Mitogenomes resolve the phylogeography and divergence times within the endemic New Zealand Callaeidae (Aves: Passerida)

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The biogeographical origins of the endemic birds of New Zealand (Aotearoa) are of great interest, particularly Palaeogene lineages such as Callaeidae, a passerine family characterized by brightly coloured wattles behind the beak and, in some cases, extreme sexual dimorphism in bill size and shape. Ancestral representatives of Callaeidae are thought to have split from their closest relatives outside New Zealand in the Oligocene, but little is known about the timing of divergences within the family. We present a fully dated molecular phylogeny of Callaeidae mitogenomes and discuss the biogeographical implications. Our results suggest that formation of Pliocene marine seaways, such as the Manawatu Strait, are likely to have played a significant role in the differentiation of North Island and South Island kōkako (*Callaeas* spp.) and saddlebacks/tīeke (*Philesturnus* spp.).

ADDITIONAL KEYWORDS: extinct birds – island biogeography – phylogenetics – speciation.

INTRODUCTION

New Zealand (Aotearoa) has long played host to biogeographical debates, such as the relative contributions of vicariance and dispersal (Waters & Craw, 2006; Wallis & Jorge, 2018), the influence of geological history (Craw *et al.*, 2016) and the impacts of Pleistocene glaciations on the evolution, speciation patterns and distribution of biota (Rawlence *et al.*,

2019). New Zealand has variously been described as 'Moa's Ark', in reference to lineages that were purported to be Gondwanan relicts, or as the 'fly paper of the Pacific' owing to the abundance of geologically recent lineages originating from long-distance dispersal (Wallis & Trewick, 2009).

Key to the debates on the origin of the biota of New Zealand is the extent of the Oligocene marine transgression, in which continental subsidence of Zealandia resulted in a dramatic marine inundation (Cooper, 1989). A complete 'drowning' in the late Oligocene/early Miocene ~23 Mya precludes a vicariant

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Gondwanan origin for any terrestrial or freshwater species. Geological evidence increasingly suggests the presence of at least some emergent land throughout this period (Mildenhall *et al.*, 2014); molecular evidence has been used both to support (Wallis & Jorge, 2018) and to challenge (McCulloch & Waters, 2019) the persistence of terrestrial land.

The role of the dramatic tectonic events during the Miocene onwards in determining present-day biotic distributions has also been the subject of extensive discussion. Uplift of the South Island Southern Alps ~5 Mya is correlated with radiations in plants, invertebrates, birds and fish (Wallis & Trewick, 2009; Craw *et al.*, 2019). Volcanic eruptions in the central North Island, most notably ~20 000 and 1850 years ago, significantly affected flora and fauna in the area, causing biological turnover events (McDowall, 1996; Trewick *et al.*, 2011) and marked population structure (Holzapfel *et al.*, 2002; Lloyd, 2003; Shepherd & Lambert, 2007; Chapple *et al.*, 2008; Bunce *et al.*, 2009).

Phylogeographical disjunctions across Cook Strait, which opened 500 000 years ago and separated the North and South Islands during interglacial high sea stands (Lewis *et al.*, 1994), also occur in many taxa, including but not limited to: fish and insects (Craw *et al.*, 2019), plants (Haase, 1992; Rawlence *et al.*, 2021), molluscs (Efford *et al.*, 2002) and birds (Miller & Lambert, 2006; Robertson & Goldstien, 2012; Boast *et al.*, 2019). At the same time, some genetic linkages straddle Cook Strait, notably in freshwater fish and marine invertebrates (Allibone, 2002; Apte & Gardner, 2002; Ayers & Waters, 2005; Apte *et al.*, 2007), reptiles (O'Neill *et al.*, 2008) and birds (e.g. Shepherd *et al.*, 2007). These linkages are sometimes associated with disjunctions across the central North Island, suggesting that older Pliocene marine seaways, such as the Manawatu Strait, might be the underlying cause of these north–south splits.

Pleistocene glacial cycles, beginning ~2.6 Mya, caused further significant changes to the landscape, resulting in glacier-driven diversification in numerous vertebrate and invertebrate taxa (Bunce *et al.*, 2009; Rawlence *et al.*, 2012; Weston & Robertson, 2015; Wallis *et al.*, 2016; Weir *et al.*, 2016); the arrival of new avian lineages (Rawlence *et al.*, 2019); and dispersal across land bridges between the main islands of New Zealand (Greaves *et al.*, 2007; O'Neill *et al.*, 2008; Marshall *et al.*, 2009; Verry *et al.*, 2022). It is within a dynamic geological history that the ancestors of modern Callaeidae arrived in New Zealand.

Callaeidae (Sundevall, 1835) are an endemic New Zealand family of wattlebirds, which form an iconic part of the avian forest assemblage, although two of the five species in this group are now extinct (Fig. 1). The huia (*Heteralocha acutirostris* Gould, 1837) is perhaps the best known, owing to its striking sexual dimorphism in bill shape, the most pronounced of any known bird species (Tomotani *et al.*, 2021). Huia were an important taonga (treasured possession) for Māori, the indigenous people of Aotearoa (New Zealand), and their feathers are highly prized. Found only on the North Island, their numbers reduced rapidly after European arrival, and the species was declared extinct in the 1920s (Phillipps & Falla, 1963). Kōkako (*Callaeas* spp. Forster, 1788) and tīeke/saddlebacks (*Philesturnus* spp. Geoffroy Saint-Hilaire, 1832) were once widely distributed across both the North and South Islands, but deforestation and mammalian predation after human arrival reduced their numbers drastically. North Island kōkako (*Callaeas wilsoni* Bonaparte, 1850) are today limited to the northern half of the North Island and a few offshore islands. The South Island kōkako (*Callaeas cinereus* Gmelin, 1788) was declared extinct in 2008 (although a tentative sighting reported in 2007 was later accepted; Milne & Stocker, 2014). North Island kōkako have fleshy blue wattles; South Island kōkako were darker overall and had orange wattles that were blue at the
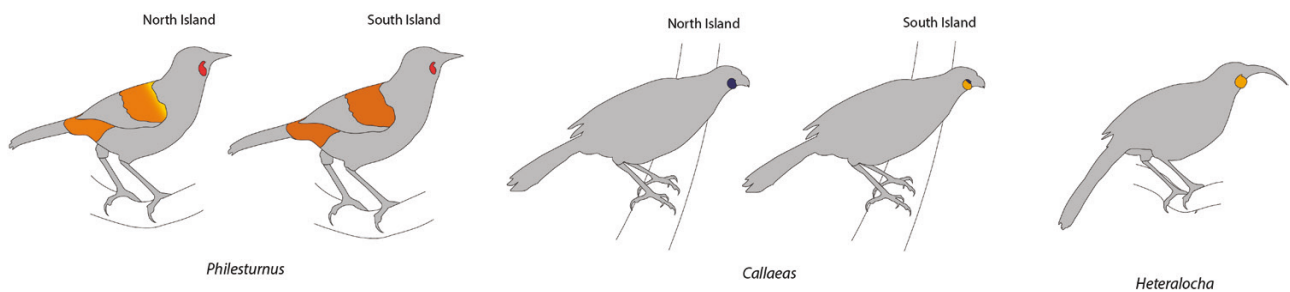

Figure 1. Callaeidae, or New Zealand wattlebirds, showing key phenotypic differences between North and South Island forms of *Philesturnus* and *Callaeas*. Differences in plumage between North and South Island *Philesturnus* are exaggerated for clarity.

base. North Island (*Philesturnus rufusater* Lesson, 1828) and South Island (*Philesturnus carunculatus* Gmelin, 1788) saddlebacks are now found only on offshore islands and predator-free fenced mainland ecosanctuaries (Hooson & Jamieson, 2003). The two species are morphologically similar, although North Island saddlebacks are slightly smaller, with larger wattles, and have a light band of colour in the 'saddle' (Fig. 1). The South Island saddleback has separate juvenile plumage not found in the North Island species. All five species have long been considered taonga by Māori, and conservation management of the three extant species is a top priority.

The wattlebirds have no close relatives outside New Zealand, which makes their taxonomic placement in Passeriformes difficult. They are currently thought to be most closely related to the cnemophiline birds of paradise in the Malesian islands, from which they diverged in the late Eocene or early Oligocene (34–39 Mya) (Barker *et al.*, 2004; Shepherd & Lambert, 2007). Evolutionary relationships within the family are also poorly known, partly because until recently, the North Island and South Island forms of kōkako (Murphy *et al.*, 2006) and saddlebacks (Gill *et al.*, 2010) were considered conspecific. Based on cranial morphology (and, subsequently, feeding habits), Burton (1974) considered the huia and the saddlebacks to be more closely related to one another than to the kōkako. Shepherd & Lambert (2007) attempted to resolve the branching order in the family but could not do so with their chosen nuclear markers, *Rag1* and *c-mos*. Using mitogenomes, Mackiewicz *et al.* (2019) supported the genus-level branching order hypothesized by Burton (1974).

Although their divergence from the cnemophiline birds of paradise and other close relatives, such as the hihi or stitchbird [*Notiomystis cincta* (Du Bus, 1839)], is estimated to be ~30 Mya (Driskell *et al.*, 2007; Irestedt & Ohlson, 2008; Gibb *et al.*, 2015; Oliveros *et al.*, 2019), the timing of divergences in the family is still unknown. Recent inclusion of Callaeidae in molecular phylogenies tends to be representative, and include only one member of the family (see Barker *et al.*, 2004; Ewen *et al.*, 2006; Driskell *et al.*, 2007; Gibb *et al.*, 2015; Selvatti *et al.*, 2015; Oliveros *et al.*, 2019). Consequently, as a result of these gaps in our knowledge, little has been written about the biogeographical origins of Callaeidae in general.

Here, we present the first complete molecular-dated phylogeny of Callaeidae using whole mitogenomes, including a new mitogenome of the South Island saddleback, *Philesturnus carunculatus*. We discuss the implications of estimated divergence times and examine the relationship of the wattlebirds to other New Zealand birds.

MATERIAL AND METHODS

For our study, we required mitogenome data from a South Island saddleback (*Philesturnus carunculatus*). These sequence data are available on GenBank (NC_029143.1; Gibb *et al.*, 2015), but the origin of the bird is listed as Tiritiri Matangi Island (Hauraki Gulf, North Island). To clarify the origin of that bird, a North Island saddleback (*Philesturnus rufusater*) from Kapiti Island was sequenced. Whole genomic DNA was extracted from blood using a MagJET Genomic Purification kit (Thermo Fisher Scientific), following the manufacturer's instructions. The mitogenome was amplified in two overlapping fragments using a KAPA Long Range Hot Start PCR kit (Sigma-Aldrich), following manufacturer's instructions and using the primer pairs F1 5′-GCTTCTTTCTCATTAAGAGGTGCT-3′/ R1 5′-CTAAGCTGCAGATGGCTAGGG-3′ and F2 5′-CAGCCATAGAAGGCCCAACA-3′/R2 5′-AGGTGGTTGTGGGCAGTATT-3′.

The PCR products were cleaned using a 1:1 ratio of magnetic beads. The fragments were pooled and sheared with a Bioruptor DNA sonicator, using 13 cycles of 30 s on and 30 s off. A double-stranded Illumina library was prepared, following Meyer & Kircher (2010), with an additional A-tailing step using Klenow fragments (New England Biolabs) after blunt end repair. The library was then sequenced on an Illumina Miseq run with a 2 × 150 bp paired-end set-up.

Sequence data were mapped following Dussex *et al.* (2021). Illumina adapters were removed using TRIMMOMATIC v.0.32 (Bolger *et al.*, 2014) with default settings. Reads were then mapped to the reference genome of *Philesturnus rufusater* (NC_029143.1) using BWA-MEM v.0.7.13 (Li & Durbin, 2010). Duplicates were sorted, indexed and removed from the alignments with SAMTOOLS (Li *et al.*, 2009). The generated BAM file was then imported into GENEIOUS PRIME v.2021.1.1 (https://www.geneious.com), and sequences were aligned using MUSCLE v.3.8.31 (Edgar, 2004). After aligning the two saddleback mitogenomes, we noticed that they were identical, indicating that NC_029143.1 is a North Island saddleback (*Philesturnus rufusater*).

In order to obtain mitogenome data for a South Island saddleback, we obtained and sequenced a *Philesturnus carunculatus* blood sample collected in 2009 on Ulva Island, off Rakiura/Stewart Island, under a permit from the New Zealand Department of Conservation (DOC; permit SO-23570-FAU). DNA extractions, library preparation, sequencing and alignment followed the same procedure as described above for the North Island saddleback sample. A consensus sequence was called for positions with coverage ≥5× using a majority consensus rule, with ambiguous and low-coverage positions called as undetermined (N). Finally, assembled sequences were inspected visually

to assess overall coverage and quality of the single nucleotide polymorphisms identified.

Publicly available sequences for the remaining members of Callaeidae were accessed from GenBank, along with 17 other passerines (Table 1). Sequences were imported into Geneious Prime, annotated using MITOS (Bernt *et al.*, 2013) and aligned with ClustalO v.1.2.4 (Sievers *et al.*, 2011) using default parameters. Preliminary investigations showed poor alignment in the control region, attributable to missing or incomplete sequence data for *Acanthisitta chloris* Sparrman, 1787, *Corvus moriorum* (Forbes, 1892) and both species of *Petroica* Swainson, 1829. This marker is also of questionable suitability in interspecific and deep-time phylogenies (e.g. Rawlence *et al.*, 2016; N. J. Rawlence, pers. obs.); hypervariability can cause poor phylogenetic resolution over long time scales and overestimation of divergence times (Duchêne *et al.*, 2011). Furthermore, control region duplications and rearrangements, common in passerines, can lead to conflicting phylogenetic topologies (Mackiewicz *et al.*, 2019). Therefore, we excluded the control region, including the duplicate control regions found in *Petroica*, *Poodytes* Cabanis, 1850 and *Notiomystis* Richmond, 1908 (in addition to the duplicate tRNA-Pro in *Notiomystis*).

Table 1. Species included in this study and associated GenBank accession numbers

Species	Accession number
Acanthisitta chloris	AY325307.1
Callaeas cinereus	NC_031350.1
Callaeas wilsoni	GCA_013398955.1
Corvus corax (California)	KX245138.1
Corvus corax (Holarctic)	KX245136.1
Corvus frugilegus	NC_002069.2
Corvus hawaiiensis	KP161620.1
Corvus macrorhynchos	NC_027173.1
Corvus moriorum	NC_031518.1
Corvus splendens	KY018687.1
Gerygone igata	NC_0229139.1
Heteralocha acutirostris	NC_031351.1
Notiomystis cincta	KC545400.1
Nucifraga columbiana	NC_022839.1
Oriolus chinensis	NC_020424.1
Petroica australis	NC_029141.1
Petroica macrocephala	NC_029142.1
Philesturnus carunculatus	This study
Philesturnus rufusater	NC_029143.1
Pica pica	HQ915867.1
Poodytes punctatus	NC_029138.1
Prosthemadera novaeseelandiae	NC_029144.1
Turnagra capensis	KU158197.1

Sequence annotations and translations were checked visually, with areas of overlap between neighbouring features re-assigned such that priority was given to protein-coding genes over other features and to the beginnings of protein-coding genes (i.e. START codon) over their ends. Sequences were split into five partitions: first, second and third positions, tRNAs and rRNAs. The most appropriate substitution model and starting estimates for the proportion of invariant sites was determined using the Akaike information criterion implemented in jModelTest2 v.2.1.10 (Darriba *et al.*, 2012) for protein-coding genes (GTR+I+G), tRNA (TVM+I+G) and rRNA (GTR+I+G). Phylogenetic trees were constructed using the maximum likelihood methods in RAxML v.8.2.11 plug-in for Geneious (Stamatakis, 2006). Inference and dating of the final phylogeny were done in BEAST v.2.6.3 (Bouckaert *et al.*, 2014). Preliminary examinations comparing strict and relaxed clocks showed significant rate variation across branches (Drummond *et al.*, 2006); therefore, only analyses based on a relaxed, uncorrelated lognormal clock are reported. These analyses also showed that the tRNA, rRNA and first codon protein-coding gene partitions shared similar clock rates, which were dissimilar to the clock rates of the second and third codon position partitions. Thus, clock models of these partitions were linked, whereas the second and third position codons were left unlinked. The tree used a birth–death speciation prior.

Molecular dating depends on fossil calibration points, but these are rare in passerines. We followed Oliveros *et al.* (2019) in calibrating the split between suboscines (represented here by *Acanthisitta chloris*) and oscines (all other members of our phylogeny) with an indeterminate suboscine fossil of minimum age 27.25 Mya and maximum age 56.0 Mya. Another passerine calibration point exists in Corvidae, the Miocene fossil *Miopica paradoxa* Kurochkin & Sobolev, 2004, which we took advantage of with the inclusion of several corvids in the phylogeny. Based on this fossil, the minimum age given to the split between *Pica* Brisson, 1760 and *Corvus* Linnaeus, 1758 is 5.3 Mya, and the maximum is 23 Mya, following Scofield *et al.* (2017). We excluded *Corvus coronoides* Vigors & Horsfield, 1827 from our analysis because it has been found to be a chimeric sequence (Sangster & Luksenburg, 2021).

Analyses ran for 75 000 000 generations and were sampled every 1000 generations. The first 10% was discarded as burn-in. Results were assessed in Tracer v.1.7.1 (Rambaut *et al.*, 2018) to ensure effective sample size values > 200 and appropriate mixing. TreeAnnotator was used to calculate maximum clade credibility trees.

RESULTS

The RAxML analysis (Fig. 2) shows good support within Calladiae (all nodes ≥ 99%) and over most of the tree, but only weakly places *Poodytes* as sister to Callaeidae (node support 41%) and *Notiomystis* as sister to *Petroica* (node support 40%). Our BEAST phylogeny (Fig. 3) places the divergence between Callaediae and its relatives at ~27.17 Mya [95% highest posterior density (HPD) 19.44–38.94 Mya] and recovers kōkako (*Callaeas*) as the earliest diverging lineage, splitting from huia (*Heteralocha acutorostris*) and the saddlebacks (*Philesturnus*) ~10.87 Mya (95% HPD 6.50–19.51 Mya). A further split of huia from the saddleback lineage is estimated at 8.14 Mya (95% HPD 4.65–15.44 Mya). Divergences between North and South Island congeners occurred around the same time; the split in kōkako occurred at 2.70 Mya (95% HPD 1.32–5.50 Mya) and in saddlebacks at 2.56 Mya (95% HPD 1.34–5.29 Mya). The split between the saddlebacks supports the designation of NC_029143.1

as *Philesturnus rufusater* and not *Philesturnus carunculatus* as initially reported and excludes the possibility of the individual being a South Island saddleback relocated to Tirititi Matangi.

In the BEAST phylogeny, wattlebirds are placed sister to *Petroica*, diverging ~27.17 Mya. This clade groups with a lineage containing the stitchbird (*Notiomystis cincta*) and the New Zealand fernbird [*Poodytes punctatus* (Quoy & Gaimard, 1832)]. Strong statistical support is found at all nodes (Bayesian posterior probability > 0.99) except for the *Notiomystis* + *Poodytes* and the *Petroica* + Callaeidae nodes (Bayesian posterior probability 0.72 in both cases).

DISCUSSION

In agreement with previous studies, we find that Callaeidae diverged from other passerines during
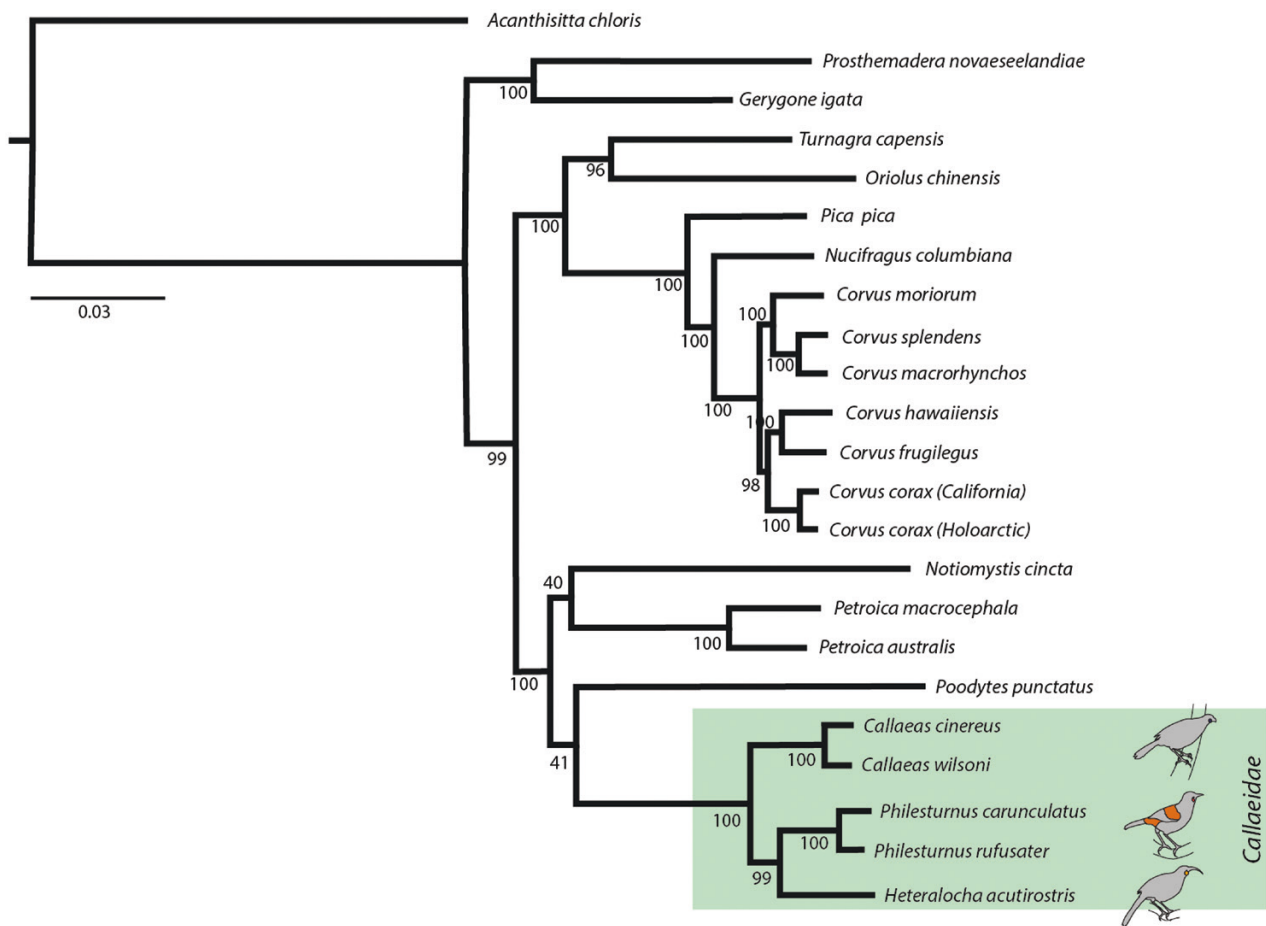
Figure 2. RAxML tree of Callaeidae mitogenomes, excluding the control region, showing different relationships and bootstrap support between Callaeidae (shaded green), *Notiomystis cincta*, *Petroica* spp. and *Poodytes punctatus*. Bootstrap support is shown at nodes.
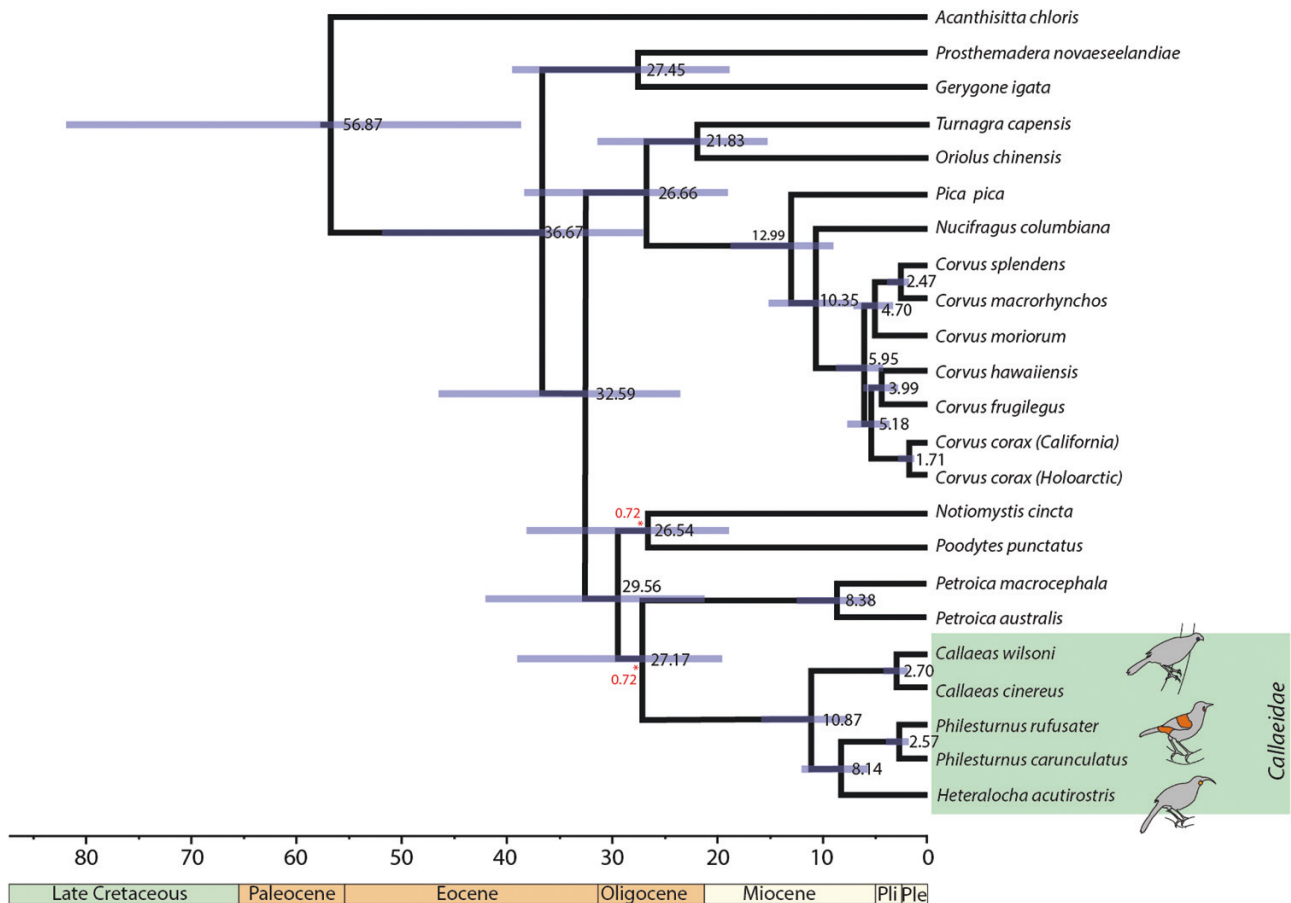
Figure 3. BEAST chronogram of Callaeidae and 17 other passerines, based on a relaxed lognormal clock and fossil calibrations from the studies by Oliveros *et al.* (2019) and Scofield *et al.* (2017). Time scale is in millions of years. Mean divergence dates are shown in black at nodes; bars represent posterior probability intervals. Bayesian posterior probability is one unless specified by a red asterisk.

the Oligocene. However, we find slightly different relationships between this family and other passerine lineages. Barker *et al.* (2004) and Lanfear & Bronham (2011) placed the wattlebird lineage as branching off before core Corvoidea, the former using two nuclear genes and the latter a supermatrix of 11 mitochondrial and three nuclear genes. Lanfear & Bronham (2011) placed the stitchbird with *Petroica* and the fernbird in a separate lineage, but could not resolve the nodes between Callaeidae, *Petroica* + *Notiomystis cincta* and *Poodytes*. Driskell *et al.* (2007), using a selection of nuclear and mitochondrial markers, found the stitchbird and wattlebirds to be sister taxa, and the lineage containing both was basal to *Petroicidae*. Close relationships between Callaeidae and *Petroica* are also found in the phylogeny of Irestedt & Olson (2008) based on two nuclear genes. Studies by Gibb *et al.* (2015) and Mackiewicz *et al.* (2019) used whole mitogenomes and placed the stitchbird and wattlebirds as each other's closest relatives, but did

not always have strong support at this node. Oliveros *et al.* (2019) used thousands of nuclear ultra-conserved elements and placed *Notiomystis* and Callaeidae as sister groups that were more closely related to *Petroica* than to *Poodytes*. The exact relationship between the wattlebirds and other passerines clearly depends on which data are used to build the phylogeny, and these relationships cannot be resolved using a small number of markers.

We note that *Notiomystis cincta*, *Petroica* and *Poodytes* share a duplicated control region not present in the Callaeidae. Exclusion of these sites in our analyses is likely to be driving the differences between our phylogeny and that of Gibb *et al.* (2015) (for a discussion on control region duplication in passerines, see Mackiewicz *et al.*, 2019). Inclusion of the control region in the alignment does improve RAxML node support slightly (see Supporting Information, Fig S1) but comes at the cost of poor alignment among most sequences. The topological discrepancies between
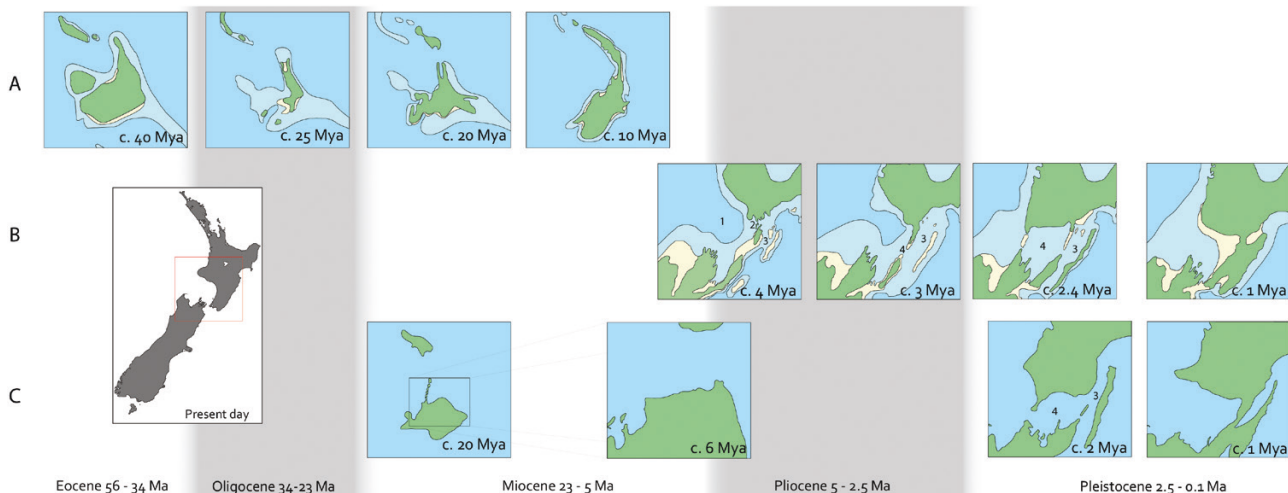
Figure 4. Palaeogeographical reconstructions of New Zealand. Land is shaded in green, coastal areas in light yellow, shallow sea in light blue, and deep sea in dark blue. Inset shows present-day map of New Zealand: (1) the Wanganui Basin; (2) the Kuripapango Strait; (3) the Ruataniwha Strait; and (4) the Manawatu Strait. Row A maps are adapted from GNS Science reconstructions based on the studies by King *et al.* (1999) and King (2000). Row B maps are adapted from the work of Trewick & Bland (2012) and are focused on the area outlined in red on the present-day inset. Row C maps are adapted from the study by Bunce *et al.* (2009); the ~20 Mya map shows the entire landmass, and subsequent ones are focused on the area outlined in the black bounding box. Background grey shading denotes changing geological periods.

An alternative third scenario, in which early divergence occurred on a proto-South Island during the Miocene, seems unlikely because it requires either that ancestral forms flew past a proto-North Island landmass from their presumed origin to reach a proto-South Island, or arrived on both landmasses but went extinct on the North Island.

Regarding the first scenario, dispersal over seaways would not typically be expected in a family of poor flyers; morphological observations in each genus emphasize weak flight muscles and powerful legs suited to hopping (Stonor, 1942). Indeed, observations of kōkako by Hay (1981) suggest that they can sustain powered flight over distances of only < 20 m, although they can glide for 150 m. Although populations of North Island kōkako have been established on offshore islands, the only naturally occurring offshore population is on Aotea (Great Barrier Island; Gill *et al.*, 2010), suggesting that these birds do not disperse over water commonly.

However, both species of saddlebacks established populations on offshore islands. North Island saddleback populations were found on Aotea, Hauturu (Little Barrier) and the Hen and Chicken Islands in northern New Zealand at the time of European arrival, the latter of which are > 12 km offshore (Gill *et al.*, 2010). South Island saddlebacks were found on D'Urville, Stewart and Stephens Islands. It is possible that these populations made their way onto these islands during the Pleistocene, when they would have been connected to the mainland when sea levels dropped by 120 m (Newnham *et al.*, 2013). It is worth noting that North Island saddlebacks were observed to self-colonize Coppermine Island after the establishment of a population on Whatupuke Island, a distance of 150 m (Newman, 1980), supporting their capability of dispersal over water. Flightlessness can also evolve rapidly (e.g. Kirchman, 2012; Garcia-R *et al.*, 2014; Hume & Martill, 2019), and ancestral forms might have been better flyers, particularly given their original transoceanic dispersal.

If dispersal over an ever-narrowing strait was indeed the mechanism by which North Island populations of kōkako and saddlebacks found their way onto the South Island, this dispersal was probably continuous, supplemented by the existence of low-lying land in the 'gap' between North and South Islands throughout the Pliocene and Pleistocene, which might have served as stepping stones. A study by Murphy *et al.* (2006) using the mitochondrial control region showed little population structure in the North Island kōkako across their range. An analysis of microsatellite markers from museum skins also failed to detect population structure in huia (Lambert *et al.*, 2009), suggesting that these birds can disperse widely across suitable habitat.

Therefore, if this dispersal was continuous, we would not expect both kōkako and saddlebacks to diverge across the strait at exactly the same time, particularly if secondary contact of the lineages occurred over

Pleistocene land bridges. Such secondary contact has been suggested to explain molecular similarities between South Island and Stewart Island forms of *Kikihia* Dugdale, 1972 cicadas (Marshall *et al.*, 2009), for example, in addition to introgression in *Oligosoma* Girard, 1857 skinks from Whenua Hou (Codfish Island) into mainland forms (Greaves *et al.*, 2007). If dispersal was continuous, it is not clear how the populations would have diverged at all, suggesting that this scenario does not explain species distributions adequately. However, this argument assumes that suitable habitat was present on the low-lying land in the straits, which would facilitate their migration. Pleistocene land bridges might not have had extensive forest cover, given the contraction of forest during glacial cycles (Newnham *et al.*, 2013), and low-lying land in Pliocene seaways might have been sandbanks unsuitable for forest.

The second scenario, overland dispersal of the kōkako and saddlebacks followed by the creation of a significant barrier to dispersal beginning 3.5–4.0 Mya in the form of the marine seaways (e.g. Manawatu Strait), does not depend on the question of continuous or non-continuous dispersal. The seaways, as a barrier to dispersal, would prevent significant gene flow between the populations and facilitate speciation. The Kuripapango and Manawatu straits, even if narrower and shorter lived than previously estimated, were still wide (< 20 km) for the wattlebirds and would have been difficult to cross, particularly if no suitable forest habitat was present on the low-lying land above the seaways (Trewick & Bland, 2012; Rawlence *et al.*, 2021). If kōkako and saddlebacks were present across both North and South Island landmasses, then huia might also have been present on both, but went extinct on the South Island. The species is typically considered to have occurred only on the North Island, although some oral reports and traditions suggest that a small population might have been living in the Nelson/Marlborough area in the late 19th century (Phillipps & Falla, 1963). These reports have never been confirmed and are not mentioned in modern bird checklists (e.g. Gill *et al.*, 2010). Worthy & Holdaway (2002) mention that huia fossils are rare and suggest that they might have preferred habitats not well represented in current fossil deposits.

CONCLUSION

Speciation patterns in saddlebacks and kōkako might be explained by one of two hypotheses: parapatric speciation on a proto-North Island followed by migration across narrowing Pliocene straits; or allopatric speciation driven by the separation of the proto-North and proto-South Islands by Pliocene straits.

To test these hypotheses, some key pieces of evidence are needed, including fossil representatives of ancestral forms and clearer palaeogeographical reconstructions of Neogene New Zealand. Although Callaeidae are well represented in subfossil and pre-European archaeological midden (i.e. rubbish dump) deposits, the oldest fossils are Late Quaternary (< 30 000 bp) and therefore too young to elucidate Neogene divergence patterns (Brodkorb, 1978; Worthy & Holdaway, 2002). The age of the Callaeidae lineages suggests that they might be found among the passerines in the 16–19 Mya South Island St Bathans fossil deposit, in which case they were already present on the South Island before the opening of the Pliocene straits (A. Tennyson, pers. comm., 2021). The extent to which North and South Islands were isolated from or connected to each other during the early to mid-Miocene is also crucial to distinguishing between these hypotheses. If the northern and southern portions of proto-New Zealand were not connected in the mid-Miocene (Fig. 4B), a north-to-south pattern of evolution might be more likely, wherein North Island kōkako and saddlebacks dispersed across the Manawatu Strait to the South Island, where they diverged. If they were connected (Fig. 4), then all three species occurred across proto-New Zealand, were isolated after the creation of the Pliocene seaways, and subsequently diverged into North and South Island forms, with South Island huia becoming extinct before North Island huia. Until more geological or palaeontological evidence comes to light, it is not possible to choose confidently between these hypotheses.

It is also important to note that geographical isolation attributable to geological upheaval and formation of a physical barrier is not the only cause of speciation, merely one whose signature is relatively easy to detect. Reproductive isolation and allopatric speciation do not require a significant geological event, such as the formation of marine straits, but could be, for example, the result of unfavourable habitat between two populations. Speciation might also be driven by niche specialization (i.e. ecological divergence) as a result of changing biotic factors that leave little to no signal in the geological record. Such factors are perhaps behind the genus-level speciations in Callaeidae, which occur at geologically unexplained times.

This study contributes to a large body of work dedicated to understanding the unique biogeographical patterns of Aotearoa (New Zealand). Species-level divergences in the wattlebirds were likely to be driven by tectonic Neogene events, and although North and South Island forms of both kōkako and saddlebacks were long considered conspecific, they diverged between 2.5 and 3.0 Mya and are distinct lineages.

DATA AVAILABILITY

Māori draw their whakapapa (genealogy) from the land and are interconnected with the plants and animals of Aotearoa. There is no cultural distinction between a living thing and its genetic data, especially for taonga (treasured) species, such as the callaeid birds. Therefore, the newly generated mitogenome will be stored in the data repository of Genomics Aotearoa at: https://repo.data.nesi.org.nz/discovery/TAONGA-AGDR00023/; access to these data is made available on the recommendation of the kaitiaki (guardians) of the sequence, Murihiku Ngai Tāhu, with whom the intellectual property associated with the data reside. Publicly available mitogenomes used in this study are available on GenBank (https://www.ncbi.nlm.nih.gov/genbank) and can be accessed with the accession numbers provided in Table 1.

REFERENCES

Allibone R. 2002. Dealing with diversity dwarf galaxias style. *Water & Atmosphere* **10:** 18–19.

Apte S, **Gardner JPA. 2002.** Population genetic subdivision in the New Zealand greenshell mussel (*Perna canaliculus*) inferred from single-strand conformation polymorphism analysis of mitochondrial DNA. *Molecular Ecology* **11:** 1617–1628.

Apte S, **Smith PJ**, **Wallis GP. 2007.** Mitochondrial phylogeography of New Zealand freshwater crayfishes, *Paranephrops* spp. *Molecular Ecology* **16:** 1897–1908.

Ayers KL, **Waters JM. 2005.** Marine biogeographic disjunction in central New Zealand. *Marine Biology* **147:** 1045–1052.

Barker FK, **Cibois A**, **Schikler P**, **Feinstein J**, **Cracraft J. 2004.** Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences of the United States of America* **101:** 11040–11045.

Bernt M, **Donath A**, **Jühling F**, **Externbrink F**, **Florentz C**, **Fritzsch G**, **Pütz J**, **Middendorf M**, **Stadler PF. 2013.** MITOS: Improved *de novo* metazoan mitochondrial genome annotation. *Molecular Phylogenetics and Evolution* **69:** 313–319.

Boast AP, **Chapman B**, **Herrera MB**, **Worthy TH**, **Scofield RP**, **Tennyson AJD**, **Houde P**, **Bunce M**, **Cooper A**, **Mitchell KJ. 2019.** Mitochondrial genomes from New Zealand's extinct adzebills (Aves: Aptornithidae: *Aptornis*) support a sister-taxon relationship with the Afro-Madagascan Sarothruridae. *Diversity* **11:** 24.

Bolger AM, **Lohse M**, **Usadel B. 2014.** Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* **30:** 2114–2120.

Bouckaert R, **Heled J**, **Kühnert D**, **Vaughan T**, **Wu C-H**, **Xie D**, **Suchard MA**, **Rambaut A**, **Drummond AJ. 2014.** BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* **10:** e1003537.

Brodkorb P. 1978. *Catalogue of fossil birds. Part 5 (Passeriformes)*. Gainesville: University of Florida.

Bunce M, **Worthy TH**, **Phillips MJ**, **Holdaway RN**, **Willerslev E**, **Haile J**, **Shapiro B**, **Scofield RP**, **Drummond A**, **Kamp PJJ**, **Cooper A. 2009.** The evolutionary history of the extinct ratite moa and New Zealand Neogene paleogeography. *Proceedings of the National Academy of Sciences of the United States of America* **106:** 20646–20651.

Burton PJK. 1974. *Anatomy of head and neck in the huia (*Heteralocha acutirostris*) with comparative notes on other Callaeidae*. London: British Museum (Natural History).

Chapple DG, **Daugherty CH**, **Ritchie PA. 2008.** Comparative phylogeography reveals pre-decline population structure of New Zealand *Cyclodina* (Reptilia: Scincidae) species. *Biological Journal of the Linnaean Society* **95:** 388–408.

Cooper RA. 1989. New Zealand tectonostratigraphic terranes and panbiogeography. *New Zealand Journal of Zoology* **16:** 699–712.

Craw D, **King TM**, **McCulloch GA**, **Upton P**, **Waters JM. 2019.** Biological evidence constraining river drainage evolution across a subduction-transcurrent plate boundary transition, New Zealand. *Geomorphology* **336:** 119–132.

Craw D, **Upton P**, **Burridge CP**, **Wallis GP**, **Waters JM. 2016.** Rapid biological speciation driven by tectonic evolution in New Zealand. *Nature Geoscience* **9:** 140–144.

Crouch EM, **Shepherd CL**, **Morgans HEG**, **Naafs BDA**, **Dallanave E**, **Phillips A**, **Hollis CJ**, **Pancost RD. 2020.** Climatic and environmental changes across the early Eocene

climatic optimum at mid-Waipara River, Canterbury Basin, New Zealand. *Earth-Science Reviews* **200:** 102961.

Darriba D, **Taboada GL**, **Doallo R**, **Posada D. 2012.** jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9:** 772.

Driskell A, **Christidis L**, **Gill BJ**, **Boles WE**, **Barker FK**, **Longmore NW. 2007.** A new endemic family of New Zealand passerine birds: adding heat to a biodiversity hotspot. *Australian Journal of Zoology* **55:** 73–78.

Drummond AJ, **Ho SYW**, **Phillips MJ**, **Rambaut A. 2006.** Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4:** e88.

Duchêne S, **Archer FI**, **Vilstrup J**, **Caballero S**, **Morin PA. 2011.** Mitogenome phylogenetics: the impact of using single regions and partitioning schemes on topology, substitution rate and divergence time estimation. *PLoS One* **6:** e27138.

Dussex N, **Van der Valk T**, **Morales HE**, **Wheat CW**, **Díez-del-Molino D**, **Von Seth J**, **Foster Y**, **Kutschera VE**, **Guschanski K**, **Rhie A**, **Phillippy AM**, **Korlach J**, **Howe K**, **Chow W**, **Pelan S**, **Mendes Damas JD**, **Lewin HA**, **Hastie AR**, **Formenti G**, **Fedrigo O**, **Guhlin J**, **Harrop TWR**, **Le Lec MF**, **Dearden PK**, **Haggerty L**, **Martin FJ**, **Kodali V**, **Thibaud-Nissen F**, **Iorns D**, **Knapp M**, **Gemmell NJ**, **Robertson F**, **Moorhouse R**, **Digby A**, **Eason D**, **Vercoe D**, **Howard J**, **Jarvis ED**, **Robertson BC**, **Dalén L. 2021.** Population genomics of the critically endangered kākāpō. *Cell Genomics* **1:** 100002.

Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32:** 1792–1797.

Efford M, **Howitt R**, **Gleeson D. 2002.** Phylogenetic relationships of *Wainuia* (Mollusca: Pulmonata)— biogeography and conservation implications. *Journal of the Royal Society of New Zealand* **32:** 445–456.

Ewen JG, **Flux I**, **Ericson PGP. 2006.** Systematic affinities of two enigmatic New Zealand passerines of high conservation priority, the hihi or stitchbird *Notiomystis cincta* and the kokako *Callaeas cinerea*. *Molecular Phylogenetics and Evolution* **40:** 281–284.

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.

Gibb GC, **England R**, **Hartig G**, **McLenachan PA**, **Smith BLT**, **McComish BJ**, **Cooper A**, **Penny D. 2015.** New Zealand passerines help clarify the diversification of major songbird lineages during the Oligocene. *Genome Biology and Evolution* **7:** 2983–2995.

Gill B, **Bell BD**, **Chambers G**, **Medway DG**, **Palma R**, **Scofield R**, **Tennyson A**, **Worthy T. 2010.** *Checklist of the birds of New Zealand, Norfolk and Macquarie Islands, and the Ross Dependency, Antarctica*. Wellington, NZ: Te Papa Press.

Greaves SNJ, **Chapple DG**, **Gleeson DM**, **Daugherty CH**, **Ritchie PA. 2007.** Phylogeography of the spotted skink (*Oligosoma lineoocellatum*) and green skink (*O. chloronoton*) species complex (Lacertilia: Scincidae) in New Zealand

reveals pre-Pleistocene divergence. *Molecular Phylogenetics and Evolution* **45:** 729–739.

Haase P. 1992. Isozyme variability and biogeography of *Nothofagus truncata* (Fagaceae). *New Zealand Journal of Botany* **30:** 315–328.

Hay JR, **Forest Bird Research Group (N.Z.)**. **1981.** *The kokako*. Wellington: New Zealand Wildlife Service.

Hayward BW, **Black PM**, **Smith IEM**, **Ballance PF**, **Itaya T**, **Doi M**, **Takagi M**, **Bergman S**, **Adams CJ**, **Herzer RH**, **Robertson DJ. 2001.** K-Ar ages of early Miocene arc-type volcanoes in northern New Zealand. *New Zealand Journal of Geology and Geophysics* **44:** 285–311.

Holzapfel S, **Faville MZ**, **Gemmill CEC. 2002.** Genetic variation of the endangered holoparasite *Dactylanthus taylorii* (Balanophoraceae) in New Zealand. *Journal of Biogeography* **29:** 663–676.

Hooson S, **Jamieson IG. 2003.** The distribution and current status of New Zealand saddleback *Philesturnus carunculatus*. *Bird Conservation International* **13:** 79–95.

Hume JP, **Martill D. 2019.** Repeated evolution of flightlessness in *Dryolimnas* rails (Aves: Rallidae) after extinction and recolonization on Aldabra. *Zoological Journal of the Linnean Society* **186:** 666–672.

Irestedt M, **Ohlson JI. 2008.** The division of the major songbird radiation into Passerida and 'core Corvoidea' (Aves: Passeriformes) — the species tree vs. gene trees. *Zoologica Scripta* **37:** 305–313.

Kamp PJJ. 1986. Late Cretaceous-Cenozoic tectonic development of the southwest Pacific region. *Tectonophysics* **121:** 225–251.

King PR. 2000. New Zealand's changing configuration in the last 100 million years: plate tectonics, basin development, and depositional setting. In: *2000 New Zealand oil exploration conference proceedings*. Wellington: Ministry of Economic Development, 132–146.

King PR, **Naish TR**, **Browne GH**, **Field BD**, **Edbrooke SW. 1999.** *Cretaceous to Recent sedimentary patterns in New Zealand*. Lower Hutt: Institute of Geological & Nuclear Sciences.

Kirchman JJ. 2012. Speciation of flightless rails on islands: a DNA-based phylogeny of the typical rails of the Pacific. *The Auk* **129:** 56–69.

Lambert DM, **Shepherd LD**, **Huynen L**, **Beans-Picón G**, **Walter GH**, **Millar CD. 2009.** The molecular ecology of the extinct New Zealand huia. *PLoS One* **4:** e8019.

Lanfear R, **Bromham L. 2011.** Estimating phylogenies for species assemblages: a complete phylogeny for the past and present native birds of New Zealand. *Molecular Phylogenetics and Evolution* **61:** 958–963.

Lee DE, **Conran JG**, **Lindqvist JK**, **Bannister JM**, **Mildenhall DC. 2012.** New Zealand Eocene, Oligocene and Miocene Macrofossil and pollen records and modern plant distributions in the Southern Hemisphere. *Botanical Review* **78:** 235–260.

Lewis KB, **Carter L**, **Davey FJ. 1994.** The opening of Cook Strait: interglacial tidal scour and aligning basins at a subduction to transform plate edge. *Marine Geology* **116:** 293–312.

Li H, **Durbin R. 2010.** Fast and accurate long-read alignment with Burrows–Wheeler transform. *Bioinformatics* **26:** 589–595.

Li H, **Handsaker B**, **Wysoker A**, **Fennell T**, **Ruan J**, **Homer N**, **Marth G**, **Abecasis G**, **Durbin R**; **1000 Genome Project Data Processing Subgroup**. **2009.** The sequence alignment/map format and SAMtools. *Bioinformatics* **25:** 2078–2079.

Lloyd BD. 2003. Intraspecific phylogeny of the New Zealand short-tailed bat *Mystacina tuberculata* inferred from multiple mitochondrial gene sequences. *Systematic Biology* **52:** 460–476.

Mackiewicz P, **Urantówka AD**, **Kroczak A**, **Mackiewicz D. 2019.** Resolving phylogenetic relationships within Passeriformes based on mitochondrial genes and inferring the evolution of their mitogenomes in terms of duplications. *Genome Biology and Evolution* **11:** 2824–2849.

Marshall DC, **Hill KBR**, **Fontaine KM**, **Buckley TR**, **Simon C. 2009.** Glacial refugia in a maritime temperate climate: cicada (*Kikihia subalpina*) mtDNA phylogeography in New Zealand. *Molecular Ecology* **18:** 1995–2009.

McCulloch GA, **Waters JM. 2019.** Phylogenetic divergence of island biotas: molecular dates, extinction, and 'relict' lineages. *Molecular Ecology* **28:** 4354–4362.

McDowall RM. 1996. Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. *Journal of Biogeography* **23:** 139–148.

McGlone MS, **Buitenwerf R**, **Richardson SJ. 2016.** The formation of the oceanic temperate forests of New Zealand. *New Zealand Journal of Botany* **54:** 128–155.

Meyer M, **Kircher M. 2010.** Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harbor Protocols* **2010:** pdb. prot5448.

Mildenhall D, **Mortimer N**, **Bassett K**, **Kennedy E. 2014.** Oligocene paleogeography of New Zealand: maximum marine transgression. *New Zealand Journal of Geology and Geophysics* **57:** 107–109.

Miller HC, **Lambert DM. 2006.** A molecular phylogeny of New Zealand's *Petroica* (Aves: Petroicidae) species based on mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **40:** 844–855.

Milne A, **Stocker R. 2014.** Evidence for the continued existence of the South Island kokako (*Callaeas cinerea*) drawn from reports collected between January 1990 and June 2012. *Notornis* **61:** 137–143.

Murphy SA, **Flux IA**, **Double MC. 2006.** Recent evolutionary history of New Zealand's North and South Island kokako (*Callaeas cinerea*) inferred from mitochondrial DNA sequences. *Emu - Austral Ornithology* **106:** 41–48.

Newman DG. 1980. Colonisation of Coppermine Island by the North Island saddleback. *Notornis* **27:** 146–147.

Newnham R, **McGlone M**, **Moar N**, **Wilmshurst J**, **Vandergoes M. 2013.** The vegetation cover of New Zealand at the Last Glacial Maximum. *Quaternary Science Reviews* **74:** 202–214.

Oliveros CH, **Field DJ**, **Ksepka DT**, **Barker FK**, **Aleixo A**, **Andersen MJ**, **Alström P**, **Benz BW**, **Braun EL**, **Braun MJ**, **Bravo GA**, **Brumfield RT**, **Chesser RT**, **Claramunt S**, **Cracraft J**, **Cuervo AM**, **Derryberry EP**, **Glenn TC**, **Harvey MG**, **Hosner PA**, **Joseph L**, **Kimball RT**, **Mack AL**, **Miskelly CM**, **Peterson AT**, **Robbins MB**, **Sheldon FH**, **Silveira LF**, **Tilson Smith B**, **White ND**, **Moyle RG**, **Faircloth BC. 2019.** Earth history and the passerine superradiation. *Proceedings of the National Academy of Sciences of the United States of America* **116:** 7916–7925.

O'Neill SB, **Chapple DG**, **Daugherty CH**, **Ritchie PA. 2008.** Phylogeography of two New Zealand lizards: McCann's skink (*Oligosoma maccanni*) and the brown skink (*O. zelandicum*). *Molecular Phylogenetics and Evolution* **48:** 1168–1177.

Phillipps WJ, **Falla RA. 1963.** *The book of the huia*. Christchurch: Whitcombe & Tombs.

Pocknall DT. 1990. Palynological evidence for the early to middle Eocene vegetation and climate history of New Zealand. *Review of Palaeobotany and Palynology* **65:** 57–69.

Pole M. 2014. The Miocene climate in New Zealand: estimates from paleobotanical data. *Palaeontologica Electronica* **17:** 1–79.

Rambaut A, **Drummond AJ**, **Xie D**, **Baele G**, **Suchard MA. 2018.** Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* **67:** 901–904.

Rawlence NJ, **Metcalf JL**, **Wood JR**, **Worthy TH**, **Austin JJ**, **Cooper A. 2012.** The effect of climate and environmental change on the megafaunal moa of New Zealand in the absence of humans. *Quaternary Science Reviews* **50:** 141–153.

Rawlence NJ, **Potter BCM**, **Dussex N**, **Scarsbrook L**, **Orlovich DA**, **Waters JM**, **McGlone M**, **Knapp M. 2021.** Plio-Pleistocene environmental changes shape present day phylogeography of New Zealand's southern beeches (Nothofagaceae). *New Zealand Journal of Botany* **59:** 55–71.

Rawlence NJ, **Scofield RP**, **McGlone MS**, **Knapp M. 2019.** History repeats: large scale synchronous biological turnover in avifauna from the Plio-Pleistocene and Late Holocene of New Zealand. *Frontiers in Ecology and Evolution* **7:** 158.

Rawlence NJ, **Scofield RP**, **Spencer HG**, **Lalas C**, **Easton LJ**, **Tennyson AJD**, **Adams M**, **Pasquet E**, **Fraser C**, **Waters JM**, **Kennedy M. 2016.** Genetic and morphological evidence for two species of *Leucocarbo* shag (Aves, Pelecaniformes, Phalacrocoracidae) from southern South Island of New Zealand. *Zoological Journal of the Linnean Society* **177:** 676–694.

Robertson BC, **Goldstien SJ. 2012.** Phylogenetic affinities of the New Zealand blue duck (*Hymenolaimus malacorhynchos*). *Notornis* **59:** 49–59.

Sangster G, **Luksenburg JA. 2021.** Sharp increase of problematic mitogenomes of birds: causes, effects and remedies. *Genome Biology and Evolution* **13:** evab210.

Scofield RP, **Mitchell KJ**, **Wood JR**, **De Pietri VL**, **Jarvie S**, **Llamas B**, **Cooper A. 2017.** The origin and phylogenetic relationships of the New Zealand ravens. *Molecular Phylogenetics and Evolution* **106:** 136–143.

Selvatti AP, **Gonzaga LP**, **de Moraes Russo CA**. **2015.** A Paleogene origin for crown passerines and the diversification

of the Oscines in the New World. *Molecular Phylogenetics and Evolution* **88:** 1–15.

Shepherd LD, **Lambert DM. 2007.** The relationships and origins of the New Zealand wattlebirds (Passeriformes, Callaeatidae) from DNA sequence analyses. *Molecular Phylogenetics and Evolution* **43:** 480–492.

Sievers F, **Wilm A**, **Dineen D**, **Gibson TJ**, **Karplus K**, **Li W**, **Lopez R**, **McWilliam H**, **Remmert M**, **Söding J**, **Thompson JD**, **Higgins DG. 2011.** Fast, scalable generation of high-quality protein multiple sequence alignments using Clustal Omega. *Molecular Systems Biology* **7:** 539.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22:** 2688–2690.

Steinthorsdottir M, **Vajda V**, **Pole M. 2019.** Significant transient pCO$_2$ perturbation at the New Zealand Oligocene-Miocene transition recorded by fossil plant stomata. *Palaeogeography, Palaeoclimatology, Palaeoecology* **515:** 152–161.

Stonor CR. 1942. Anatomical notes on the New Zealand wattled crow (*Callæas*), with especial reference to its powers of flight. *Ibis* **84:** 1–18.

Suggate RP, **Stevens GR**, **Te Punga MT**. **1978.** *The Geology of New Zealand*. Wellington: E.C. Keating, Government Printer.

Tomotani BM, **Salvador RB**, **Sabadel AJM**, **Miskelly CM**, **Brown JCS**, **Delgado J**, **Boussès P**, **Cherel Y**, **Waugh SM**, **Bury SJ. 2021.** Extreme bill dimorphism leads to different but overlapping isotopic niches and similar trophic positions in sexes of the charismatic extinct huia. *Oecologia* **198:** 67–77.

Trewick S, **Bland K. 2012.** Fire and slice: palaeogeography for biogeography at New Zealand's North Island/South Island juncture. *Journal of the Royal Society of New Zealand* **42:** 153–183.

Trewick SA, **Wallis GP**, **Morgan-Richards M. 2011.** The invertebrate life of New Zealand: a phylogeographic approach. *Insects* **2:** 297–325.

Verry AJF, **Schmidt M**, **Rawlence NJ. 2022.** A partial skeleton provides evidence for the former occurrence of moa populations on Rakiura Stewart Island. *New Zealand Journal of Ecology* **46:** 3458.

Wallis GP, **Jorge F. 2018.** Going under down under? Lineage ages argue for extensive survival of the Oligocene marine transgression on Zealandia. *Molecular Ecology* **27:** 4368–4396.

Wallis GP, **Trewick SA. 2009.** New Zealand phylogeography: evolution on a small continent. *Molecular Ecology* **18:** 3548–3580.

Wallis GP, **Waters JM**, **Upton P**, **Craw D. 2016.** Transverse alpine speciation driven by glaciation. *Trends in Ecology & Evolution* **31:** 916–926.

Waters JM, **Craw D. 2006.** Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Systematic Biology* **55:** 351–356.

Weir JT, **Haddrath O**, **Robertson HA**, **Colbourne RM**, **Baker AJ. 2016.** Explosive ice age diversification of kiwi. *Proceedings of the National Academy of Sciences of the United States of America* **113:** E5580–E5587.

Weston KA, **Robertson BC. 2015.** Population structure within an alpine archipelago: strong signature of past climate change in the New Zealand rock wren (*Xenicus gilviventris*). *Molecular Ecology* **24:** 4778–4794.

Worthy TH, **Holdaway RN. 2002.** *The lost world of the moa: prehistoric life of New Zealand*. Bloomington: Indiana University Press.

SUPPORTING INFORMATION

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

Figure S1. RAxML tree of Callaeidae mitogenomes, including the control region, showing different relationships between Callaeidae, *Notiomystis cincta*, *Petroica* spp. and *Poodytes punctatus*. Bootstrap support is shown at nodes.