Zoological Journal of the Linnean Society, 2018, **182**, 681–694. With 3 figures.

At the end of the line: independent overwater colonizations of the Solomon Islands by a hyperdiverse trans-Wallacean lizard lineage (*Cyrtodactylus*: Gekkota: Squamata)

PAUL M. OLIVER[1*], SCOTT L. TRAVERS[2], JONATHAN Q. RICHMOND[3], PATRICK PIKACHA[4] and ROBERT N. FISHER[3]

[1]*Division of Ecology and Evolution, and Centre for Biodiversity Analysis, Research School of Biology, Australian National University, Canberra, ACT 0200, Australia*
[2]*Department of Ecology and Evolutionary Biology; Biodiversity Institute, University of Kansas, Dyche Hall, 1345 Jayhawk Blvd, Lawrence, KS 66045, USA*
[3]*U.S. Geological Survey, 4165 Spruance Rd, Suite 200, San Diego, CA 92101, USA*
[4]*Aquatic Research Group, School of Civil Engineering, University of Queensland, Brisbane, QLD 4072, Australia*

Received 25 January 2017; revised 29 April 2017; accepted for publication 26 June 2017

The islands of East Melanesia have generated key insights into speciation processes and community assembly. However, when and how these islands began to form, emerge and accumulate endemic taxa remains poorly understood. Here, we show that two divergent lineages within the world's most diverse genus of geckos (*Cyrtodactylus*) occur in the Solomon Islands. One large-bodied species is nested within a radiation from far eastern New Guinea, with inferred colonization, spread and diversification since the late Miocene. In contrast, a newly sampled and relatively small species with a restricted distribution on Guadalcanal Island is a relict that diverged from extant congeners around the early to mid-Miocene. Similar Miocene divergences from extralimital relatives have been inferred for other endemic bird, bat and lizard lineages in East Melanesia. In contrast, across all lineages (including divergent relictual lineages), there is little evidence for endemic *in situ* diversification within East Melanesia predating the Pliocene (especially in the Solomon Islands). While some East Melanesian endemic lineages may have origins on progenitor islands during the Miocene or even earlier, current evidence suggests the *in situ* diversification and assembly of extant biological communities commenced around the end of the Miocene.

ADDITIONAL KEYWORDS: East Melanesia – Guadalcanal – insular relicts – island biogeography – Makira – phylogeography.

INTRODUCTION

The endemic and often distinctive biotas of isolated islands have provided model systems for understanding the processes that shape biological diversity at varying spatial and temporal scales (Whittaker & Fernandez-Palacios, 2007). The Solomon Islands occur in a broader region referred to here as East Melanesia (also including the Admiralty Islands, New Ireland and New Britain to the west). They are situated to the east of Papua New Guinea and northwest of Vanuatu and comprise six major islands (including Bougainville, politically associated with Papua New Guinea) and over 900 smaller islands. The main archipelago consists of a double-chain of NW–SE oriented islands at the collision zone between the Indo-Australian Plate and the Pacific Plate (Hackman, 1980; Coulson & Vedder, 1986; Wells, 1989; Petterson *et al.*, 1999; Hall, 2002). These islands are encompassed by deep ocean floor to the northeast and southwest and, although they have never been connected

---

*Corresponding author. E-mail: paul.oliver@anu.edu.au

by land to other regions, nonetheless have a diverse and highly endemic biota (Flannery, 1995; McCoy, 2006; Menzies, 2006; Pikacha, Morrison & Richards, 2008; Dutson, 2012). These terrestrial biotic communities provide a rich framework for analyses of speciation processes, and community ecology and assembly (Mayr & Diamond, 2001; Weeks & Claramunt, 2014; Lavery *et al.*, 2016).

The timing of when land became subaerial and the subsequent terrestrial biota evolved in the Solomon Islands, and other geologically complex insular regions of Melanesia, is poorly understood. Although many taxa occurring in this region have ultimate origins on continental plates to the west, the timing of colonization events has received little focussed attention using modern phylogenetic approaches. Most recent molecular phylogenetic analyses have focussed on patterns of differentiation between major islands, especially in volant taxa which tend to have high vagility and lower persistence over long timescales: birds (Smith & Filardi, 2007), bats (Pulvers & Colgan, 2007; Lavery, Leung & Seddon, 2014) and butterflies (Toussaint *et al.*, 2016). The Solomon Islands also have a moderately rich reptile and amphibian fauna (McCoy, 2006; Menzies, 2006; Pikacha *et al.*, 2008). This includes lineages closely related to or even conspecific with taxa that occur across Australasia, and other endemics that appear to be much more divergent (McCoy, 2006; Austin *et al.*, 2010; Brown *et al.*, 2015; Strickland *et al.*, 2016).

Among the endemic reptiles of the Solomon Islands are two species of bent-toed geckos in the genus *Cyrtodactylus* (Fig. 1). *Cyrtodactylus* is the most diverse genus of geckos in the world (over 235 species) and has a wide distribution spanning much of India, the Himalayas, Southeast Asia and as far south as Australia and Melanesia (Oliver, Richards & Sistrom, 2012; Wood *et al.*, 2012; Uetz, Freed & Hošek, 2017). The two Solomon Island endemics occur at the far eastern extremity of this wide distribution. *Cyrtodactylus salomonensis* is a large species [~150-mm snout–vent length (SVL)] widespread across the archipelago (excluding the easternmost large island of Makira) and phylogenetically nested within a complex of taxa (the *louisiadensis* group) from the easternmost portion of New Guinea (the Papuan Peninsula) and surrounding islands to the south (Oliver *et al.*, 2012; Worthington-Wilmer & Couper, 2016). The second much smaller (~90-mm SVL) species, *Cyrtodactylus biordinis*, occurs in lowland forests (up to 700-m elevation) and is known only from the northwest coast of Guadalcanal Island (Brown & McCoy, 1980; McCoy, 2006). *Cyrtodactylus biordinis* has a distinctive morphology that suggests it is not closely related to any other Melanesian *Cyrtodactylus*, in particular males have two continuous femoral pore rows on each hindlimb (all other Melanesian *Cyrtodactylus* have one or no rows). Where these two species co-occur, field observations indicate they are ecologically differentiated, with the smaller species using small trees and vines, while the larger is associated with large forest trees (McCoy, 2006).

The wide distribution and phylogenetic relationships of *C. salomonensis* indicate it has colonized and radiated across the Solomon Islands relatively recently (Worthington-Wilmer & Couper, 2016). In contrast, the phylogenetic placement of the morphologically distinctive *C. biordinis* has yet to be tested. The unique morphology and much more restricted and isolated distribution of *C. biordinis* suggest this taxon may be a relict, possibly reflecting the historical isolation of Guadalcanal. However, two converse hypotheses are that while it is morphologically distinctive, *C. biordinis* may have (1) evolved *in situ* from within the outwardly different *C. salomonensis* or (2) colonized the Solomon Islands more recently, and be allied to other outwardly different taxa that occur nearby (for instance eastern New Guinea). Resolving the phylogenetic relationships and history of *C. biordinis*, and patterns of diversity within *C. salomonensis*, are key steps towards addressing these questions. Recently, we obtained tissue samples from *C. biordinis* for the first time, as well as additional samples of *C. salomonensis* from new localities and islands. Here, we use these samples to determine the biogeographic history of these two congeneric, but distinctively different lineages from the Solomon Islands. To give context to these results, we also present a broad summary of available information on the biogeographic origins and timing of divergences in other endemic or near endemic lineages from East Melanesia.

MATERIAL AND METHODS

SAMPLING

New tissue samples are stored in ethanol (liver) and accessioned at the University of Kansas Biodiversity Institute and in the Museum of Comparative Zoology at Harvard University. We obtained sequence data from seven *C. biordinis* (from two localities) and 23 *C. salomonensis* from 11 localities on six islands, including new samples from Guadalcanal (not previously sampled), Choiseul and Malaita. To make our sampling for all *Cyrtodactylus* taxa as complete as possible for potential source islands around New Guinea, we also added new sequence data for a single sample of *Cyrtodactylus* from Kai Island to the west of New Guinea (sp. Kai Islands). All sequence data for material from the Solomon Islands included in this study

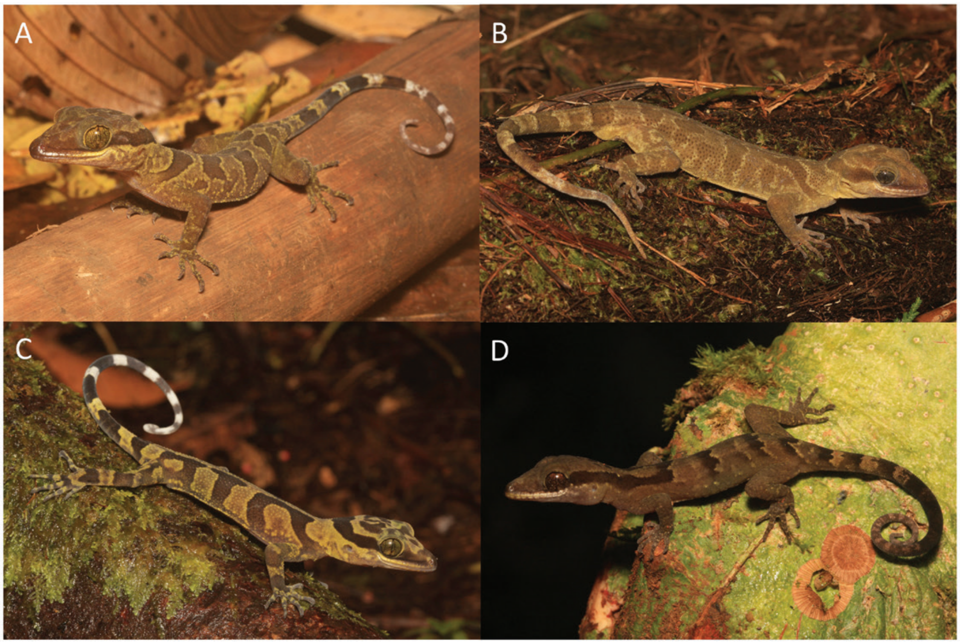

Figure 1. Solomon Island bent-toed geckos in life. A, adult female *Cyrtodactylus salomonensis* from Choisuel Island (MCZ R-193032). B, adult male *C. salomonensis* from Malaita Island (KU 343700). C, juvenile *C. salomonensis* from Malaita Island (KU 343690). D, juvenile *Cyrtodactylus biordinis* from Guadalcanal Island (KU 341118). All Photos by Scott Travers.

are summarized in Supporting Information, Table SI1. For an overall alignment spanning the global diversity of *Cyrtodactylus*, selected new sequences were aligned with pre-existing data from Wood *et al.* (2012), Oliver, Skipwith & Lee (2014) and Worthington-Wilmer & Couper (2016) (Supporting Information, Table SI2).

SEQUENCING PROTOCOLS

We extracted DNA from liver samples using a Qiagen DNeasy Blood and Tissue Kit following the manufacturer protocol. We used Sanger methods (Sanger, Nicklen & Coulson, 1977) to sequence the mitochondrial *ND2* gene and adjacent tRNAs (tRNA-trp and tRNA-ala) and two nuclear genes, *RAG-1* and Phosducin. We sequenced these genes for compatibility with other phylogenetic studies on *Cyrtodactylus* (Wood *et al.*, 2012; Oliver *et al.*, 2012; Worthington-Wilmer & Couper, 2016). Polymerase chains reactions (12.5 µL) were composed of 1× PCR buffer, 2 mM $MgCl_2$, 0.2 mM of each dNTP, 1 µM of each primer (listed in Supporting Information, Table SI3), 1.25 U *Taq* polymerase and ~100 ng DNA (see Supporting Information, Table SI3 for details of the primer sequences). Polymerase chain reaction cycling conditions were as follows: 94 °C for 2 min, 30 cycles of 94 °C for 30 s, 56–58 °C for 45 s, 72 °C for 60 s and a 5-min extension at 72 °C. We sequenced all PCR products in two directions using an ABI PRISM 3730 Analyser (Applied Biosystems) at Genewiz, Inc. (La Jolla, CA, USA). We edited all sequences using Sequencher 5.0 (Gene Codes Corp., Ann Arbor, MI, USA).

PHYLOGENY AND GENETIC DISTANCE ESTIMATION

We estimated phylogenetic relationships using maximum likelihood (RAxML v.8.0.24; Stamatakis, 2014) and Bayesian analytical approaches (BEAST v.1.8.0; Drummond *et al.*, 2012). To initially place the two Solomon Islands taxa into a broader phylogenetic context, we used a species-level data set (four genes, single examplars of 91 taxa). For this alignment, we used a three-partition strategy following previous analyses of Melanesian *Cyrtodactylus* (Oliver *et al.*, 2014) (mitochondrial first and second codons; mitochondrial third codons; and nuclear genes) with all partitions given the GTR + G model. Maximum likelihood trees were estimated using the CIPRES data portal for online phylogenetic analyses (http://www.phylo.org/).

To visualize diversity and estimate relationships among populations of the more widespread *C. salomonensis*, we ran an additional maximum likelihood analysis of an mtDNA alignment including all samples of this taxon, related taxa in the *Cyrtodactylus louisiadensis* group from the Papuan Peninsula, and *Cyrtodactylus equestris* as an outgroup. We selected partitions and models (three codons GTR + G; HKY + G; GTR + G) for this data set using the Bayesian information criteria as implemented in Partitionfinder v.1.0.1 (Lanfear *et al.*, 2012).

Genetic divergences (uncorrected *p*-distances) in the mitochondrial *ND2* gene between all samples from the Solomon Islands and additional samples in the *C. louisiadenisis* group were calculated using MEGA v.7.0.20 (Kumar, Stecher & Tamura, 2016).

Divergence time estimation

All dating analyses were undertaken in BEAST v.1.8.0 (Drummond *et al.*, 2012) using the uncorrelated lognormal model, birth–death speciation prior, run for 20 million generations, sampling every 20 000 with the first 20% of trees discarded as burn-in. Initial BEAST analyses focussed on the species-level combined nuclear mitochondrial data sets. Dating calibrations largely followed those used by Oliver *et al.* (2014) with the addition of a broad normally distributed prior at the base of *Cyrtodactylus* (mean 32, SD 5.0), derived from a reanalysis of a five nuclear gene alignment containing the majority of recognized gecko genera and major lineages (see Gamble *et al.*, 2015; Oliver *et al.*, 2017). We also ran this analysis with third codons removed to see how the removal of these potentially saturated sites affected date estimates.

To estimate time frames for divergence between lineages of *C. salomonensis* occurring across the Solomon Islands, we ran an additional dating analysis focussed specifically on a mitochondrial data set for the *C. louisiadensis* group. Sampling was reduced to a single example of each divergent lineage (including samples from all major islands in the Solomon Islands), and analyses were secondarily calibrated using the mean height and 95% highest posterior distribution estimates for the *C. louisiadensis* crown age estimated from the species-level combined alignment with third codons removed (10.7, 8.3–13.4). All other settings and partitioning strategies for this analysis were as indicated above.

RESULTS

The species-level alignment includes 91 taxa or candidate taxa, including all but three of the 30 recognized species from Australia and Melanesia. This species-level data set supports previous work showing that only two *Cyrtodactylus* lineages have successfully crossed Lydekker's Line into Melanesia (Fig. 2A, B). One of these shows an estimated early Miocene split from extralimital lineages and has diversified extensively (at least 29 recognized taxa), while the other includes only a single recognized Melanesian taxon, and is less divergent from taxa occurring to the east. A further widespread lineage of apparently specialist island taxa occurs in close geographic proximity to this region (including a newly sampled lineage from the Kai Islands just to the west of New Guinea), but does not appear to have crossed into Melanesia.

In all phylogenetic analyses, the two Solomon Islands endemic taxa are placed in the strongly supported and moderately diverse radiation of Melanesian and Australian *Cyrtodactylus* taxa. Within this clade, the newly sampled *C. biordinis* is sister to all other taxa, but with very weak support (Fig. 2A). When weakly supported nodes were collapsed, *C. biordinis* forms one of the nine well-supported lineages within what appears to be a relatively rapid initial radiation of Melanesian *Cyrtodactylus* (in addition to eight lineages delineated by Oliver *et al.*, 2012). As per the previous analyses (Worthington-Wilmer & Couper, 2016), *C. salomonensis* is nested within a strongly supported lineage from the Milne Bay region of eastern New Guinea (the *louisiadensis* group), specifically it is inferred to be the sister lineage to a clade comprising *Cyrtodactylus epiroticus* (Papuan Peninsula and D'Entrecasteaux Islands) and *C. louisiadensis* (Sudest Island).

The seven samples of *C. biordinis* from three sites on Guadalcanal show very low genetic divergence (uncorrected *ND2* *p*-distances = 0.000–0.002). Within *C. salomonensis*, both islands from which we had samples from multiple localities show evidence of much deeper intra-island haplotypic diversity. Samples from Malaita form a clade with moderate divergences (*p*-distances = 0.000–0.042), while three divergent lineages (*p*-distance = 0.056–0.059) are identified on Choiseul, of which one is more closely allied to a sample from Bougainville than other localities from the same island (*p*-distance = 0.030, bootstrap support 100). Samples from New Georgia and Guadalcanal form a clade with moderate support (maximum likelihood bootstrap 78, Bayesian posterior 0.99). All other relationships between islands were unresolved (Figs 2D, 3). Samples of *C. salomonensis* from all major islands (Fig. 2C, D) are moderately divergent from each other. Excluding closely related lineages on Bougainville and Choiseul, average net between group mean divergences between islands range from 0.037 to 0.077 (Table 1), approaching the mean genetic divergence between other insular populations recognized as species in this species complex (e.g. *Cyrtodactylus murua* and *Cyrtodactylus tripartitus* = 0.068) (Table 2).

Date estimates based on the overall species-level data set suggest *C. biordinis* diverged from all other sampled taxa around the time of the initial diversification of the main Melanesian *Cyrtodactylus* radiation in the early Miocene (Table 3). In the same data set and analysis, *C. salomonensis* diverged from its

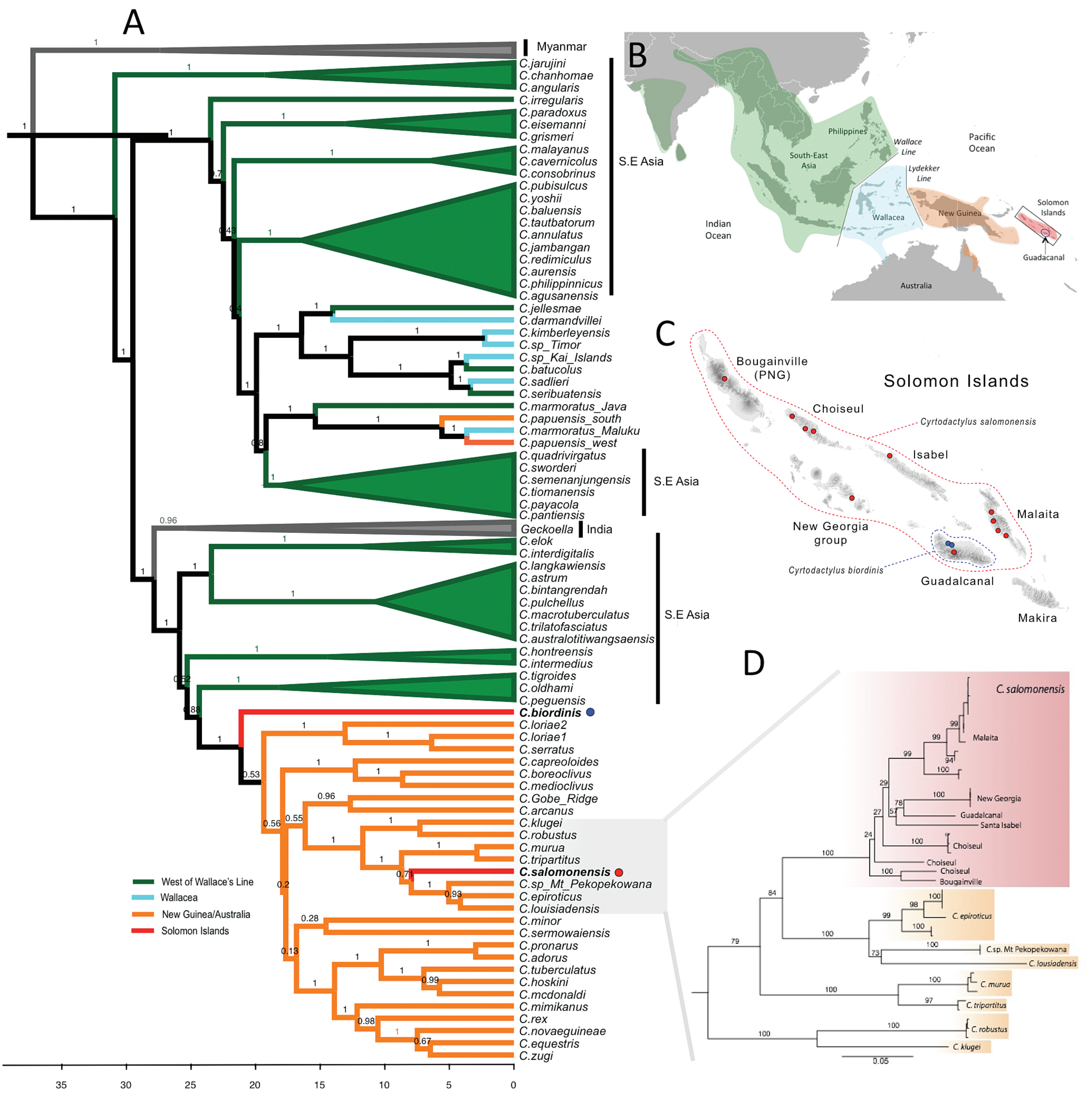

Figure 2. A, Species-level chronogram for *Cyrtodactylus* estimated from combined data set using BEAST with major lineages colour coded according to the region in which they occur. B, overall distribution the genus *Cyrtodactylus* with major regions of occurrence highlighted. C, genetically sampled localities with the Solomon Islands. D, maximum likelihood tree for *Cyrtodactylus salomonensis* and allied taxa estimated from the *ND2* sequences.

closest relatives in the late Miocene (Table 3). Given the nesting of *C. salomonensis* within a cluster of other species from Milne Bay, we interpret this as the maximum age estimate of the time of colonization in the Solomon Islands from eastern New Guinea. Dating analyses focussed on a mitochondrial alignment of the *C. louisiadensis* group suggest an initial radiation of lineages of *C. salomonensis* in the Pliocene and a relatively rapid spread across the Solomon Islands (Fig. 3).

DISCUSSION

The isolated and endemic biota of the Solomon Islands offers great potential for testing major questions about

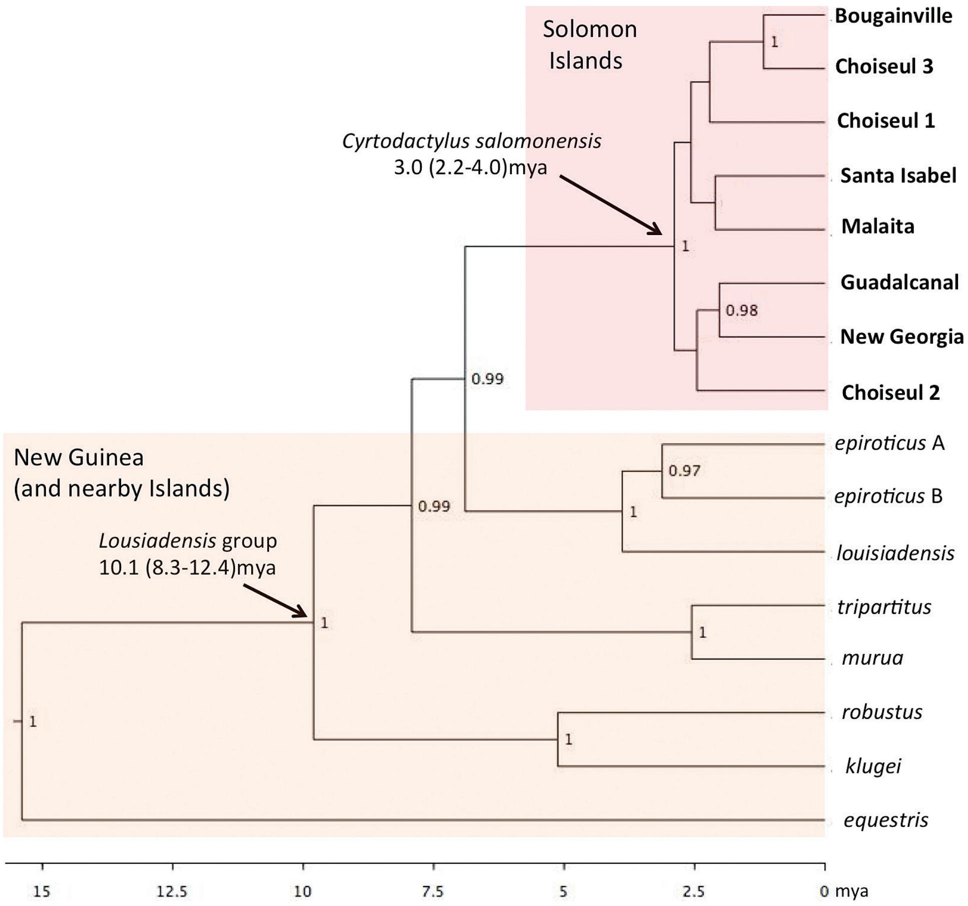

Figure 3. Chronogram for species and lineages within the *Cyrtodactylus louisiadensis* group estimated from the mitochondrial *ND2* gene and secondary calibrations. Bayesian posterior support values greater than 0.95 for key nodes are also indicated. Timescale on bottom axis in Mya. Details of different lineages are provided in Supporting Information, Table SI1.

Table 1. Mean genetic divergences (*p*-distances) within and between islands and major lineages of *Cyrtodactylus salomonensis* in the Solomon Islands

ND2 p-distances between and within islands (*Cyrtodactylus salomonensis*)

	Bougainville/ Choiseul 3	Choiseul 1	Choiseul 2	Isabel	New Georgia	Guadalcanal	Malaita
Bougainville/ Choiseul 3	**0.030**						
Choiseul 1	0.037	**n/a**					
Choiseul 2	0.043	0.062	**0.002**				
Isabel	0.058	0.077	0.069	**n/a**			
New Georgia	0.059	0.077	0.057	0.074	**0.000**		
Guadalcanal	0.049	0.062	0.053	0.062	0.053	**n/a**	
Malaita	0.039	0.057	0.039	0.064	0.051	0.052	**0.019**

Bold values indicate intralineage divergences. n/a, not applicable.

how species form and biological communities develop (Mayr & Diamond, 2001). However, more baseline data are needed to assemble stronger biogeographic and phylogenetic data sets for understanding the early evolutionary history of this archipelago (and other island systems of Melanesia). Here, we show that two

Table 2. Mean genetic divergences (*p*-distances) between *Cyrtodactylus* geckos in the *louisadensis* group, including *Cyrtodactylus salomonensis*

ND2 p-distances between and within taxa

	salomonensis	*klugei*	*epiroticus* A	*epiroticus* B	*louisiadensis*	*murua*	*robustus*	*tripartitus*	*equestris*
salomonensis	**0.048**								
klugei	0.129	**n/a**							
epiroticus A	0.060	0.125	**0.016**						
epiroticus B*	0.090	0.175	0.067	**0.000**					
louisiadensis	0.114	0.166	0.106	0.134	**n/a**				
murua	0.110	0.148	0.115	0.152	0.143	**0.010**			
robustus	0.143	0.126	0.150	0.182	0.179	0.170	**0.002**		
tripartitus	0.127	0.160	0.127	0.163	0.160	0.068	0.178	**0.003**	
equestris	0.150	0.190	0.175	0.196	0.208	0.182	0.218	0.209	**n/a**

Bold values indicate intraspecific divergences. n/a, not applicable.
*Normanby Island.

Table 3. Age estimates (height and 95% highest posterior distribution) for key divergence events in *Cyrtodactylus* estimated using the combined mitochondrial and nuclear gene alignment and secondary calibrations

Clade	All data	No third codons
Cyrtodactylus (crown group)	37.4 (32.0–42.2)	40.0 (33.9–45.9)
Main Melanesian clade (crown group)	21.1 (17.8–25.2)	20.4 (16.6–25.6)
louisiadensis group (crown group)	11.7 (9.6–14.0)	10.7 (8.3–13.4)
Cyrtodactylus salomonensis (vs. nearest relatives)	8.0 (6.5–9.7)	7.7 (5.7–9.9)
Cyrtodactylus biordinis (vs. nearest relatives)	21.1 (17.8–25.2)	17.2 (13.6–21.2)

All estimates are in Mya.

endemic lizards in the Solomon Islands have contrasting patterns of distribution, diversity and divergence. One is a relatively ancient relict with a restricted distribution, while the other is more recent colonist that has spread and diversified across islands.

A MELANESIAN INSULAR RELICT BIOTA?

Some of the world's most spectacular and rapid radiations have occurred on the islands of the Pacific, especially some of the more isolated islands (Wagner & Funk, 1995; Moyle *et al.*, 2009; Chiba, 2010). However, many Pacific islands, especially those closer to larger continental landmasses, are also home to distinctive relict lineages – moderately to deeply divergent taxa with low species diversity – that are geographically disjunct from (or even completely lack) close living relatives (Ota, 1998; Grandcolas, Nattier & Trewick, 2014).

Here, we found that *C. biordinis* is a relict species of uncertain biogeographic origin that probably diverged from all other living relatives in Melanesia around the early Miocene. A growing number of phylogenetic studies are providing similar evidence for divergent and endemic lineages in East Melanesia (Table 4). This includes relict lineages endemic to single islands (this study), and more widespread taxa either endemic to specific archipelagos (Lucky & Sarnat, 2010; Skinner, Hugall & Hutchinson, 2011, Lavery *et al.*, 2014) or occurring across archipelagos (Oliver *et al.*, 2016; Strickland *et al.*, 2016). Divergence dates for the separation of these taxa from nearest relatives in Australia/New Guinea generally date to the mid- to late-Miocene. Thus, while many endemic taxa are probably more recently derived, there is growing evidence for an older insular fauna potentially predating the major accretion and uplift of the much larger nearby landmass of New Guinea in the later Miocene (Hall, 2002; Cloos *et al.*, 2005).

Within the Solomon Islands, the high islands of Guadalcanal (and Bougainville) show notable levels of endemism, especially for lizards, birds and mammals (Flannery, 1995; McCoy, 2006; Dutson, 2012). However, while many of these endemics occur in montane habitats, the four endemic lizard species currently known only from Guadalcanal (including *C. biordinis*) have so far only been reported from lower elevations, suggesting montane gradients have not played a role in the diversification of these taxa (although high elevation habitats in Guadalcanal are poorly explored). These

Table 4. Summary of published estimates of mean divergence times for East Melanesian endemic animal lineages, including both splits from nearest extralimital relatives, and ages for diversification events within East Melanesia

Group	East Melanesian endemic taxa	Extralimital relatives	Split time (era)	Split time (Mya)	Crown age (era)	Crown age (Mya)	Reference
Birds	*Stresemannia bougainvillei**	Ambiguous	Late Miocene	10–15	–	–	Marki *et al.* (2017)
	Ducula brenchleyi	Ambiguous	Late Miocene	~10	–	–	Cibois *et al.* (2017)
	*Guadalcanaria inexpectata**	Ambiguous	Late Miocene	5–10	–	–	Marki *et al.* (2017)
	*Meliarchus sclateri**	Ambiguous	Late Miocene	5–10	–	–	Marki *et al.* (2017)
	Ptilinopus viridis/*eugeniae* clade	New Guinea	Miocene-Pliocene	5–10	Pleistocene	< 1.5	Cibois *et al.* (2014)
	Ptilinopus richardsii	Oceania	Plio-Pleistocene	< 5	–	–	Cibois *et al.* (2014)
	Ptilinopus greyi	Oceania	Plio-Pleistocene	< 5	–	–	Cibois *et al.* (2014)
	Myzomela clade	Ambiguous	Plio-Pleistocene	< 5	–	–	Marki *et al.* (2017)
	Corvus woodfordi/*meeki* clade	Ambiguous	Plio-Pleistocene	~5	Plio-Pleistocene	2–3	Jønsson, Fabre & Irestedt (2012)
	Charmosyna meeki	Melanesia	Plio-Pleistocene	~3	–	–	Schweizer *et al.* (2015)
	Myiagra ferrocyanae	Ambiguous	Pleistocene	< 3	–	–	Fabre *et al.* (2014)
	Myiagra cervinicauda	Ambiguous	Pleistocene	< 3	–	–	Fabre *et al.* (2014)
	Zosterops clade	Ambiguous	Pleistocene	< 2.3	Pleistocene	< 2	Moyle *et al.* (2009)
	Coracina salomonis	Ambiguous	Pleistocene	< 2	–	–	Jønsson *et al.* (2010b)
	Lorius chlorocercus	Melanesia	Pleistocene	~2	–	–	Schweizer *et al.* (2015)
	Coracina holopolia	Ambiguous	Pleistocene	~1–2	–	–	Jønsson *et al.* (2010b)
	Nesoclopeus woodfordi	Ambiguous	Pleistocene	~1–2	–	–	Garcia-R, Gibb & Trewick (2014)
	Pachycephala orioloides	Ambiguous	Pleistocene	~1	–	–	Jønsson *et al.* (2010a)
	Todiramphus leucopygius	Australia	Pleistocene	~0.5	–	–	Andersen *et al.*, 2014)
	Monarcha castaneiventris clade	Ambiguous	Pleistocene	~0.5	Pleistocene	~0.5	Filardi & Moyle (2005), Uy *et al.* (2009)
Mammals	*Anthops ornatus**	Ambiguous	Early Miocene	~22	–	–	Lavery *et al.* (2014)
	Hipperosideros calcaratus	Ambiguous	Early Miocene	~18	Pleistocene	< 1	Lavery *et al.* (2014)
	Hipperosideros cervinus	Australasia	Plio-Pleistocene	~3	Pliocene	< 3	Lavery *et al.* (2014)

Table 4. *Continued*

Group	East Melanesian endemic taxa	Extralimital relatives	Split time (era)	Split time (Mya)	Crown age (era)	Crown age (Mya)	Reference
	Hipperosideros diadema group	New Guinea	Plio-Pleistocene	~3	Pliocene	< 3	Lavery *et al.* (2014)
	*Solomys**	New Guinea	Pleistocene	~2	Pliocene	< 1	Bryant *et al.* (2011)
Reptiles	*Tribolonotus* sp.	Australasia	Pre-Eocene	~55	–	–	Skinner *et al.* (2011)
	*Corucia zebrata**	Australia	Early Miocene	~25	Plio-Pleistocene	~1	Skinner *et al.* (2011), Hagen *et al.* (2012)
	Lepidodactylus guppyi group	Philippines	Early Miocene	~20	Plio-Pleistocene	~10	P. M. Oliver, R. M. Brown, F. Kraus, E. Rittmeyer, S. L. Travers, C. S. Siler (unpubl. data)
	Cyrtodactylus biordinis	New Guinea	Mid-Miocene	15–20	–	–	This study
	Gehyra rohan	Fiji/Vanuatu	Late Miocene	~10	–	–	Oliver *et al.* (2016)
	Cyrtodactylus salomonensis	East New Guinea	Late Miocene	~5	Plio-Pleistocene	~3	This study
	Emoia cyanura group†	Ambiguous	–	–	Mid-Miocene	~10	Klein *et al.* (2016)
	Emoia impar group†	Ambiguous	–	–	Late Miocene	~5	Klein *et al.* (2016)
Insects	*Ornithoptera victoriae*	East New Guinea	Pliocene	~5	–	–	Condamine *et al.* (2015)
	Polyura epigenes	East New Guinea	Pleistocene	1.3	Pleistocene	~0.25	Toussaint *et al.* (2016)

Divergence estimates are given both as eras and to the nearest Mya.
*Endemic genera.
†Near endemic radiations, with widespread likely anthropogenically dispersed lineages.

divergent or endemic lowland lineages on Guadalcanal may reflect differing histories of uplift and isolation of key islands through the Miocene. The Solomon Islands are a montage of obducted crustal units with separate geological histories that occurred in two phases (62–24 Mya and 7 Mya–present; Petterson *et al.*, 1999; Hall, 2002). The Solomon Islands initially formed as the Pacific Plate was subducting westward beneath the Australian Plate in the Mid-Oligocene (*c*. 40 Mya) along the Vitiaz Trench. Guadalcanal (with Choiseul) is part of this initial 'old' island arc. In the early Late Miocene (*c*. 12 Mya), there was a reversal of subduction that drove the formation of a second arc that includes the New Georgia and Russell groups (Petterson *et al.*, 1999; Hall, 2002; Polhemus, 2007, 2008). These data suggest that Guadalcanal could be older than the surrounding islands; however, in the face of this complex geology, how and when different fragments of the Solomon Islands became subaerial still remains uncertain. Some islands containing the oldest rocks may not have been subaerial the longest: Isabel and Malaita have basement rocks that are ~120 Mya, but apparently did not emerge as subaerial islands until the Miocene (*c*. 6 Mya). In contrast, Choiseul and Guadalcanal may have been emergent since at least the Miocene but have basement rocks that are < 100 Mya (Petterson *et al.*, 1999). Further dated phylogenies for other endemic taxa may provide an alternative means to better resolve the history of isolation and uplift of key islands.

Another, not necessarily exclusive, hypothesis for the restricted distribution of *C. biordinis* is that species interactions may have played a role. For instance, it has been suggested that larger lizards may displace smaller congeners in sympatry (especially on islands) [e.g. Roughgarden & Pacala, 1989 (but see Losos, 1992); Rocha, Posada & Harris, 2013]. Ancestral state reconstructions also suggest that Melanesian *Cyrtodactylus* lineages have independently evolved large body size from smaller ancestors relatively recently in their radiation (Oliver *et al.*, 2014). Unfortunately, given that there are only two taxa in the example studied here, it is difficult to test these ideas further, although better data on inter-island variation in body size and shape, habitat usage and ecology may provide some insight.

Plio-pleistocene divergences within the Solomon Islands

In contrast to *Cyrtodactylus biordinis*, *C. salomonensis* is widespread and clearly nested within a complex of taxa occurring at the far eastern edge of New Guinea and surrounding islands in Milne Bay Province, Papua New Guinea (Worthington-Wilmer & Couper, 2016). The only large island from which this taxon has not been reported is Makira, the most geographically distant island from likely source areas for colonists to the west (i.e. present day New Guinea and Australia). Makira was not connected by recent glacial sea-level fluctuations to other large islands (Neall & Trewick, 2008; Polhemus *et al.*, 2008; Lavery *et al.*, 2016). This isolation is likely reflected in both Makira's large number of endemic birds (Danielsen *et al.*, 2010; Dutson, 2012), insects (Greenslade, 1969) and other genetically distinct subspecific lineages (Pulvers & Colgan, 2007; Uy, Moyle & Filardi, 2009; Andersen *et al.*, 2014), and depauperate fauna for other terrestrial vertebrate groups (e.g. frogs; Pikacha *et al.*, 2008).

Across the islands where *C. salomonensis* is present, genetic structuring and molecular dating analysis suggests rapid spread during the Pleistocene, followed by periods of isolation sufficient to cause moderate diversification across (and in some cases within) major islands. *Cyrtodactylus salomonensis* shows variation in colour pattern that may provide further evidence of differentiation (Fig. 1; McCoy, 2006), although in many areas (such as Malaita) this appears to be within, not between, populations (S. L. Travers, pers. observ.). Similar moderate genetic structuring and morphological divergence across major islands, or paleo-island complexes, has been detected in other widespread Solomon Islands species or 'super-species' (Table 4), including other lizards (Hagen, Donnellan & Bull, 2012; Klein *et al.*, 2016), bats (Pulvers & Colgan, 2007), butterflies (Toussaint *et al.*, 2016) and especially birds (Filardi & Smith, 2005; Smith & Filardi, 2007; Uy *et al.*, 2009; Andersen *et al.*, 2013, 2014). Broadly, while geographic patterns vary across these taxa, overall levels of genetic and morphological differentiation between allopatric populations all show relatively recent (i.e. Plio-Pleistocene) expansion and divergence (Table 4). Importantly, this tendency towards post-Miocene diversification within the Solomon Islands is observed across both old relictual lineages that have subsequently diversified (see above) and those inferred to have colonized more recently. This common pattern suggests that while some lineages may have longer history in the general region, biotic assemblages across the Solomon Islands have largely developed their current configuration since the end of the Miocene.

Dispersal, colonization and diversification in a hyperdiverse genus

Recent work on *Cyrtodactylus* in different parts of the range has presented evidence for numerous evolutionary processes in shaping the substantial phyletic diversity of this genus, including parallel niche evolution

(Grismer *et al.*, 2015), shifts in macroevolutionary regimes (Oliver *et al.*, 2014) and ecological plasticity coupled with refugial dynamics (Worthington-Wilmer & Couper, 2016). In Melanesia, distributional data suggest that *Cyrtodactylus* have been less effective at dispersal than other co-occcuring gecko genera, most of which extend further across the Solomon Islands (including Makira) and well out into the Pacific. This suggests that while *Cyrtodactylus* can clearly disperse, they are apparently less able to do so than many other gekkonine taxa (at least in Melanesia), probably increasing the likelihood of speciation by geographic isolation (Weeks & Claramunt, 2014). Of the many islands inhabited by *Cyrtodactylus* in eastern Melanesia, Guadalcanal is thus far also one of only two instances of sympatry [the other being *C. louisiadensis* (133 mm) and *Cyrtodactylus klugei* (143 mm) on Sudest Island in the Louisiade Archipelago] (Kraus, 2008). This further suggests a dominant role of dispersal and geographic isolation in shaping *Cyrtodactylus* diversity (at least in insular Melanesia); however, further work on the roles of ecological diversification and species interactions is certainly warranted.

CONCLUSION

For 50 years, biogeographers have focussed on East Melanesia as a model region to ask questions about how lineages diversify, and especially how biotic communities are assembled; however, the history of these communities has remained largely unexamined. Here, a summary of available phylogenetic data suggest that islands with associated endemic lineages may have been present in Melanesia since at least the early Miocene. However, *in situ* diversification within Eastern Melanesia tends to be much younger, suggesting that while an earlier biota may have present, extant communities may largely be explained by geological and biological processes since the late Miocene.

ACKNOWLEDGEMENTS

P.M.O. was supported by a Discovery Early Career Researcher Fellowship from the Australian Research Council and a grant from the Australia Pacific Science Foundation. S.L.T. was supported by grants from the National Geographic Society, Society of Systematic Biologists, Society for the Study of Amphibians and Reptiles, American Society of Ichthyologists and Herpetologists, the University of Kansas and NSF grant number DEB 1557053 to R. Moyle and R. Brown. J.Q.R. and R.N.F. were supported by funds from the Museum of Comparative Zoology, Harvard University and the USGS Ecosystems Mission Area. We are especially indebted to Ecological Solutions Solomon Islands; the Solomon Island Community Conservation Partnership; the Lauru Land Conference of Tribal Communities on Choiseul; the Secretariat of the Pacific Regional Environment Programme; University of the South Pacific; and the many local tribes, land owners and field assistants that facilitated aspects of our fieldwork. Tyrone Lavery helped with field collections and provided advice on protective footwear. S.L.T. and J.Q.R. also thank David Boseto, Rob Moyle and Rafe Brown for guidance during fieldwork. We thank Mike McCoy for providing useful insight into the distribution and ecology of *Cyrtodactylus* in the Solomon Islands, and Adam Backlin and Edgar Pollard for field assistance. Fieldwork was made possible by the National and Provincial Governments of the Solomon Islands, undertaken under permits from Solomon Island Ministry of Environment, Climate Change, Disaster Management and Meteorology issued to the University of Kansas (Permit No. RP/2014/007), and export permits issued to USGS and KU by the Department of Environment, Conservation, and Meteorology, Solomon Islands Government (EX2014/128, EX2015/080, EX2014/116, EX2015/122). Any use of trade, product or firm names in this report is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

Andersen MJ, Nyári ÁS, Mason I, Joseph L, Dumbacher JP, Filardi CE, Moyle RG. 2014. Molecular systematics of the world's most polytypic bird: the *Pachycephala pectoralis / melanura* (Aves: Pachycephalidae) species complex. *Zoological Journal of the Linnean Society* **170:** 566–588.

Andersen MJ, Oliveros CH, Filardi CE, Moyle RG. 2013. Phylogeography of the variable dwarf-kingfisher *Ceyx lepidus* (Aves: Alcedinidae) inferred from mitochondrial and nuclear DNA sequences. *The Auk* **130:** 118–131.

Austin CC, Rittmeyer EN, Richards SJ, Zug GR. 2010. Phylogeny, historical biogeography and body size evolution in Pacific island crocodile skinks *Tribolonotus* (Squamata; Scincidae). *Molecular Phylogenetics and Evolution* **57:** 227–236.

Brown WC, McCoy M. 1980. A new species of gecko of the genus *Cyrtodactylus* from Guadalcanal Island, Solomon Islands. *Herpetologica* **36:** 66–69.

Brown RM, Siler CD, Richards DJ, Diesmos AC, Cannatella DC. 2015. Multilocus phylogeny and a new classification for Southeast Asian and Melanesian forest frogs (family Ceratobatrachidae). *Zoological Journal of the Linnean Society* **174:** 130–168.

Bryant LM, Donnellan SC, Hurwood DA, Fuller SJ. 2011. Phylogenetic relationships and divergence date estimates among Australo-Papuan mosaic-tailed rats from the *Uromys* division (Rodentia: Muridae). *Zoologica Scripta* **40:** 433–447.

Chiba S. 2010. Species diversity and conservation of *Mandarina*, and endemic land snail of the Ogasawara Islands. In: Kawakami K, Okochi I, eds. *Restoring the Oceanic Island ecosystem: impact and management of invasive alien species in the Bonin Islands*. Tokyo: Springer, 29–37.

Cibois A, Thibault JC, Bonillo C, Filardi CE, Pasquet E. 2017. Phylogeny and biogeography of the imperial pigeons (Aves: Columbidae) in the Pacific Ocean. *Molecular Phylogenetics and Evolution* **110:** 19–26.

Cibois A, Thibault JC, Bonillo C, Filardi CE, Watling, D, Pasquet E. 2014. Phylogeny and biogeography of the fruit doves (Aves: Columbidae). *Molecular Phylogenetics and Evolution* **70:** 442–453.

Cloos M, Sapiie B, van Ufford AQ, Weiland RJ, Warren PQ, McMahon TP. 2005. Collisional delamination in New Guinea: the geotectonics of subducting slab breakoff. *Geological Society of America Special Papers* **400:** 1–51.

Condamine FL, Toussaint EFA, Clamens AL, Genson G, Sperling FAH, Kergoat GJ. 2015. Deciphering the evolution of birdwing butterflies 150 years after Alfred Russel Wallace. *Scientific Reports* **5:** 11860.

Coulson FI, Vedder JG. 1986. Geology of the central and western Solomon Islands. In: Vedder JG, Pound KS, Boundy SQ, eds. *Geology and offshore resources of Pacific island arcs – Central and Western Solomon Islands, Vol. 4*. Houston: Circum-Pacific Council for Energy and Mineral Resources, Earth Science Series, 59–87.

Danielsen F, Filardi CE, Jønsson KA, Kohaia V, Krabbe N, Kristensen JB, Moyle RG, Pikacha P, Poulsen MK, Sørensen MK, Tatahu C, Waihuru J, Fjeldså J. 2010. Endemic avifaunal biodiversity and tropical forest loss in Makira, a mountainous Pacific island. *Singapore Journal of Tropical Geography* **31:** 100–114.

Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* **29:** 1969–1973.

Dutson G. 2012. *Birds of Melanesia: Bismarcks, Solomons, Vanuatu, and New Caledonia*. Princeton: Princeton University Press.

Fabre PH, Moltensen M, Fjeldså J, Irestedt M, Lessard JP, Jønsson KA. 2014. Multiple waves of colonization by monarch flycatchers (Myiagra, Monarchidae) across the Indo-Pacific and their implications for coexistence and speciation. *Journal of Biogeography* **41:** 274–286.

Filardi CE, Moyle RG. 2005. Single origin of a pan-Pacific bird group and upstream colonization of Australasia. *Nature* **438:** 216–219.

Filardi CE, Smith CE. 2005. Molecular phylogenetics of monarch flycatchers (genus *Monarcha*) with emphasis on Solomon Island endemics. *Molecular Phylogenetics and Evolution* **37:** 776–788.

Flannery T. 1995. *The mammals of the South-West Pacific and Moluccan Islands*. Chatswood: Reed Books.

Gamble T, Greenbaum E, Jackman TR, Bauer AM. 2015. Into the light: diurnality has evolved multiple times in geckos. *Biological Journal of the Linnean Society* **115:** 896–910.

Garcia-R JC, Gibb GC, Trewick SA. 2014. Deep global evolutionary radiation in birds: diversification and trait evolution in the cosmopolitan bird family Rallidae. *Molecular Phylogenetics and Evolution* **81:** 96–108.

Grandcolas P, Nattier R, Trewick S. 2014. Relict species: a relict concept? *Trends in Ecology and Evolution* **29:** 655–663.

Greenslade PJM. 1969. Insect distribution patterns in the Solomon Islands. *Philosophical Transactions of the Royal Society B: Biological Sciences* **255:** 271–284.

Grismer LL, Wood PL, Ngo VT, Murdoch ML. 2015. The systematics and independent evolution of cave ecomorphology in distantly related clades of Bent-toed Geckos (Genus *Cyrtodactylus* Gray, 1827) from the Mekong Delta and islands in the Gulf of Thailand. *Zootaxa* **3980:** 106–126.

Hackman BD. 1980. The geology of Guadalcanal, Solomon Islands. *Vol. 6. London: Institute of Geological Sciences*, 115.

Hagen IJ, Donnellan SC, Bull CM. 2012. Phylogeography of the prehensile-tailed skink *Corucia zebrata* on the Solomon Archipelago. *Ecology and Evolution* **2:** 1220–1234.

Hall R. 2002. Cenozoic geological plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, models and animations. *Journal of Asian Earth Sciences* **20:** 353–431.

Jønsson KA, Bowie RC, Moyle RG, Christidis L, Norman JA, Benz BW, Fjeldså J. 2010a. Historical biogeography of an Indo-Pacific passerine bird family (Pachycephalidae): different colonization patterns in the Indonesian and Melanesian archipelagos. *Journal of Biogeography* **37:** 245–257.

Jønsson KA, Bowie RC, Nylander JA, Christidis L, Norman JA, Fjeldså J. 2010b. Biogeographical history of cuckoo-shrikes (Aves: Passeriformes): transoceanic colonization of Africa from Australo-Papua. *Journal of Biogeography* **37:** 1767–1781.

Jønsson KA, Fabre PH, Irestedt M. 2012. Brains, tools, innovation and biogeography in crows and ravens. *BMC Evolutionary Biology* **12:** 72.

Klein ER, Harris RB, Fisher RN, Reeder TW. 2016. Biogeographical history and coalescent species delimitation of Pacific island skinks (Squamata: Scinidae: *Emoia cyanura* species group). *Journal of Biogeography* **43:** 1917–1929.

Kraus F. 2008. Taxonomic partitioning of *Cyrtodactylus louisiadensis* (Lacertilia: Gekkonidae) from Papua New Guinea. *Zootaxa* **1883:** 1–27.

Kumar S, Stecher G, Tamura K. 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* **33:** 1870–1874.

Lanfear R, Calcott B, Ho SY, Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29:** 1695–1701.

Lavery T, Leung LK-P, Seddon JM. 2014. Molecular phylogeny of hipposiderid bats (Chiroptera: Hipposideridae) from Solomon Islands and Cape York Peninsula, Australia. *Zoologica Scripta* **43:** 1–14.

Lavery TH, Olds AD, Seddon JM, Leung LKP. 2016. The mammals of northern Melanesia: speciation, ecology, and biogeography. *Mammal Review* **46:** 60–76.

Losos JB. 1992. A critical comparison of the taxon-cycle and character-displacement models for size evolution of *Anolis* lizards in the Lesser Antilles. *Copeia* **2:** 279–288.

Lucky A, Sarnat EM. 2010. Biogeography and diversification of the Pacific ant genus *Lordomyrma* Emery. *Journal of Biogeography* **37:** 624–634.

Marki PZ, Jønsson KA, Irestedt M, Nguyen JM, Rahbek C, Fjeldså J. 2017. Supermatrix phylogeny and biogeography of the Australasian Meliphagides radiation (Aves: Passeriformes). *Molecular Phylogenetics and Evolution* **107:** 516–529.

Mayr E, Diamond J. 2001. *The birds of northern Melanesia: speciation, ecology, and biogeography*. Oxford: Oxford University Press.

McCoy M. 2006. *Reptiles of the Solomon Islands*. Sofia: Pensoft.

Menzies JI. 2006. *The frogs of New Guinea and the Solomon Islands*. Sofia: Pensoft.

Moyle RG, Filardi CE, Smith CE, Diamond J. 2009. Explosive Pleistocene diversification and hemispheric expansion of a "great speciator". *Proceedings of the National Academy of Sciences of the United States of America* **106:** 1863–1868.

Neall VE, Trewick SA. 2008. The age and origin of the Pacific Islands: a geological overview. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363:** 3293–3308.

Oliver PM, Clegg JR, Fisher RN, Richards SJ, Taylor PN, Jocque MMT. 2016. A new biogeographically disjunct giant gecko (*Gehyra*: Gekkonidae: Reptilia) from the East Melanesian Islands. *Zootaxa* **4208:** 61.

Oliver PM, Laver RJ, De Mello Martins F, Pratt RC, Hunjan S, Moritz CC. 2017. A novel hotspot of vertebrate endemism and an evolutionary refugium in tropical Australia. *Diversity and Distributions* **23:** 53–66.

Oliver PM, Richards SJ, Sistrom M. 2012. Phylogeny and systematics of Melanesia's most diverse gecko lineage (*Cyrtodactylus*, Gekkonidae, Squamata). *Zoologica Scripta* **41:** 437–454.

Oliver PM, Skipwith P, Lee MS. 2014. Crossing the line: increasing body size in a trans-Wallacean lizard radiation (*Cyrtodactylus*, Gekkota). *Biology Letters* **10:** 20140479.

Ota H. 1998. Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu archipelago, Japan, with special reference to their paleogeographical implications. *Researches on Population Ecology* **40:** 189–204.

Petterson MG, Babbs T, Neal CR, Mahoney JJ, Saunders AD, Duncan RA, Tolia D, Magu R, Qopoto C, Mahoa H, Natogga D. 1999. Geological–tectonic framework of Solomon Islands, SW Pacific: crustal accretion and growth within an intra-oceanic Setting. *Tectonophysics* **301:** 35–60.

Pikacha P, Morrison C, Richards S. 2008. *Frogs of the Solomon Islands*. Suva: Quality Print Ltd.

Polhemus DA. 2007. Tectonic geology of Papua. In: Marshall AJ, Beehler BM, eds. *Ecology of Papua, part 1*. Singapore: Periplus Editions (HK) Ltd., 137–164.

Polhemus, DA, Englund RA, Allen GR, Boseto D, Polhemus JT. 2008. Freshwater biotas of the Solomon Islands analysis of richness, endemism and threats. *Bishop Museum Technical Report* **45:** 126.

Pulvers JN, Colgan DJ. 2007. Molecular phylogeography of the fruit bat genus *Melonycteris* in northern Melanesia. *Journal of Biogeography* **34:** 713–723.

Rocha S, Posada D, Harris DJ. 2013. Phylogeography and diversification history of the day-gecko genus *Phelsuma* in the Seychelles islands. *BMC Evolutionary Biology* **13:** 3.

Roughgarden J, Pacala S. 1989. Taxon cycles among *Anolis* lizard populations: review of evidence. In: Otte D, Endler JA, eds. *Speciation and its consequences*. Sunderland: Sinauer Associates, 403–432.

Sanger F, Nicklen S, Coulson AR. 1977. DNA sequencing with chain-terminating inhibitors. *Proceedings of the National Academy of Sciences of the United States of America* **74:** 5463–5467.

Schweizer M, Wright TF, Peñalba JV, Schirtzinger EE, Joseph L. 2015. Molecular phylogenetics suggests a New Guinean origin and frequent episodes of founder-event speciation in the nectarivorous lories and lorikeets (Aves: Psittaciformes). *Molecular Phylogenetics and Evolution* **90:** 34–48.

Skinner A, Hugall AF, Hutchinson MN. 2011. Lygosomine phylogeny and the origins of Australian scincid lizards. *Journal of Biogeography* **38:** 1044–1058.

Smith CE, Filardi CE. 2007. Patterns of molecular and morphological variation in some Solomon Island land birds. *The Auk* **124:** 479–493.

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30:** 1312–1313.

Strickland JL, Carter S, Kraus F, Parkinson CL. 2016. Snake evolution in Melanesia: origin of the Hydrophiinae (Serpentes, Elapidae), and the evolutionary history of the enigmatic New Guinean elapid *Toxicocalamus*. *Zoological Journal of the Linnean Society* **178:** 663–678.

Toussaint EFA, Morinière J, Lam A, Turlin B, Balke M. 2016. Bayesian Poisson tree processes and multispecies coalescent models shed new light on the diversification of Nawab butterflies in the Solomon Islands (Nymphalidae, Charaxinae, *Polyura*). *Zoological Journal of the Linnean Society* **178:** 241–256.

Uetz P, Freed P, Hošek J. 2017. The Reptile Database. Available at: http://reptile-database.reptarium.cz/

Uy JAC, Moyle RG, Filardi CE. 2009. Plumage and song differences mediate species recognition between incipient flycatcher species of the Solomon Islands. *Evolution* **63:** 153–164.

Wagner WL, Funk VA. 1995. *Hawaiian biogeography: evolution of a hotspot archipelago*. Washington: Smithsonian Institution Press.

Weeks BC, Claramunt S. 2014. Dispersal has inhibited avian diversification in Australasian archipelagos. *Proceedings* *of the Royal Society of London B: Biological Sciences* **281:** 20141257.

Wells RE. 1989. The oceanic basement of the Solomon Islands arc and its relationship to the Ontong Java Plateau – insights from Cenozoic plate motion models. In: Vedder JG, Bruns TR, eds. *Geology and offshore resources of Pacific Islands Arcs – Solomon Islands und Bougainville, Papua New Guinea Regions, Vol. 12*. Houston: Circum-Pacific Council for Energy and Mineral Resources, Earth Science Series, 7–22.

Whittaker RJ, Fernandez-Palacios JM. 2007. *Island biogeography: ecology, evolution and conservation*. Oxford: Oxford University Press.

Worthington-Wilmer J, Couper P. 2016. Phylogeography of north-eastern Australia's *Cyrtodactylus* radiation: a habitat switch highlights adaptive capacity at a generic level. *Australian Journal of Zoology* **63:** 398–410.

Wood PL Jr, Heinicke MP, Jackman TR, Bauer AM. 2012. Phylogeny of bent-toed geckos (*Cyrtodactylus*) reveals a west to east pattern of diversification. *Molecular Phylogenetics and Evolution* **65:** 992–1003.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table SI1. *Cyrtodactylus* from the Solomon Islands included in this study.
Table SI2. Data and samples included in the four gene all species analyses (largely following Oliver *et al*., 2014, and data primarily from Wood *et al*., 2012).
Table SI3. Primers and details.