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ISSN: 0158-4197 (Print) 1448-5540 (Online) Journal homepage: http://www.tandfonline.com/loi/temu20

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**To cite this article:** Anna M. Kearns, Leo Joseph, Aude Thierry, John F. Malloy, Maria Nandadevi Cortes-Rodriguez & Kevin E. Omland (2018): Diversification of *Petroica* robins across the Australo-Pacific region: first insights into the phylogenetic affinities of New Guinea's highland robin species, Emu - Austral Ornithology, DOI: 10.1080/01584197.2018.1498744

**To link to this article:** https://doi.org/10.1080/01584197.2018.1498744

EMU - AUSTRAL ORNITHOLOGY
https://doi.org/10.1080/01584197.2018.1498744

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# Diversification of *Petroica* robins across the Australo-Pacific region: first insights into the phylogenetic affinities of New Guinea's highland robin species

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**ABSTRACT**

Complex spatial and temporal phylogenetic patterns have emerged among Pacific Island radiations and their Australian and New Guinean congeners. We explore the diversification of Australo-Pacific *Petroica* robins using the first phylogeny with complete species-level sampling of the genus. In doing so we provide the first assessment of the phylogenetic affinities of two poorly known species with highly restricted ranges in the highlands of New Guinea – Subalpine Robin (*Petroica bivittata*) and Snow Mountain Robin (*P. archboldi*). Our analyses suggest that *Petroica* underwent an initial diversification during the Plio-Pleistocene that established four major lineages restricted to New Zealand (four species), Australia (four species), New Guinea (two species) and Pacific Islands + Australia (three or four species). All lineages appear to have undergone species diversification *in situ* with the exception of the Pacific Islands + Australia lineage where long-distance over-water dispersal must be invoked to explain the placement of the Red-capped Robin (*P. goodenovii*) within the iconic Pacific robin species complex (*P. multicolor* + *pusilla*). Two scenarios fit this biogeographic pattern: (1) a single 'upstream' colonisation of mainland Australia from a Pacific Island ancestor resulting in *P. goodenovii*, or (2) two or three 'downstream' colonisations from a mainland Australian or New Guinean ancestor resulting in the distinct Pacific robin lineages that occur in the south-west Pacific. Overall, biogeographic patterns in *Petroica* suggest that long-distance dispersal and island colonisations have been rare events in this group, which contrasts with other Australo-Pacific radiations that show evidence for repeated long-distance dispersals and multiple instances of secondary sympatry on islands across the Pacific.

**ARTICLE HISTORY**
Received 13 December 2017
Accepted 1 July 2018

**KEYWORDS**
Australian birds; biogeography; conservation; evolution; genetics; Pacific Ocean; threatened species; taxonomy

## Introduction

Patterns of biodiversity in the Australo-Pacific region (Australia, New Guinea, New Zealand and south-west Pacific Islands) have originated through a diverse range of colonisation and diversification scenarios. Both the timing and routes of colonisation have varied – many involving 'downstream' dispersal of colonists from mainland Australia to the Pacific Islands, others from 'upstream' dispersal from the Pacific Islands to Australia (MacArthur and Wilson 1967; Filardi and Moyle 2005; Bellemain and Ricklefs 2008; Jønsson *et al.* 2010; Cibois *et al.* 2011; Schweizer *et al.* 2015). Pacific Island radiations have also been shaped by repeated exchange of colonists among islands resulting in secondary sympatry of divergent non-sister lineages (Andersen *et al.* 2015). These diverse colonisation and diversification histories have left geographically and temporally complex phylogenetic signatures within the Australo-Pacific biota that pose considerable challenges for developing robust hypotheses (Ericson *et al.* 2002; Filardi and Moyle 2005; Jønsson *et al.* 2010, 2011; Cibois *et al.* 2011, 2014; Joseph *et al.* 2011; Irestedt *et al.* 2013; Andersen *et al.* 2014a,2015; Schweizer *et al.* 2015). For example, the extent to which the Australo-Pacific biota have experienced concordant vs. taxon-specific idiosyncratic diversification histories remains unclear owing to the difficulty in teasing apart signatures left by older vs. more recent processes (e.g. intra-archipelago colonisations leading to secondary sympatry). Another continuing issue for studies of this region is the limited availability of scientific collections for key taxon groups such as widespread Pacific Island radiations, with numerous distinct island forms scattered across Melanesia, Oceania and Polynesia (i.e. the

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'great speciators') (Diamond *et al.* 1976; Mayr and Diamond 2001), and species with restricted ranges in remote areas of New Guinea. One of the main gaps in our knowledge stemming from these issues is understanding the extent to which New Guinea has acted as an important island 'stepping-stone' enabling colonisation between Australia and the south-west Pacific (see Filardi and Moyle 2005).

Recent work on the Australo-Pacific robins (Aves: Petroicidae: *Petroica*) illustrates the limitations of having incomplete taxonomic and geographic sampling for developing robust biogeographic hypotheses (Miller and Lambert 2006; Loynes *et al.* 2009; Christidis *et al.* 2011; Kearns *et al.* 2016). *Petroica* robins are a charismatic group of passerines known for their striking variability in plumage carotenoids, repeated losses and gains of sexual dichromatism among island and mainland forms and diversification of species across the Australo-Pacific region (Boles 2007). The 13 *Petroica* species are distributed across a range of habitats in Australia, New Zealand, New Guinea and the south-west Pacific (Bougainville, Solomon Islands, Vanuatu, Fiji, Samoa, Norfolk Island). Consensus from previous phylogenetic studies supports three major lineages within *Petroica*: (1) New Zealand (four species: *P. australis*, *P. longipes*, *P. traversi*, *P. macrocephala*), (2) Australia (four species: *P. rosea*, *P. rodinogaster*, *P. phoenicea*, *P. boodang*) and (3) the Pacific Islands/Australia (three species: *P. multicolor*, *P. pusilla*, *P. goodenovii*) (Miller and Lambert 2006; Loynes *et al.* 2009; Christidis *et al.* 2011; Kearns *et al.* 2016). Notably, the most widespread species in Australia, the Red-capped Robin (*P. goodenovii*), is more closely related to the species in the Pacific Islands than to the other four species in Australia. This biogeographic pattern could result from either upstream colonisation of Australia by *P. goodenovii* from a Pacific Island ancestor or multiple downstream colonisations of the Pacific Islands from a mainland Australian or New Guinean ancestor (Kearns *et al.* 2016). Critically, the lack of complete taxonomic sampling in previous phylogenetic studies has hindered robust tests of these hypotheses. No previous study had complete species sampling of all members of the above three major lineages, and none have sampled the two species that are restricted to the highlands of New Guinea – the Subalpine Robin *Petroica bivittata* (De Vis, 1897) and the Snow Mountain Robin *Petroica archboldi* (Rand 1940) (see Figure 1 for species ranges).

Here, we provide the first analysis of the phylogenetic placement of New Guinea's *P. archboldi* and *P. bivittata*, and in doing so present the first phylogeny for *Petroica* with complete species sampling. Like many of New Guinea's highland species, little is known of the behaviour, life history, precise range limits and taxonomic affinities of *P. archboldi* and *P. bivittata*. Plumage and body size strongly differentiate the two species (Boles 2007; see Figure 1 for plumage differences), and they also show differences in foraging behaviour and habitat preferences – *P. archboldi* is the only bird inhabiting the highest rocky scree habitats at 3800–4200 m elevation (Pratt and Beehler 2015), while *P. bivittata* occupies high mountain forest and alpine/subalpine shrublands above 2700–3500 m elevation (Beehler and Pratt 2016; Figure 1). Given that phylogenetic patterns across the rest of *Petroica* support geography, rather than phenotype, as the best predictor of phylogenetic affinities (Kearns *et al.* 2016), we predict that *P. archboldi* and *P. bivittata* could be sister species despite their major phenotypic differences. In the absence of recent tissue collections, we use an ancient DNA approach to sequence an informative region of mtDNA from museum specimens of *P. archboldi* and *P. bivittata* that were collected by the American Museum of Natural History between 1898 and 1938. Given how little is known about *P. archboldi* and *P. bivittata*, we complement phylogenetic analyses with an assessment of morphometric differentiation between the two species, and contrast this with morphometric differentiation among close relatives in the Pacific Islands and

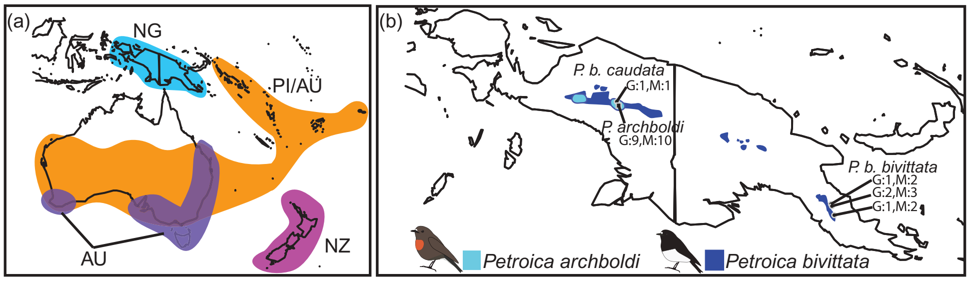

**Figure 1.** Distribution of *Petroica* across the Australo-Pacific. (a) Distribution of major lineages of *Petroica* from New Guinea (NG), Australia (AU), Pacific Islands/Australia (PI/AU) and New Zealand (NZ). (b) Details of sampling localities and distribution of the Snow Mountain Robin *P. archboldi* and Subalpine Robin *P. bivittata* from New Guinea. Sample sizes in genetic (G) and morphometric (M) datasets are given for each locality. Distributions of New Guinea robins are re-drawn from BirdLife International and NatureServe (2011). *Petroica* lineages are based on inferences from this study, and previous studies (Loynes *et al.* 2009; Christidis *et al.* 2011; Kearns *et al.* 2016).

Australia. We use our data to (1) establish the distinctiveness and phylogenetic placement of *P. archboldi* and *P. bivittata*, and (2) further develop and test hypotheses about the colonisation routes and diversification history of *Petroica*. Specifically, we explore the role of New Guinea as a 'stepping-stone' between Australia and the south-west Pacific, and evaluate the extent to which 'upstream', 'downstream' and repeated colonisations have shaped the biogeographic history of *Petroica*.

## Methods

### Molecular sampling

Few cryo-frozen tissues or blood samples are available from birds from the highlands of New Guinea owing to logistical difficulties in collecting there, and none are available for *P. archboldi* and *P. bivittata*. We therefore used ancient DNA techniques to sequence the mitochondrial *ND2* locus from nine *P. archboldi* and five *P. bivittata* (1 *P. b. caudata*, 4 *P. b. bivittata*) museum study skin specimens that were collected by the American Museum of Natural History between 1898 and 1938 (supplementary Table 1). We obtained *ND2* sequences from GenBank for all Australian species, all Pacific Island species and for *P. macrocephala* from New Zealand, which were sequenced in previous phylogenetic studies (Loynes *et al.* 2009; Christidis *et al.* 2011; Dolman and Joseph 2015; Kearns *et al.* 2015, 2016). New Zealand species have only been extensively sequenced for mtDNA *cyt b* and control region loci (Miller and Lambert 2006). Thus, in order to obtain complete taxon sampling of *Petroica* we also sequenced the three New Zealand species that have yet to be sequenced for mtDNA *ND2* – North Island Robin (*P. longipes*), South Island Robin (*P. australis*) and the endangered Chatham Island Black Robin (*P. traversi*) (see supplementary Table 1 for sample details). We also sequenced three individuals from the Chatham Island subspecies of the Tomtit *P. macrocephala chathamensis*, and from *P. goodenovii* to expand subspecies and geographic sampling. We obtained multiple *ND2* sequences from GenBank for *Eugerygone*, *Amalocichla* and *Pachycephalopsis*, and single representatives from four more distantly related genera in the Petroicidae to use as outgroups in phylogenetic analyses (Christidis *et al.* 2011). All sequences generated in this study were deposited in GenBank (accessions: MG676885–MG676913).

### DNA extraction and sequencing

DNA was extracted from small pieces of skin sampled from the toepads or feet of historical museum specimens. All laboratory work was performed in a laboratory at the University of Maryland, Baltimore County that is dedicated to non-avian species in order to limit the risk of contamination from contemporary bird tissues. DNA was extracted using a DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) with a modified protocol to increase the yield obtained from these degraded tissue sources. We used 25 µl of DTT (dithiothreitol) solution and 20 µl of Proteinase K for the initial digestion step, and DNA was eluted with 60 µl of elution buffer instead of 200 µl. *ND2* was amplified in five overlapping fragments that were between 163 and 251 bp in length using *Petroica*-specific internal primers designed for this study (supplementary Table 2). PCRs were carried out on a PTC-200 Thermal Cycler PCR (MJ Research, Hercules, CA, USA) and PCR products were verified on a 1% agarose gel with 5 µl of ethidium bromide. Samples were then cleaned using ExoSAP-IT (Affymetrix, Cleveland, OH, USA) and sent to Genewiz (South Plainfield, NJ, USA) for sequencing. Blood samples from New Zealand robins and tissue samples from *P. goodenovii* were extracted using a DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) with a modified protocol used for the blood samples, which were preserved on filter paper. This involved an additional step where the blood-soaked filter paper was incubated at 55°C overnight in lysis buffer prior to adding proteinase K. PCR amplification of *ND2* followed Kearns *et al.* (2015, 2016). *ND2* sequences were edited and checked for stop codons and indels using Sequencher 4.7 (Gene Codes, Ann Arbor, MI). Following this, we combined our newly generated sequences with those from GenBank using MUSCLE with default alignment settings implemented in MEGA 5 (Tamura *et al.* 2011).

### Phylogenetic analysis

We estimated a rooted phylogeny for *ND2* using both maximum likelihood (ML) and Bayesian inference (BI). PartitionFinder v1.1.1 (Lanfear *et al.* 2012) was used to select the best partitioning scheme and substitution models under BIC. The best partitioning scheme and models were as follows: first codon position – HKY+I, second codon position – HKY+I+G and third codon position – HKY+G. Bayesian inference was implemented in MrBayes 3.6 (Huelsenbeck and Ronquist 2001) for 25 million generations using four runs with four chains each, a temperature of 0.2 and trees were sampled every 1000 generations on the CIPRES Science Gateway HPC (Miller *et al.* 2010). Mixing and convergence of parameters across the four BI runs was assessed using TRACER 1.5 (Drummond and Rambaut 2007) and by ensuring split frequencies of each run had dropped below 0.01 and harmonic means between all four runs did not differ by more than four. Maximum likelihood was implemented in RAxML 7.0.3 (Stamatakis 2006) under the 'fast ML' algorithm with 100 bootstrap pseudoreplicates and imposing the GTRGAMMA model across all partitions as recommended (Stamatakis 2006). We estimated uncorrected mean net nucleotide divergences between each major lineage and species using MEGA 5 (Tamura *et al.* 2011). Divergences were estimated from two datasets – one that was 623 bp long, allowing the inclusion of our single specimen of *P. b. caudata* (AMNH 341,295), which was missing the first 117 bp of *ND2*, and the other was 740 bp long and excluded the short *P. b. caudata* sequence (AMNH 341,295).

### *Divergence dating*

BEAST v1.7.5 (Drummond and Rambaut 2007) was used to estimate divergence times of *Petroica* lineages. We used an uncorrelated lognormal relaxed clock with a yule speciation prior on the tree model and an HKY+I+G substitution model. Substitution model parameters and base frequencies were estimated within BEAST. The *ucld. stdev* parameter and coefficient of variation were both greater than one, indicating that an uncorrelated lognormal relaxed clock was more appropriate for the data than a strict clock (Drummond *et al.* 2007). Divergence times were estimated using a mean substitution rate of $2.9 \times 10^{-2}$ substitutions per site per million years and a standard deviation of 0.004 under a normal prior distribution to reflect the 95% HPD intervals estimated for *ND2* in Lerner *et al.* (2011) ($2.4–3.3 \times 10^{-2}$ substitutions per site per million years). We ran three independent runs under these specifications for 200 million generations, sampling every 1000 generations. TRACER v1.6 was used to check for convergence – we applied a 25% burn-in and verified that marginal probabilities were similar across independent runs, traces of each parameter had reached stationarity in all runs, and effective sample sizes (ESS) on posterior parameter estimates were greater than 100 in all runs. LOGCOMBINER v1.75 was then used to combine tree and log files from the three independent runs after excluding a 25% burn-in from each run and resampling states at a lower frequency of 20 000. We then verified that ESS values were above 100 and parameters had reached stationarity in the combined down-sampled dataset. A maximum clade credibility tree was calculated from the combined down-sampled dataset using mean heights in TREEANNOTATOR v1.75.

### *Morphometric measurements*

To explore the phenotypic distinctiveness of *P. bivittata* and *P. archboldi* we performed morphometric measurements of wing length, tail length and bill length for 15 *P. archboldi* (4 females, 9 males, 2 unknown sex) and 13 *P. bivittata* (2 females, 6 males, 5 unknown sex) (supplementary Table 1) following the methods described in Kearns *et al.* (2016). Samples with unknown sex or suspected to be juveniles (based on plumage characters or specimen labels) were excluded from subsequent analyses (supplementary Table 1). These data were combined with published morphometric measurements from all described species and subspecies in the Pacific + Australia lineage, which phylogenetic analyses determined to be the most closely related to the New Guinean robins (see Results). This dataset included 46 *P. multicolor* (27 males, 19 females), 186 *P. pusilla* (116 males, 70 females), and 33 *P. goodenovii* (17 males, 16 females) (data from Kearns *et al.* 2016). Little difference was observed between sexes in *P. archboldi*, *P. bivittata* (supplementary Table 1) and species in the PI/AU lineage (see Kearns *et al.* 2016). Thus, for simplicity and to maximise sample sizes, we did not perform separate analyses for each sex. Differences in wing length, tail length and bill length were explored using scatter-plots and principal components analysis (PCA) performed in R using the prcomp function. Samples with missing data (due to damage to the bill, wing or tail) were omitted from these analyses (supplementary Table 1). Principal component one (PC1) explained 61% of the variation and had the highest loadings for wing and tail length. PC2 explained 32% of the variation and had the highest loadings for bill length. As patterns of differentiation between the species were similar between PCA and pairwise comparisons of wing length, tail length and bill length, we show only the PCA results.

## Results

### *Phylogenetics*

A total of 740 bp of *ND2* was sequenced for nine *P. archboldi* and four *P. b. bivittata*. The single *P. b. caudata* specimen (AMNH 341295) had poorer DNA quality and only 623 bp were sequenced. Samples from four New Zealand species and *P. goodenovii* sequenced in this study were obtained for the full length of *ND2* (~1040 bp), and then truncated to 740 bp for phylogenetic analyses. *ND2* sequences had no premature stop codons, indels or polymorphic base pairs.

*Petroica archboldi* and *P. bivittata* were 12.2% divergent and reciprocally monophyletic with respect to each other (Figure 2). All nine *P. archboldi* had a single haplotype whereas *P. bivittata* showed population structuring in mtDNA. The western subspecies *P. b. caudata* and the eastern subspecies *P. b. bivittata* were 4.8% divergent. Individuals of eastern *P. b. bivittata* were divided into two

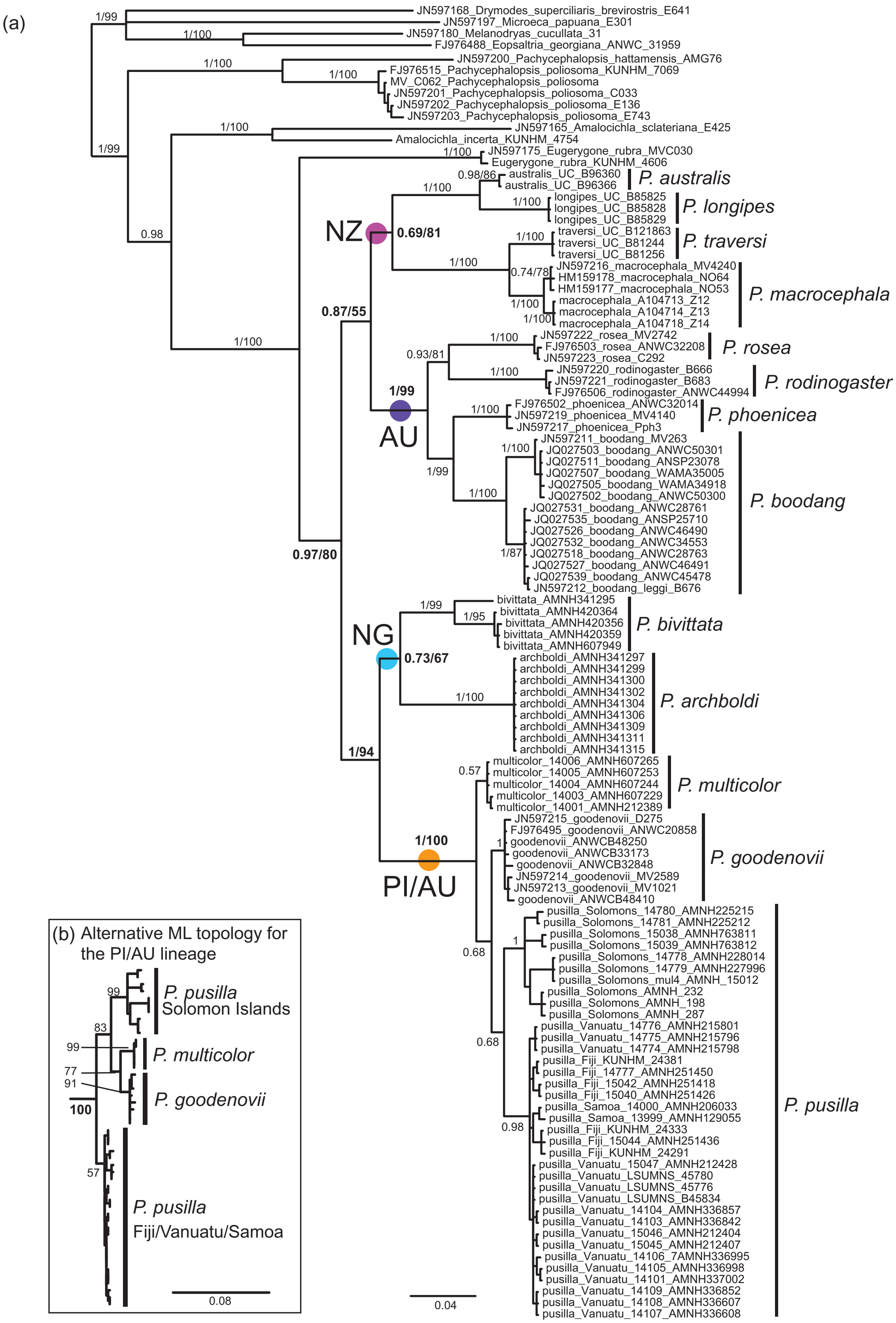

**Figure 2.** Phylogenetic affinities of the Australo-Pacific *Petroica* robins inferred from mtDNA *ND2* using complete species-level sampling. (a) Bayesian consensus tree with Bayesian posterior probabilities and maximum likelihood bootstrap support indicated for each node except those for the PI/AU lineage where Bayesian and maximum likelihood topologies differed. (b) Alternative maximum likelihood topology for the PI/AU lineage showing the sister relationship of *P. multicolor* and *P. goodenovii*, and paraphyly of *P. pusilla* lineages from the Solomon Islands and Vanuatu/Fiji/Samoa.

haplotypes that were 0.13% divergent – one was sampled from three different sampling localities (AMNH 420356 from Mt Albert Edward, AMNH 420359 from Murray Pass, AMNH 607949 from Mt Knutsford), and the other contained a single individual from Mt Albert Edward (AMNH 420364).

There was strong support for the reciprocal monophyly of all species in *Petroica* except those within the PI/AU lineage as was first documented in Kearns *et al.* (2016) (Figure 2). Bayesian analyses support a topology where *P. multicolor* is sister to a lineage comprising *P. goodenovii* and *P. pusilla* as sisters (Figure 2(a)), whereas ML supports a topology where *P. multicolor* and *P. goodenovii* are sisters and nested within *P. pusilla* rendering it paraphyletic (Figure 2(b)). The ML topology supports a sister relationship between *P. pusilla* from the Solomon Islands and a clade containing *P. multicolor* + *P. goodenovii* to the exclusion of *P. pusilla* from Vanuatu, Samoa and Fiji, which is consistent with divergence levels within the PI/AU lineage (Table 1). Bayesian inference and ML analyses support four major lineages in *Petroica* containing (1) all species from New Guinea (NG lineage: 0.73/67), (2) all species from the Pacific Islands plus *P. goodenovii* from mainland Australia (PI/AU lineage: 1/100), (3) all species from Australia except *P. goodenovii* (AU lineage: 1.0/99), and (4) all species from New Zealand (NZ lineage: 0.69/81). However, support was weak for the monophyly of both the New Guinea (NG lineage: 0.73/67) and New Zealand (NZ lineage: 0.69/81) lineages (Figure 2).

Mean net nucleotide divergences between the four major lineages ranged from 11.7 to 16.2% (AU vs. NZ = 15.0; AU vs. NG = 14.9; AU vs. PI/AU = 14.1; NZ vs. NG = 16.2; NZ vs. PI/AU = 15.7; NG vs. PI/AU = 11.7) (Table 1). Within the New Zealand lineage there are two major lineages that are ~16% divergent – grey plumaged *P. australis* and *P. longipes*, which are themselves 5.4% divergent, and black plumaged *P. traversi* and *P. macrocephala*, which are 4.7% divergent from each other (Table 1). These results mirror those of Miller and Lambert (2006) based on *cyt b* and control region mtDNA loci. Species within the Australia lineage are ~10% divergent except for *P. phoenicea* and *P. boodang* which are only 6.4% divergent from each other (Table 1). Species within the PI/AU lineage have the shallowest divergences, ranging from 1.6 to 3.3% (Table 1).

Divergence within each of the four major lineages of *Petroica* is estimated to have occurred over the past 1–6 million years (Figure 3). The New Zealand and Australian lineages are estimated to have begun their divergences earlier than the New Guinea and Pacific Islands/Australia lineages (Figure 3). Crown ages (i.e. time to most recent common ancestor, TMRCA) for New Guinea's *P. archboldi* (95% HPD = 0.1–2.09 mya) and *P. bivitatta* (95% HPD = 0.05–1.82 mya) were similar to those of species in the Australia lineage (95% HPD: lower range = 0.01–0.38 mya; upper range = 1.45–2.76 mya) and New Zealand lineage (95% HPD: lower range = 0–0.13 mya; upper range = 0.93–1.89 mya), as well as for *P. multicolor* (95% HPD = 0.04–1.6 mya) and *P. goodenovii* (95% HPD = 0.18–1.9 mya) in the Pacific Islands/Australia lineage (Figure 3). In contrast, divergences were deeper for the two possibly paraphyletic lineages of *P. pusilla* from the Solomon Islands (95% HPD = 0.39–2.76 mya) and Vanuatu/Fiji/Samoa (95% HPD = 0.49–3.26 mya) (Figure 3).

## Morphometrics

*Petroica archboldi* and *P. bivittata* are discretely differentiated in wing, tail and bill length (data not shown).

**Table 1.** Mean net nucleotide divergence estimates between each species of *Petroica*. Comparisons between major lineages are highlighted in grey, those within lineages are shown in white. Species names are abbreviated to the first four letters. Divergence estimates were calculated separately for the Solomon Islands and Vanuatu/Fiji/Samoa lineages of *P. pusilla* (abbreviated as *pusi* SOL and *pusi* VFS). Net-nucleotide divergences are expressed as percentages

| | | AU | | | | NZ | | | | NG | | PI/AU | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *bood* | *phoe* | *rose* | *rodi* | *aust* | *long* | *macr* | *trav* | *arch* | *bivi* | *mult* | *good* | *pusi* VFS | *pusi* SOL |
| AU | *bood* | | | | | | | | | | | | | | |
| | *phoe* | 6.4 | | | | | | | | | | | | | |
| | *rose* | 9.8 | 10.4 | | | | | | | | | | | | |
| | *rodi* | 11 | 10.8 | 9.9 | | | | | | | | | | | |
| NZ | *aust* | 12.2 | 12.7 | 13.9 | 14.3 | | | | | | | | | | |
| | *long* | 14.3 | 15.6 | 17.1 | 17.6 | 5.4 | | | | | | | | | |
| | *macr* | 14.2 | 15.1 | 15 | 17 | 13.3 | 15.8 | | | | | | | | |
| | *trav* | 13.9 | 14.7 | 15.3 | 17.7 | 14.4 | 16.1 | 4.7 | | | | | | | |
| NG | *arch* | 14.4 | 14.9 | 14.7 | 15.8 | 15.9 | 16 | 17.7 | 16.9 | | | | | | |
| | *bivi* | 15.1 | 14.4 | 14.5 | 15.3 | 14.2 | 16.2 | 16.7 | 16.3 | 12.2 | | | | | |
| PI/AU | *mult* | 12.4 | 11.7 | 15 | 14.5 | 14.4 | 15.1 | 14.8 | 14.2 | 11.5 | 11 | | | | |
| | *good* | 13.1 | 12.2 | 15.9 | 14.4 | 15.5 | 16.5 | 16.3 | 15.9 | 12.5 | 11.7 | 1.6 | | | |
| | *pusi* VFS | 13.3 | 13.1 | 16 | 15.5 | 15.2 | 16.2 | 16.6 | 15.4 | 12.3 | 10.1 | 3.3 | 3.1 | | |
| | *pusi* SOL | 13.1 | 13.2 | 16.5 | 16.1 | 16 | 16.8 | 16.6 | 15.7 | 12.5 | 12 | 2.8 | 2.6 | 3 | |

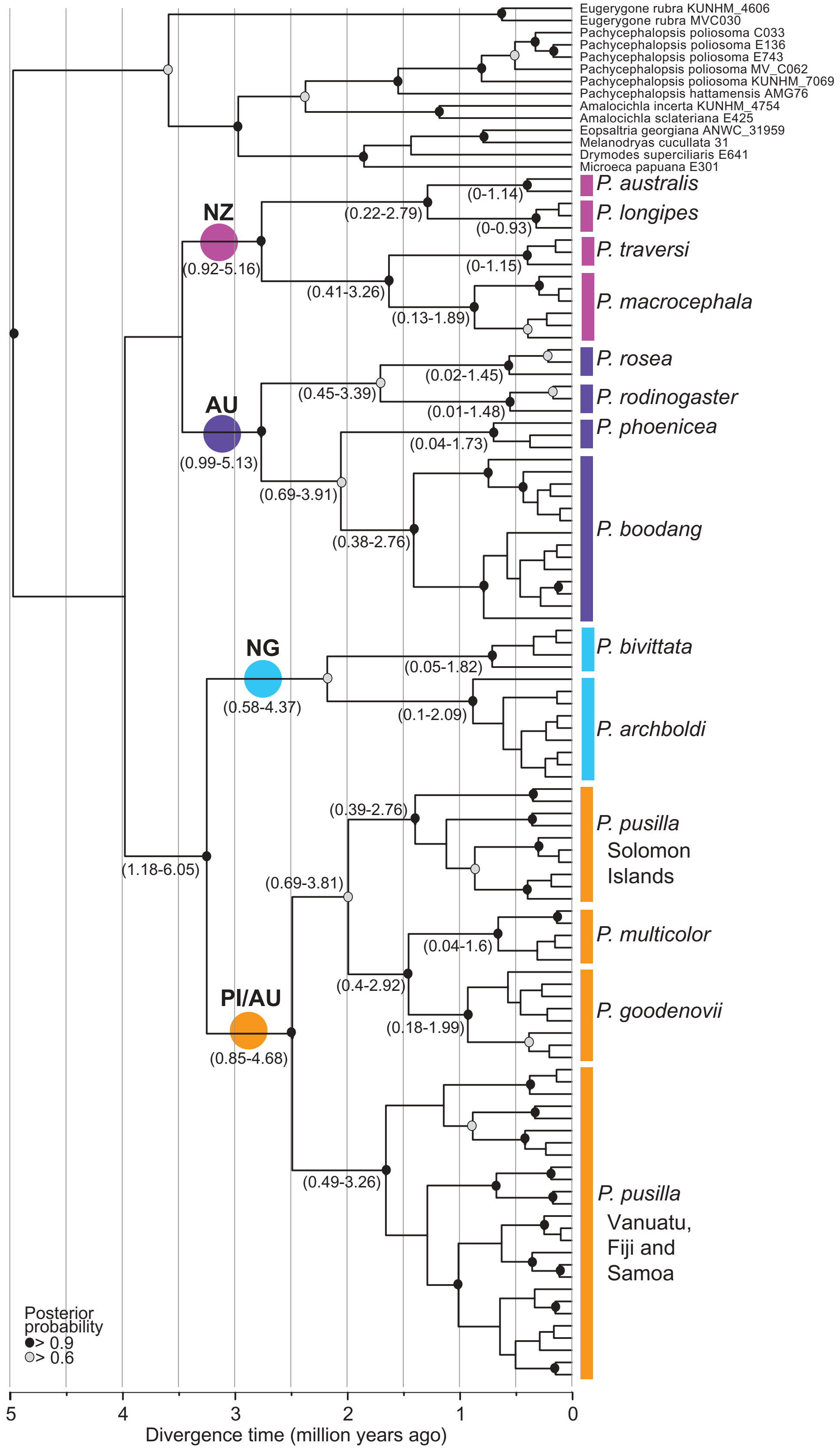

**Figure 3.** Time-scaled phylogeny for the Australo-Pacific *Petroica* robins. Posterior probabilities above 0.6 are indicated for each node (0.6–0.89, grey circle; >0.9, black circle). Ninety-five per cent highest posterior densities (HPD) for estimates of the time to most recent common ancestor (TMRCA) for the major lineages and species in *Petroica* are given in parentheses at each node.

*Petroica archboldi* was larger than *P. bivittata* for all measured variables, but overlapped with members of the PI/AU lineage in bill length (*P. goodenovii* and *P. pusilla*) and tail length (*P. multicolor*). *Petroica bivittata* had similar wing length to *P. multicolor*, and similar bill and tail lengths to *P. goodenovii*. Despite this overlap in trait space, *P. bivittata* occupied distinct morphometric PCA space, as did *P. archboldi* (Figure 4). These analyses confirm the morphometric distinctiveness of *P. archboldi* and *P. bivittata*, and also reconfirm the phenotypic distinctiveness of the endangered Norfolk Robin with broader taxonomic sampling (see Kearns *et al.* 2016).

## Discussion

Our results provide strong evidence that the two New Guinea representatives of the Australo-Pacific robins, *Petroica archboldi* and *P. bivittata*, are most closely related to the Pacific robin radiation, which is widespread across the south-west Pacific and Australia. The two New Guinea species are likely sister taxa that have been evolving separately for several million years; however, we cannot rule out that either *P. archboldi* or *P. bivittata* is sister to the Pacific robin radiation with the other New Guinea species sister to this clade. Although we acknowledge the limitations of studies based solely on a single maternally inherited mtDNA locus (especially for the shallowest divergences, see Funk and Omland 2003; Joseph and Omland 2009), we stress that phylogenetic patterns inferred here from *ND2* are similar to those inferred from nuclear loci and other mtDNA loci in previous studies with incomplete sampling of *Petroica* (Loynes *et al.* 2009; Christidis *et al.* 2011; Kearns *et al.* 2016). Given that there are no modern tissue collections for *P. bivittata*, *P. archboldi* and most taxa in the Pacific robin group, our *ND2* phylogeny offers a valuable framework for understanding the biogeography and evolution of this important Australo-Pacific radiation.

### *Diversification of the Australo-Pacific robins*

Biogeographic patterns within *Petroica* suggest that long-distance over-water dispersal has been rare and restricted mostly to the earlier stages of diversification in *Petroica* (Figures 2 and 3). This contrasts with other so-called ‘great speciators’ and ‘supertramps’ in the Pacific (Moyle *et al.* 2009; Andersen *et al.* 2014b, 2015; Pedersen *et al.* 2018), which have much more complex biogeographic histories involving multiple temporal signatures of colonisation and secondary sympatry. We suggest a reasonably simple diversification scenario for *Petroica*. An initial diversification occurred across the Australo-Pacific region some time over the past 1–6 mya during the Plio-Pleistocene. Four major lineages established and diversified in New Guinea, Australia, New Zealand and the Pacific Islands/Australia (the Pacific robin radiation) beginning around 3 mya (Figure 2). Sister relationships between Australian and New Zealand, and New Guinean and Pacific/Australian lineages imply that Australo-Papua (i.e. Australia and/or New Guinea) could have been the ancestral source of *Petroica* (Figure 2). However, poor support at key nodes (Figure 2) inhibit understanding of colonisation routes at the earlier stages of diversification (Loynes *et al.* 2009; Christidis *et al.* 2011; Kearns *et al.* 2016). For

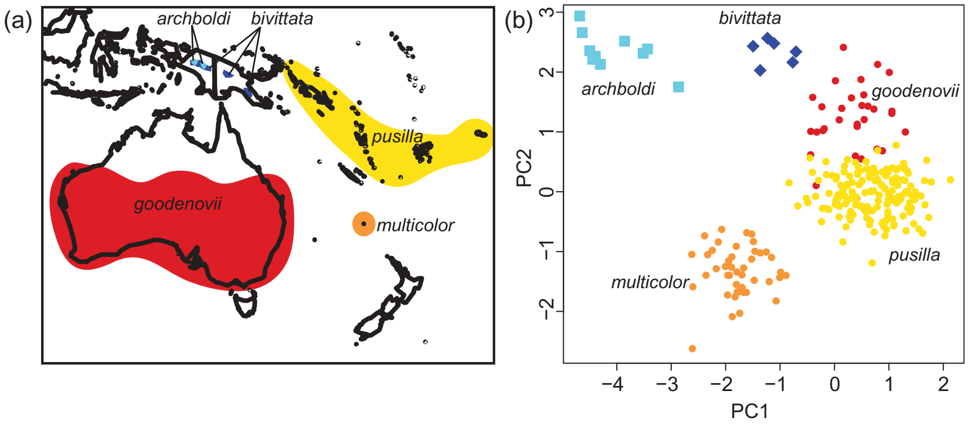

Figure 4. Morphometric variation of New Guinea robins and Pacific/Australia lineage robins. (a) Distribution of species (see Figure 1 for further details of ranges in New Guinea). (b) Principal components analysis (PCA) of measurements of wing length, tail length and bill length showing the differentiation of *P. archboldi* (squares) and *P. bivittata* (diamonds) vs. the PI/AU lineage (circles) (*P. multicolor*, *P. pusilla* and *P. goodenovii*) across PC1 (highest loadings for wing and tail length) and PC2 (highest loadings for bill length).

example, we cannot rule out that the major lineages within both the New Zealand and New Guinea lineages were founded by separate colonisation events owing to weak support for their monophyly (i.e. at the nodes supporting the sister relationship of *P. australis* + *P. longipes* and *P. macrocephala* + *P. traversi* in the New Zealand lineage, and *P. archboldi* and *P. bivittata* in the New Guinea lineage) (Figure 2). This topological uncertainty likely reflects saturation of *ND2*, and more work is still needed to produce a well-resolved phylogenetic and biogeographic hypothesis for *Petroica*. Notably, we find clear evidence that the two species from New Guinea (Snow Mountain Robin *P. archboldi*, Subalpine Robin *P. bivittata*) are most closely related to the Pacific/Australia lineage (Figure 2). Weak support for the monophyly of the New Guinea lineage itself means that at least three alternative patterns of relationships are plausible for the species within the NG+PI/AU clade, including some where the New Guinea species are not sister species. Critically, however, because the monophyly of the NG+PI/AU clade is strongly supported, this uncertainty does not strongly affect inferences about the role of New Guinea as a 'stepping-stone' in the diversification and colonisation history of *Petroica.*

Like previous studies, our data suggest that the Pacific/Australia lineage represents the only example of major over-water dispersal in *Petroica* that occurred after the initial radiation and diversification of the genus across the Australo-Pacific (Figures 2 and 3) (Christidis *et al.* 2011; Kearns *et al.* 2016). Estimates of divergence times suggest that the Pacific/Australia lineage diversified during the Pleistocene (Figure 3), a period of severe global oscillations between glacial and interglacial climates involving changes to sea level, ocean circulation and the severity of south-east tradewinds and westerlies (Hope 1996; Shulmeister *et al.* 2004; Head and Gibbard 2005). Changing sea levels in the Australo-Pacific resulted in repeated land connections between Australia and New Guinea, and between currently isolated islands within most south-west Pacific archipelagos, including within Bougainville and the Solomon Islands, Vanuatu and Fiji (Hope 1996; Worthy and Holdaway 2002; Steadman 2006). However, these changing sea levels did not result in land connections between the south-west Pacific archipelagos. Therefore, the biogeographic history of the Pacific/Australia lineage had to involve long-distance over-water dispersal. Two scenarios fit the data. One is a single 'upstream' colonisation event from the Pacific Islands to Australia resulting in secondary sympatry of *P. goodenovii* with species in the Australian lineage. The other is multiple 'downstream' colonisation events from an ancestor in either Australia or New Guinea to establish the divergent lineages of *P. multicolor* on Norfolk Island and *P. pusilla* in the Solomon Islands, Fiji, Vanuatu and Samoa (also see Cook and Crisp 2005; Keppel *et al.* 2009). Australia's *P. goodenovii* is one of the few widespread birds in the arid interior of Australia with no recognised subspecies (Schodde and Mason 1999). It shows limited genetic diversity in mtDNA *ND2* (Figure 2). These observations accord with its having recently colonised mainland Australia from a Pacific ancestor, perhaps as recently as 0.18 mya (Figure 3). Similar 'upstream' origins have been argued in other birds of mainland Australia (Filardi and Moyle 2005; Cibois *et al.* 2011; Schweizer *et al.* 2015), and elsewhere in the world (Nicholson *et al.* 2005; Bellemain and Ricklefs 2008; Sturge *et al.* 2009).

It remains unclear whether the drivers of long-distance dispersal by *Petroica* were stochastic (chance), deterministic (e.g. easterlies/tradewinds or west-wind drift), or evolutionary shifts from high to intermediate or poor dispersal ability after colonisation (Diamond *et al.* 1976; Mayr and Diamond 2001). Notably, many species of *Petroica* currently undergo small-scale seasonal migrations. Most species from the Australian lineage are seasonal migrants within Australia, and several regularly migrate between Tasmania and mainland Australia (Higgins and Peter 2002). New Zealand robins tend to be much more sedentary (Higgins and Peter 2002; Richard and Armstrong 2010), but they likely engage in some over-water dispersal among islands (Higgins and Peter 2002; Oppel and Beaven 2002). Comparatively little is known about the movement patterns of species from the Pacific/Australia lineage. The furthest recorded dispersal of *P. goodenovii* is 36 km (Dowling *et al.* 2003), but seasonal variation in occurrences across Australia is well known for this species (Higgins and Peter 2002). Seasonal altitudinal migration has been reported for *P. pusilla* in the Solomon Islands (Sardell 2016). Notably, deep divergences, strong phylogeographic structuring and phenotypic differentiation argue for little to no contemporary dispersal among robins distributed across the archipelagos and islands of the south-west Pacific (Figure 2) (Kearns *et al.* 2015, 2016, in prep.).

Finally, we consider whether extinction affects our inferences about species relationships and biogeographic hypotheses for *Petroica*. Extinction of key lineages/species can drastically change phylogeny-based interpretations of ancestral source areas and modes of colonisation (e.g. differentiating between 'stepping-stone' models and long-distance dispersal) (Keppel *et al.* 2009). Subfossils of *P. australis* found throughout New Zealand and subfossils of Pacific robin found in Tonga suggest that both species once had more widespread ranges than at present (Worthy and Holdaway 2002; Steadman 2006). Our *ND2* dataset shows possible signatures of extinction (long branches and deep divergences within the New Guinean and New Zealand lineages in particular). Our biogeographic interpretations of New Guinea's role as a 'stepping-stone' between the Pacific and mainland Australia could be affected if there were extinctions of lineages/species within these regions. Thus, even a well-resolved nuclear dataset could be insufficient to develop a robust biogeographic hypothesis for *Petroica*, and to determine New Guinea's role as a 'stepping-stone' in the colonisation route between mainland Australia and the south-west Pacific Islands. Notably, this is not an issue unique to *Petroica* – subfossil data predict that only 50% of Pacific bird species present before humans arrived persist today (Steadman 2006).

## Taxonomic implications

Molecular phylogenetic analyses show phenotypic traits to be poor indicators of taxonomic affinities and evolutionary history in *Petroica* (Christidis *et al.* 2011; Kearns *et al.* 2016). Instead, geography is a better predictor of phylogenetic relationships among the Australo-Pacific robins (also see Kearns *et al.* 2016). This is further exemplified by the likely close relationship of New Guinea's *P. archboldi* and *P. bivittata*, which share few phenotypic traits (Figures 3 and 4). *Petroica archboldi* has never been closely aligned with any other species owing to its large body size, brown-slate-grey plumage and small badge of orange-red breast plumage, which are distinctive within *Petroica* (Rand 1940). In contrast, *P. bivittata* is smaller and has black dorsal plumage with a large white breast that is reminiscent of other *Petroica* species (Figure 3) (Schodde and Mason 1999). Based on plumage, Schodde and Mason (1999) hypothesised that *P. bivittata* aligned most closely with *P. macrocephala, P. boodang, P. multicolor* (and *P. pusilla*) and *P. goodenovii*. Our phylogenetic analysis differs, finding these six species to be dispersed across the phylogeny and in all four major lineages of *Petroica* (Figure 2).

Our study offers further support for the recognition of the Solomon Islands and Vanuatu/Fiji/Samoa lineages of the Pacific robin radiation as two distinct species (see also Kearns *et al.* 2016). They are currently treated as one species, *P. pusilla*, which is widely distributed across the south-west Pacific (Figure 4(a)). However, sequence divergence (Table 1) and divergence times for the Solomon Islands and Vanuatu/Fiji/Samoa lineages are of the same order of magnitude as the rest of the species in *Petroica* (Figure 3), and there is weak support for a sister relationship between the two lineages. We follow Kearns *et al.* (2016) in suggesting that *polymorpha* Mayr, 1934, could be used as the species rank epithet for the Solomon Islands lineage, while *pusilla* Peale, 1848, has priority for the Vanuatu/Fiji/Samoa lineage. Nuclear loci would provide additional information on this taxonomic issue and we have examined this in a separate paper (Kearns *et al.* in prep.). Note that we find little molecular support for elevating the Samoan subspecies of Pacific robins, *P. pusilla pusilla*, to species rank as Pratt and Mittermeier (2016) advocated based on its distinctive song and plumage. We do not recommend this taxonomic change, given that the Samoan subspecies is one of the least differentiated populations in the Pacific robin radiation. Furthermore, elevating it to species rank would also require that the four other weakly differentiated haplo-groups/lineages within the Vanuatu/Fiji/Samoa lineage be elevated to species rank in order to avoid creating a paraphyletic species (Figure 2). We examine this issue further in a separate paper (see Kearns *et al.* in prep.).

Finally, we note that denser geographic sampling will be required to determine whether the deep genetic divergence between the two Subalpine Robin subspecies, *P. b. bivittata* (represented by four specimens from the most eastern part of the range) and *P. b. caudata* (represented by a single specimen, AMNH 341295) (net-divergence = 4.8%), warrants species-level recognition. Similarly, as samples were available only for one locality within the range of *P. archboldi* (Puncak Trikora/Mt Wilhelmina; Figure 1), an assessment of range-wide genetic diversity and taxonomic limits awaits denser geographic sampling within this species.

## Conclusion

The *Petroica* robins of New Guinea and the Pacific Islands are facing increasing threats from habitat destruction and climate change (Kingsford *et al.* 2009; Keppel *et al.* 2012; Kearns *et al.* 2016). However, this problem is especially acute for New Guinea's Snow Mountain Robin (*P. archboldi*), which has the highest range of any bird species in New Guinea and is the only bird species inhabiting the highest rocky scree habitats at 3800–4200 m elevation (Pratt and Beehler 2015; Beehler and Pratt 2016). Mining is occurring within the ranges of both of New Guinea's endemic robin species and global warming has already caused ice-caps to melt on Puncak Trikora/Mt Wilhelmina – one of the few locations where *P. archboldi* is found (Beehler and Pratt 2016). Here, our use of museum specimens collected as early as the 1800s has provided valuable insight into the evolutionary history and genetic diversity of these vulnerable Australo-Pacific species despite the absence of contemporary tissue collections. Our results provide a much-needed phylogenetic context that can be used to prioritise future research and conservation efforts of these under-studied taxa. Overall, biogeographic patterns in *Petroica* suggest that long-distance dispersal and island colonisations have been rare events in this group, which contrasts with other Australo-Pacific radiations that show evidence for repeated long-distance dispersal and multiple instances of secondary sympatry on islands across the Pacific.

## Acknowledgements

Thanks to Paul Sweet, Thomas Trombone, Lydia Garetano, Peter Capainolo and Chris Filardi at the American Museum of Natural History for allowing us to destructively sample historical museum specimens of *P. archboldi* and *P. bivittata* from New Guinea. Thanks to Jim Briskie, Marie Hale and Tammy Steeves at the University of Canterbury for blood samples from the four species of New Zealand robins. Thanks to Robert Palmer at the Australian National Wildlife Collection, CSIRO for samples of *P. goodenovii*. Bayesian and BEAST analyses were run on CIPRES Science Gateway HPC. This research was funded by NSF grant DEB-1119506 to K.E.O. and partially supported by an Australian Biological Resources Study Churchill Fellowship to A.M.K.

## Funding

This work was supported by the Australian Biological Resources Study [Churchill Fellowship]; National Science Foundation [DEB-1119506].

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