



Review article

Vicars, tramps and assembly of the New Zealand avifauna: a review of molecular phylogenetic evidence

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The avifauna of New Zealand is taxonomically and ecologically distinctive, as is typical of island biotas. However, the potential for an old geological age of New Zealand has encouraged a popular notion of a 'Moa's ark' based on the idea that much of the fauna was isolated when Zealandia broke from Gondwana *c.* 83 million years ago. Molecular phylogenetics has proved useful for exploring the relative importance of different biogeographical processes, revealing for example that 'tramp' species (widely dispersing taxa) have arrived in New Zealand even in the last few hundred years, and that some avian taxa have close phylogenetic relatives overseas (predominantly Australian), indicating their recent ancestors were tramps, too. Distinctive taxa with deep phylogenetic ancestry might be 'vicars' that owe their presence to vicariance, but lack of close morphological, taxonomic and phylogenetic affinity provides only tenuous evidence for this. Disproving the alternative possibility that apparent vicars are descended from tramps that dispersed in earlier times remains challenging, but molecular analyses have yielded startling insights. Among New Zealand's iconic taxa, the world's largest eagle shared a Pleistocene ancestor with a small Australian eagle, and giant, flightless moa are phylogenetic sisters of the much smaller, flying tinamous of South America. The New Zealand avifauna is neither isolated nor stable, but demonstrative of prolonged and ongoing colonization, speciation and extinction.

Keywords: colonization, dispersal, migration, molecular clock, Neoaves, vicariance, Zealandia.

The biotas of islands (whether oceanic or other habitat patches) are modelled both as equilibrium communities assembled by migration and balanced by extinction (MacArthur & Wilson 1967) as well as foci of speciation and adaptation (Darwin 1859). Birds have provided exemplars of both paradigms (e.g. Diamond 1974, Fleischer *et al.* 1998), making it clear that assembly of biotas even on strictly oceanic islands is complex. Where the islands concerned are deemed continental (Cowie & Holland 2006) and are seemingly of considerable age, we might expect the processes of assembly to have stabilized and their contributions to be readily inferred.

New Zealand's (NZ) biota has been variously described as ill-balanced, unique, small, Gondwanic

and a hotspot (e.g. Keast 1971, Daugherty *et al.* 1993, Gibbs 2006, McDowall 2008). It is well recognized that although endemism is high, representation among taxonomic groups is highly variable and the overall diversity in many groups is low. This is true for birds, which provide an amenable group for the study of biogeography, as they are taxonomically well resolved in comparison with most other animal groups. Interestingly, although authors in the 1950s and 1960s were pragmatic about the origins of the NZ avifauna and recognized that the assemblage was largely what would be expected on a large oceanic island (e.g. Falla 1953, Fleming 1962, Caughley 1964), by the 1970s and 1980s a shift in biogeographical reasoning had taken place. Acceptance of continental drift, explained by plate tectonics (Tarling &

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Tarling 1971, Sutherland 1999, Graham 2008), stimulated a resurgence of interest in vicariance as an important process in the formation of the NZ biota and placed emphasis on its putatively ancient origins. As continental drift would seem to have limited influence on flying birds, evidence for ancient isolation has generally been drawn from other sections of the biota. However, the distinctiveness of NZ's avifauna is nonetheless routinely attributed to 'its long period of isolation' and linked with the observation of low taxonomic diversity (Baker 1991). In fact there is no readily apparent reason to connect low diversity with protracted isolation, as many other much smaller, more isolated and younger islands have high diversity and endemism in birds and other taxa (Goldberg *et al.* 2008).

Caughley (1964) attempted to predict retrospectively the vertebrate composition of the NZ biota given its size, position relative to Australia and inferences about dispersal ability. Caughley (1964) and Falla (1953) made inferences that did not require continental drift to explain distribution patterns, except perhaps for the existence of ratites (Kiwī and Mōa) in NZ: 'It must be admitted that the fauna of the NZ archipelago conforms, in the main, to what should be expected on large oceanic islands' (Falla 1953). Even the presence of the iconic kiwis (Apterygidae) and moas (Dinornithidae) has been ascribed to overland invasions (Fleming 1962) or from flying ancestors (De Beer 1956, Mayr 1963). Each of the endemic passerine families might also represent separate colonizations (McDowall 1968). These authors were interested in the possibility, and perhaps presumed, that dispersal was the primary or only method by which taxa could reach NZ. The necessity for this explanation diminished with acceptance of continental drift (Skipworth 1974), which provided a simple mechanism to explain the distribution of lineages that appear to be poor dispersers. However, recent molecular studies cast doubt on assumptions of limited dispersal ability and hence colonization opportunity of several different taxa; for example, the Gondwanan vicariance icon *Nothofagus* beech arrived after NZ formed (Cook & Crisp 2005b, Knapp *et al.* 2005).

Three classes of information can illuminate our understanding of the way that biotas develop: (1) observation of the local and neighbouring modern faunas and floras, (2) the fossil record and (3) phylogenetic inference from DNA sequence data.

The extant biota is our primary point of reference, but it represents a single time-slice through evolution, whereas fossils provide the only means of observing, albeit partial, biotas from other times. Since the 1980s, molecular phylogenetics has rapidly transformed our perceptions of the rates and modes of speciation, and allowed the effective inclusion of time in biogeographic and systematic inference. Although molecular phylogenetic and genomic approaches can only inform directly on living and recently extinct organisms, the resulting evolutionary lessons can be applied to interpretation of fossil evidence. Here we review the contributions of molecular phylogenetics to our understanding of the assembly of the NZ avifauna.

A BRIEF HISTORY OF NEW ZEALAND

NZ is an archipelago in the southwest Pacific Ocean consisting of two major islands and numerous smaller ones with a total area a little less than 270 000 km² (Fig. 1). In the Pacific, only the Japanese archipelago has a greater land area. The nearest substantial land area to NZ is the continent of Australia; at least 1520 km to the west across the Tasman Sea (Neall & Trewick 2008). Unlike most islands in the Pacific and elsewhere, which are



Figure 1. New Zealand and neighbouring islands (modified from Wallis & Trewick 2009). The approximate extent of the submerged continent of Zealandia is indicated with grey fill and dashed line. The approximate position of the Alpine Fault in the South Island is indicated with a white line.

predominantly of volcanic origin, NZ is formed primarily of continental crust (Trewick *et al.* 2007) and is described as a continental island (Cowie & Holland 2006). The formation of modern NZ began in the early Miocene when activity on the boundary between the Australian and Pacific continental plates became vigorous (26–22 Ma, Campbell & Hutchings 2007). This plate boundary developed through the largely submerged continent of Zealandia, such that NZ sits astride a major fault zone referred to as the Alpine Fault (Fig. 1). At that stage, most and perhaps all of Zealandia (Landis *et al.* 2008) was submerged beneath the sea, and even today some 90% is under water (Mortimer 2004).

A spreading ridge producing new oceanic crust had developed by 83 Ma between Zealandia and the Australian/Antarctic part of Gondwana, thereby forming the Tasman Sea. This sea-floor spreading continued until about 53 Ma, but by 75 Ma Zealandia was already isolated from Australia and Antarctica, and by the start of the Tertiary (65 Ma) Zealandia was low-lying and surrounded by deep seas (Graham 2008, Fig. 2). A process of crustal spreading and thinning may explain the gradual submergence of Zealandia in the late Oligocene (Campbell & Hutchings 2007). Australia and South America finally separated from Antarctica in the late Eocene (*c.* 35 Ma), initiating the circumpolar current (Sanmartin & Ronquist 2004). Although biologists frequently refer to NZ separating from Australia, NZ has never had any direct physical contact with other parts of Gondwana. The question of whether there was any continually habitable land in the Zealandia region throughout the period of maximum inundation in the Oligocene is unresolved (Campbell & Hutchings 2007, Landis *et al.* 2008). Importantly, at about the size of India, Zealandia was large and there can be little doubt that it began with a substantial terrestrial biota. This Zealandian biota is one possible source of modern lineages.

However, almost nothing is known about the Zealandian biota beyond that inferred from the extant faunas of NZ and neighbouring islands. Fossils provide some insights into the terrestrial fauna, with evidence of Cretaceous dinosaurs (Long 1998), Miocene mammals, crocodiles and birds (Molnar & Pole 1997, Worthy *et al.* 2006, 2007, 2009), and Plio-Pleistocene vertebrates (Worthy & Holdaway 2002). NZ fossils of terrestrial animals are relatively few and give only glimpses of the

past, although they confirm that assemblages changed through time, and are useful for dating phylogenies if appropriate methods are used (see Discussion). However, spatially and temporally isolated fossils fail to demonstrate continuity of occupation by particular bird lineages through time and provide little information on biogeographical processes given the absence of comparable, well-sampled fossil biotas elsewhere.

OVERVIEW OF THE NEW ZEALAND AVIFAUNA

Approximately 245 birds were breeding in NZ on human contact with the islands (estimated from late Holocene fossils and the extant fauna; Holdaway *et al.* 2001, Worthy & Holdaway 2002). This number is dependent to some degree on opinion about subspecies/species status and on the inclusion/exclusion of recent colonists and vagrants. For instance, Worthy and Holdaway (2002) exclude the self-introduced and highly successful Silvereye *Zosterops lateralis* (Robertson *et al.* 2007b), but include as species many populations that are elsewhere treated as subspecies. Perceptions about composition are also influenced by the inclusion/exclusion of species found in the wider NZ archipelago (from subantarctic islands in the south to Norfolk Island in the north). Offshore islands tend to have their own representatives of many taxa due to allopatric divergence (Fleming 1976); the Chatham Islands, for example, have in some taxonomic treatments more than 10 endemic land birds, each of which is almost certainly sister to a species on mainland NZ (Worthy & Holdaway 2002). The avifaunas of offshore islands are, therefore, perhaps better treated as independent units for the purposes of inventory. A large proportion of NZ birds occupy freshwater, marine and coastal habitats, including seabirds (57 Procellariiformes, 14 Pelecaniformes and 10 Sphenisciformes), shorebirds (32 Charadriiformes) and ducks (18 Anseriformes). If we exclude offshore island endemics and seabirds, but include North Island and South Island forms of many taxa as distinct species (following Worthy & Holdaway 2002) there were 95 mainland breeding bird species in NZ at human contact, including 29 passerines, 14 shorebirds, 13 ducks and nine rails (Rallidae).

Analysis of NZ's pre-human (Holocene fossil bones in caves and swamps) and modern avifauna indicates two phases of extinction associated with

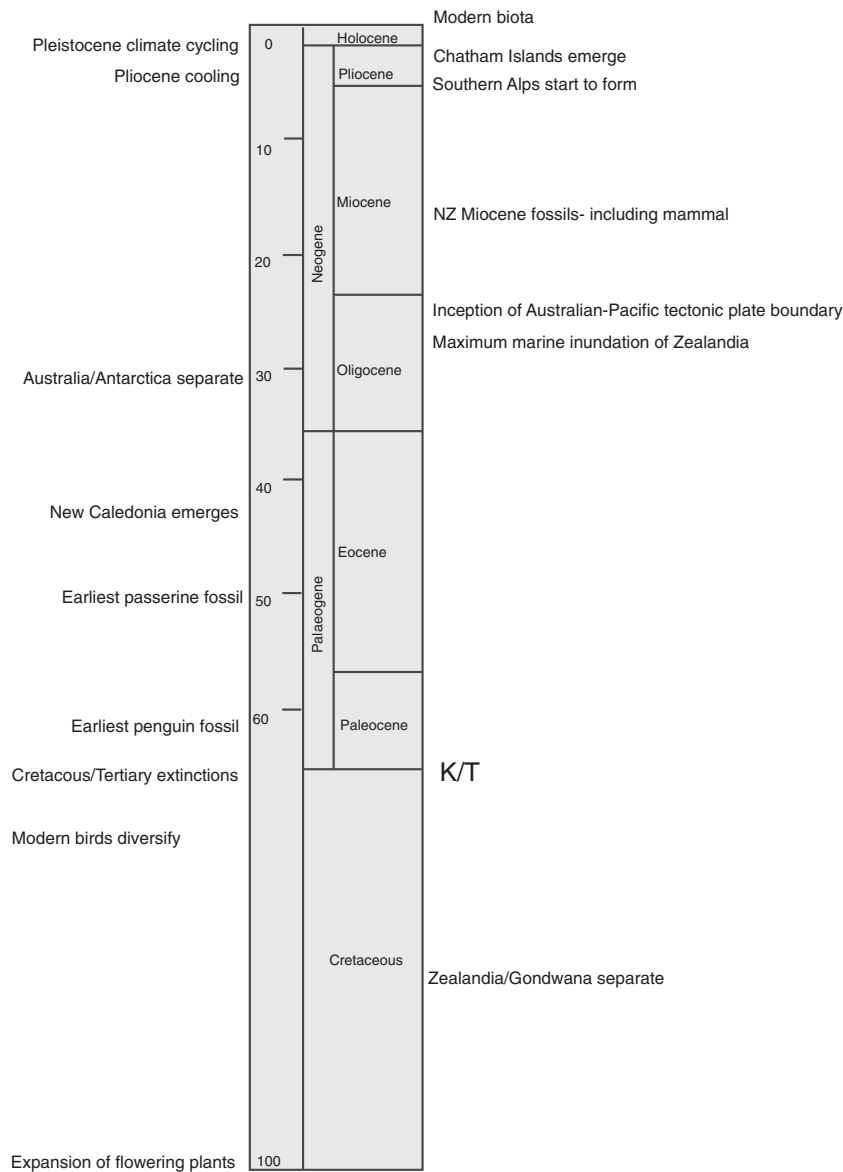


Figure 2. Geological timescale with some relevant ecological, evolutionary and geophysical events indicated. Values indicate millions of years before present (Ma).

human colonization. The first, or Polynesian, phase started around 1280 AD (Wilmshurst *et al.* 2008) and resulted in the extinction of the larger and possibly least fecund taxa, including 11 species of moa, a swan, two geese, two giant coots and a giant eagle. Habitat modification, and introduced predators such as dogs (kuri) and Pacific Rats (kiore) *Rattus exulans* must have had some impact, but direct hunting may have been sufficient to reduce populations below sustainable levels (Turvey & Holdaway 2005). The contents of mid-dens indicate that hunting of large birds was an

important component of Maori (or pre-Maori) culture at that time (Anderson 2003, King 2003). Settlement by Europeans in the 19th century corresponds with extinction of additional endemic birds, including the Huia *Heteralocha acutirostris*, New Zealand Quail *Coturnix novaezelandiae*, Laughing Owl *Sceloglaux albifacies*, New Zealand Little Bittern *Ixobrychus novaezelandiae* and Bush Wren *Xenicus longipes*. Most of these were forest inhabitants whose populations were depleted by large-scale habitat modification (e.g. pastoralization), a plethora of mammalian predators (rats,

mice, mustelids, cats, pigs, possums) and hunting with guns (see Worthy & Holdaway 2002, Tennyson & Martinson 2006). In total, about 31% of the estimated 245 species of birds breeding in the wider NZ region have become extinct since human contact. Of the non-marine taxa, the largest losses were among ducks, ratites, rails and passerines.

The modern element in the NZ avifauna arrived in two ways: intentional introductions mostly mediated by various Acclimatization Societies (Thomson 1922, McDowall 1994) and self-colonization. Intentional introductions were primarily of northern European species brought to NZ as part of a colonization ethic that prevailed in the 1860s, or in early attempts at biological control (McDowall 1994, Walrond 2008). For birds, these include some 137 species of which about 20% are recorded as successfully 'acclimatizing', including: Blackbird *Turdus merula*, Song Thrush *Turdus philomelos*, Rock Dove *Columba livia*, Skylark *Alauda arvensis*, House Sparrow *Passer domesticus*, a number of finches and allies, Little Owl *Athene noctua*, Rook *Corvus frugilegus*, Starling *Sturnus vulgaris* and Common Mynah *Acridotheres tristis* (Veltman *et al.* 1996). The success of introduced birds was primarily dependent on the number of individuals introduced and their migratory behaviour (Veltman *et al.* 1996). Introduction of species that were migratory in their natural range tended to be less successful, although many species introduced to mainland NZ quickly reached and colonized other parts of the archipelago over distances of up to 900 km (Williams 1953).

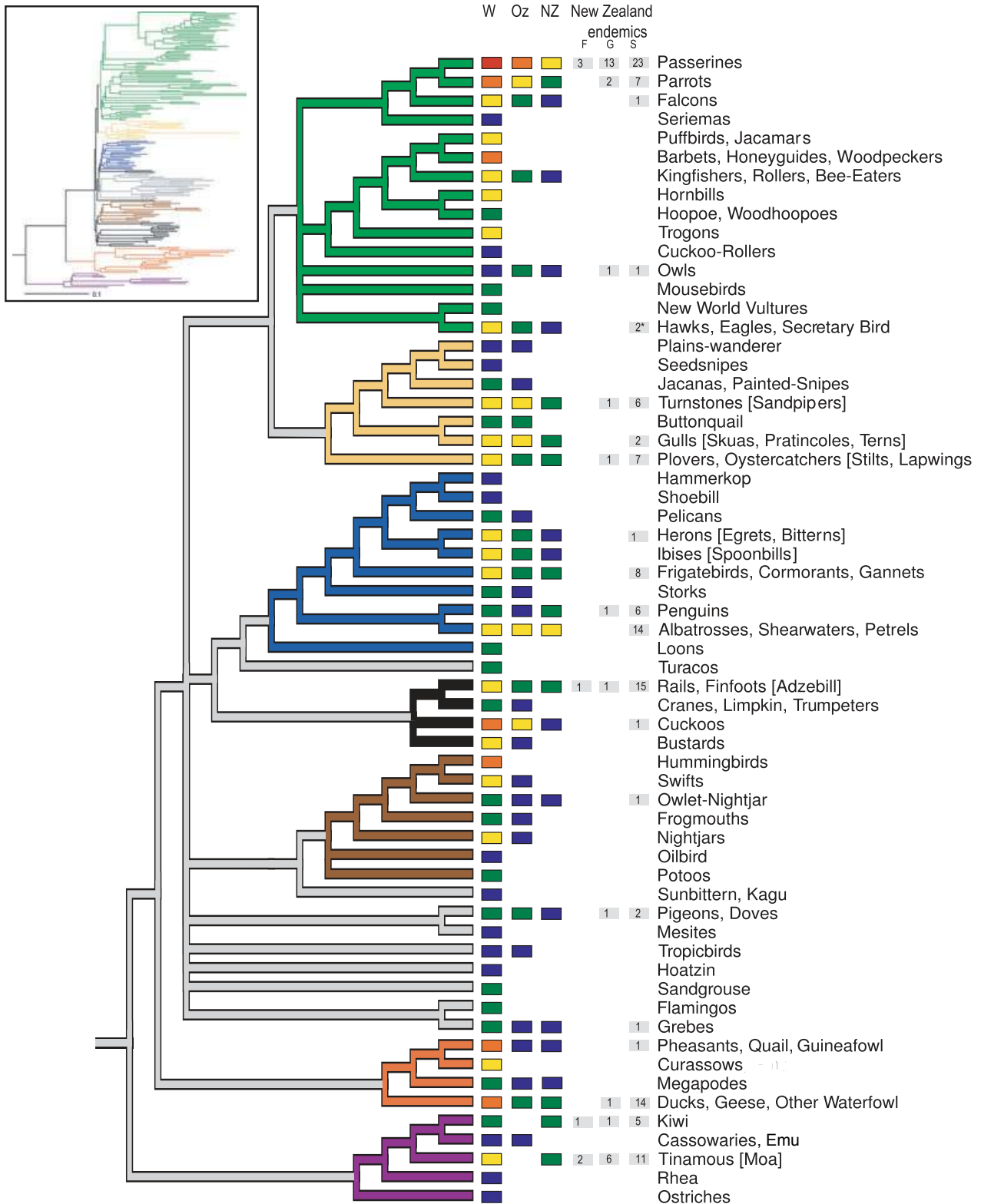
A separate group of species have arrived entirely by their own efforts, traversing at least 1500 km of ocean and founding viable NZ populations. These provide valuable insight into dispersal and colonization. The first arrival times of several species are known, including: Silveryeye 1856, Pacific Swallow

Hirundo tahitica 1958, Cattle Egret *Bubulcus ibis* 1963, Masked Plover *Vanellus miles* 1932, Coot *Fulica atra australis* 1954, White-faced Heron *Ardea novaehollandiae* 1940 and Black-fronted Dotterel *Charadrius melanops* 1954 (Falla 1953, Baker 1991, see also Robertson *et al.* 2007b). Additional species appear to be aviary escapees, including parrots, doves and a kingfisher.

Among the most mobile species visiting NZ are seabirds, including terns, gannets, petrels, penguins and albatrosses, which nest mostly on offshore islands. Some nested on mainland NZ prior to human contact (Worthy & Holdaway 2002) and a few continue to do so today (e.g. Southern Royal Albatross *Diomedea epomophora*, Yellow-eyed Penguin *Megadyptes antipodes*, Hutton's Shearwater *Puffinus huttoni*, Australasian Gannet *Morus serrator*). Migratory shorebirds include the Bar-tailed Godwit *Limosa lapponica*, Knot *Calidris canutus* and Ruddy Turnstone *Arenaria interpres*. Two species of cuckoo, Shining Bronze-cuckoo *Chrysococcyx lucidus* and Long-tailed Cuckoo *Eudynamis taitensis*, migrate to NZ to breed. The Great White Egret *Egretta alba* currently breeds locally in NZ, but has sometimes reached as far afield as the Auckland, Campbell, Chatham and Maquarie islands (Falla 1953).

Inferring the timing and process of assembly prior to human contact is much more difficult, but given observation of the modern element it is clear that something can be gleaned from taxonomic distinctiveness. Indeed, evidence of hierarchical variation in taxonomic distinctiveness led Falla (1953) and others (e.g. Fleming 1962, Caughley 1964) to propose that colonization of NZ occurred several times. Thus, species with recognizable NZ subspecies, such as Grey Fantail *Rhipidura fuliginosa*, Banded Rail *Gallirallus philippensis*, Pacific Black (Grey) Duck *Anas superciliosa*, Spotless Crake

Figure 3. Phylogeny of birds based on multiple genes (redrawn from Hackett *et al.* 2008, fig. 4). Branch colours are those given by Hackett *et al.* (2008) and indicate major clades supported: land birds (green), Charadriiforms (yellow), water birds (blue), core Gruiforms and cuckoos (black), Apodiforms and Caprimulgiforms (brown), Galloanserae (orange), and Paleognaths (purple). Bird groups not cited by Hackett *et al.* (2008) are placed on the tree [in square brackets], sometimes tentatively, according to other phylogenetic or taxonomic evidence (e.g. the New Zealand endemic Adzebills (*Aptornis*) are currently assigned to their own family, which is usually placed tentatively within Rallidae). Coloured boxes indicate species diversity on a base 5 log-scale (1–4 blue, 5–24 green, 25–124 yellow, 125–624 orange, > 3125 red), worldwide (W), in Australia (Oz) and in New Zealand (NZ), respectively. Statistics for species numbers came from Clements (2007) (World), Walter Boles (pers. comm.) (Australia), NZRBN (Robertson & Medway 2003) and Holdaway *et al.* (2001) (New Zealand). New Zealand taxa do not include Norfolk Island. Also indicated are estimates from current taxonomy of New Zealand endemics per bird group, at Family, Genus and Species level (note endemic species and genera are not always nested within endemics of higher taxonomic levels). New Zealand passerine data are as in Table 1. The inset tree provides an indication of molecular rate variation among lineages and short internodes at the base of the Neoaves and is derived from Hackett *et al.* (2008, fig. 3).



Porzana tabuensis, Little Black Shag *Phalacrocorax sulcirostris*, Purple Swamphen (Pukeko) *Porphyrio porphyrio*, White Egret and Southern Boobook (Morepork) *Ninox novaeseelandiae*, are likely to be derived from relatively recent colonists. Endemic species such as the New Zealand Robin *Petroica australis* and Tomtit *Petroica macrocephala* are likely to be the products of earlier arrivals. In some cases it appears that particular lineages have reached NZ on more than one occasion and thus contributed multiple times to bird diversity. Many of the examples cited by Fleming (1974) have been confirmed by molecular and traditional taxonomy (see order-specific sections below, and supplementary Table S1).

MOLECULAR PHYLOGENY AND THE NEW ZEALAND AVIFAUNA

We review the available molecular phylogenetic analyses of bird groups that include data from NZ taxa. In the following section and in Table S1, the sequence of orders follows Christidis and Boles (2008). Direct searches of the NCBI GenBank database (<http://www.ncbi.nlm.nih.gov/>) were designed to identify all published DNA sequence data for NZ birds and their associated publications (Table S1). We also used web searches and citation searches to track information on particular taxa. Important background to understanding the assembly of the NZ avifauna comes from deep phylogenetic analyses of bird orders and families undertaken with large datasets of mitochondrial and nuclear DNA sequences (see 'multiple orders' in Table S1). Some of these do not include representatives of NZ species, whereas others do (Slack *et al.* 2006, Gibb *et al.* 2007, Morgan-Richards *et al.* 2008, Pratt *et al.* 2009), but all contribute to a framework for interpreting evolutionary history of local lineages (Fig. 3). Many studies consist of local sampling of NZ taxa with overseas relatives as outgroups or include NZ species such as Rifleman *Acanthisitta chloris* as the outgroup for other taxa (e.g. Barker *et al.* 2004). All levels provide important insights into the timing and mode of assembly of the modern NZ avifauna.

There are many gaps in available phylogenetic and taxonomic information even among the extant avifauna. Many extant NZ taxa are so similar to overseas species that their phylogenetic placement with molecular data would probably yield few surprises. Nonetheless, additional phylogeographical

analyses, especially in the wider geographical context of the Oceania region, would be of interest for many taxa (e.g. warblers, robins, owls and kingfishers). The situation is less clear for the recently extinct species with the notable exception of the moa, which have been intensively studied (Table S1). Some extinct lineages have received little or no attention as yet, but would doubtless yield useful insights into the manner in which the fauna has assembled. Among these are *Aptornis*, a distinctive flightless gruiform currently placed in a monotypic family, and several less enigmatic taxa including a goose, crow or raven, swan, Laughing Owl and Piopio *Turnagra capensis*.

Struthioniformes (ratites & tinamous)

The ratites and tinamous are sometimes placed in separate orders, partly on the basis of morphology associated with flight in the tinamous, but there has long been debate about this (e.g. Cracraft 1974, Parkes & Clark 1996). Several molecular studies have constrained ratite monophyly by treating tinamous as an outgroup (Cooper *et al.* 2001, Paton *et al.* 2002, Pereira & Baker 2006). Living tinamous are restricted to Central and South America, whereas ratites live on all southern hemisphere continents except Antarctica. Ratites have usually been inferred to be a monophyletic group derived from a single flightless ancestor (Cracraft 1974). In NZ, ratites are represented by two families: moa and kiwi. Despite their extinction, a large body of molecular data has been gathered on moa from late Pleistocene and Holocene fossil bones (Table S1). This has contributed to revision of their taxonomic diversity and identified sexual dimorphism, which had previously been a cause of taxonomic oversplitting (Bunce *et al.* 2003, Huynen *et al.* 2003).

Early molecular phylogenetics revealed that the two NZ ratite families do not form a monophyletic group (Cooper *et al.* 1992, 2001), implying either that the moa, kiwi and other ratite lineages coexisted prior to separation of Zealandia, which would suggest that living bird groups evolved much earlier than is supported by other evidence, or that the kiwis' ancestor dispersed to Zealandia/NZ over water (Cooper *et al.* 2001). Haddrath and Baker (2001) used whole mitochondrial DNA sequences to date ratite divergence times with an Australian fossil representing the ancestor of Emu *Dromaius novaehollandiae* and cassowaries *Casuarius* spp. Their estimates of 62 Ma and 79 Ma, respectively,

for the origin of kiwi and moa supported the notion that kiwi arrived after separation of Zealandia, but moa ancestors might have been present on Zealandia.

However, recent analyses using larger, multigene datasets and more thorough phylogenetic analyses have revealed that tinamous and ratites are probably not monophyletic sister groups, but rather that the clade of (flying) tinamous is nested within the ratites (Hackett *et al.* 2008, Harshman *et al.* 2008, Phillips *et al.* 2010). Furthermore, moa and tinamous appear to be sister lineages within ratites (Phillips *et al.* 2010). This has important evolutionary and biogeographical implications because it indicates that flight has been lost several times in the group rather than being the ancestral and defining condition for ratites (Harshman *et al.* 2008), and it weakens the arguments favouring a vicariant explanation for their presence in NZ. Dispersal of ratite lineages thus becomes more plausible and analogous to the numerous independent instances of loss of flight in groups such as Rallidae (see Gruiformes below). Molecular dating based on complete mitochondrial DNA sequences and a suite of calibration points indicates that both the kiwi and moa lineages post-date separation of Zealandia and the K/T boundary (Phillips *et al.* 2010).

Moa represent the most extensive and best-documented avian radiation in NZ. At one time some 27 species were recognized (Archey 1941, Oliver 1949), but this has recently been reduced to 11 taxa associated with a range of lowland and alpine environments (Worthy & Holdaway 2002). This radiation has been dated to the late Miocene and Pliocene (10–4 Ma) using an 82 Ma date for the split between moa and an outgroup comprising other ratites and tinamous (Baker *et al.* 2005). However, the justification for this molecular clock calibration is questionable, so the moa radiation is likely to be younger and primarily associated with habitat heterogeneity that developed with the formation of the Southern Alps starting in the Pliocene (Bunce *et al.* 2009).

Analyses of mtDNA sequence data that included extinct populations revealed that kiwi comprise five largely allopatric lineages (Shepherd & Lambert 2006). Burbidge *et al.* (2003) estimated that Brown and Spotted Kiwi (*Apteryx* spp.) species group diversity might date to the Miocene and splitting in the Brown Kiwi group to the Pliocene, based on the calibration of ratite phylogeny by Haddrath and Baker (2001).

Anseriformes (ducks & geese)

Diversity among ducks and their allies in NZ is almost entirely a product of numerous independent colonizations (Worthy & Olson 2002). These have resulted in species-level endemism, and it is evident that at least some apparently endemic genera are more likely to be island forms of widespread genera; for example the extinct duck *Euryanas finschi* is, on the basis of morphology, better placed in *Chenonetta* with the Australian Wood Duck *Chenonetta jubata* (Worthy & Olson 2002). However, molecular data testing this and other hypotheses do not yet exist. The New Zealand Brown Teal *Anas aucklandica* includes closely related taxa on several offshore islands in a shallow, allopatric radiation (Kennedy & Spencer 2000). The molecular phylogeny of *Anas*, although incompletely resolved, indicates substantial dispersal of different dabbling duck lineages around the globe (Johnson & Sorenson 1999). The Pacific Black Duck appears to have colonized NZ twice in recent geological time and support for the subspecific status of the NZ 'Grey Duck' is weak (Rhymer *et al.* 2004). The shallow phylogenetic history of *Anas* (Johnson & Sorenson 1998, 1999) is evident in their capacity to hybridize successfully, as documented in NZ between *Anas superciliosa* and introduced Mallard *Anas platyrhynchos* (Gillespie 1985, Rhymer *et al.* 1994, 2004). The endemic Blue Duck *Hymenolaimus malacorhynchos* shows strong phylogeographical structure between North Island and South Island (Robertson *et al.* 2007a), but its phylogenetic placement is unresolved. The two extinct large geese *Cnemiornis* are thought to be closely allied to the Australian Cape Barren Goose *Cereopsis novaehollandiae*, an inference from morphology supported by a small amount of DNA data (Worthy *et al.* 1997). The Merganser *Mergus australis* is known from Holocene fossils in mainland NZ but the last population to go extinct was that on the sub-Antarctic Auckland Islands. Other mergansers occur in Europe, Asia, North America and Brazil but are not otherwise known in Australasia.

Galliformes (game birds)

Morphology indicates that the single extinct native galliform, the New Zealand Quail, was closely related to the Australian Stubble Quail *Coturnix pectoralis*, a relationship confirmed by molecular

analysis (Seabrook-Davison *et al.* 2009). There is a closer relationship between *Coturnix novaeseelandiae* and *Coturnix pectoralis*, which are estimated to have diverged in the Pliocene, than there is between the two Australian quails *Coturnix pectoralis* and *Coturnix ypsilophora* (Seabrook-Davison *et al.* 2009). The latter species has since been introduced to NZ (Thomson 1922, Robertson *et al.* 2007b).

Podicipediformes (grebes)

NZ has one endemic grebe, the New Zealand Dabchick *Poliiocephalus rufopectus*. The genus includes the Hoary-headed Grebe *Poliiocephalus poliocephalus*, which is a vagrant from Australia, but there has been no molecular analysis of these taxa. Two other widespread grebes, Great Crested *Podiceps cristatus* and Australasian *Tachybaptus novaehollandiae*, are also recorded in NZ. Analysis of complete mitochondrial DNA sequences of these species has confirmed the sister relationship of grebes and flamingos (Morgan-Richards *et al.* 2008), as has nuclear DNA sequence data (Hackett *et al.* 2008), a relationship originally proposed by van Tuinen *et al.* (2001).

Columbiformes (pigeons)

The endemic New Zealand Pigeon (Kereru) *Hemiphaga novaeseelandiae* forms a clade with the monotypic Australian Topknot Pigeon *Lophalaimus antarcticus* and the small genus *Gymnophaps* of Indonesia, New Guinea and the Solomon Islands (Pereira *et al.* 2007). A molecular analysis with multiple fossil calibrations estimated that these lineages diverged in the early- to mid-Miocene (Pereira *et al.* 2007). If correct, this provides a maximum age for the arrival of the *Hemiphaga* lineage in NZ. There is little taxonomic diversity in *Hemiphaga* with an extinct subspecies *Hemiphaga novaeseelandiae spadicaea* known from Norfolk Island and a sister species *Hemiphaga chathamensis* from the Chatham Islands. These islands are no older than 4 Ma, but the distribution appears to be of even more recent origin. Control region sequences reveal low genetic distances and a sister relationship between *H. chathamensis* and the two *H. novaeseelandiae* subspecies consistent with structuring during the Pleistocene (J. Goldberg & S. Trewick unpubl. data).

Apodiformes (Owlet Nightjar)

The New Zealand Owlet Nightjar *Aegotheles novaeseelandiae* is extinct, but is considered to have been most similar to the New Caledonia species *Aegotheles savesi* (Tennyson & Martinson 2006). A molecular analysis of this small genus, which has its centre of diversity in Papua New Guinea, indicates that the NZ and New Caledonian species are sister to species in New Guinea/Australia (Dumbacher *et al.* 2003). The comparatively large size, long legs and short wings of *A. novaeseelandiae* and *A. savesi* imply a more terrestrial rather than arboreal habit (Dumbacher *et al.* 2003), which could have been derived independently in each lineage after island colonization.

Procellariiformes (tubenosed birds)

Tubenoses are among the most mobile birds in the world, although they are also frequently philopatric (Shaffer *et al.* 2006). Many of the world's Procellariiformes (~45%) take advantage of coastal and island nesting sites in the NZ region where they account for a high proportion of all avian species (~22%). It is not surprising that most molecular analyses of NZ seabirds concern population structuring across the oceans (Abbott & Double 2003b) and in many cases focus on identifying the provenance of birds killed as fisheries by-catch (Abbott *et al.* 2006). Species that breed in NZ waters tend to have genetically close sister taxa on nearby islands outside the region. For example, White-capped Albatross *Diomedea steadi* that nest on the sub-Antarctic Auckland islands are closely related to Shy Albatross *Diomedea cauda* on small islands near Tasmania, Australia (Abbott & Double 2003a). Shallow divergences exist between South Georgia Diving Petrel *Pelecanoides georgicus* populations in southern NZ and the Indian Ocean (Paterson *et al.* 2000), and among Black-browed *Diomedea melanophrys* and Wandering *Diomedea exulans* Albatrosses from southern NZ, South America and the Kerguelen Islands (Alderman *et al.* 2005). The Chatham Island endemic Magenta Petrel (Taiko) *Pterodroma magentae* forages as far as Chile, and is closely related to other Southern Ocean petrels including *Pterodroma macroptera* and *Pterodroma lessonii* (Lawrence *et al.* 2008). Shearwaters in the NZ region are members of an Australasian clade (Austin 1996, Austin *et al.* 2004).

Sphenisciformes (penguins)

Penguins have a long history in the region, and early penguin fossils are recorded from South Island (Jadwiszczak 2009). Fossils demonstrate that the penguin lineage extends at least to the early Tertiary and this has provided a valuable molecular clock calibration (Slack *et al.* 2006, Ho & Phillips 2009). The group may have originated in the Australasian/Antarctic region, and its current distribution continues to be the southern hemisphere. However, extant diversity is much younger (Baker *et al.* 2006, Ksepka *et al.* 2006). Penguins are highly mobile, seeking land only when breeding. Speciation appears to have resulted from numerous dispersal events presumably enhanced by subsequent philopatric behaviour, and the modern NZ assemblage reflects this.

The lineage leading to Yellow-eyed Penguin may have evolved in the Miocene (Baker *et al.* 2006) but has arrived on the NZ mainland, from sub-Antarctic islands, since the arrival of humans. This appears to have happened after the extinction of a previously undescribed and closely related species, *Megadyptes waitaha* (Boessenkool *et al.* 2009). The implication of repeated waves of colonization, is a pattern also evident in Little Blue Penguin *Eudyptula minor*. The diversity of *E. minor* indicates more than one exchange between NZ and Australia since the start of the Pleistocene (Banks *et al.* 2002, Overeem *et al.* 2008, Peucker *et al.* 2009) and lineage sharing with Australia might also be explained by extinction and recolonization. Sister to *Megadyptes* is the *Eudyptes* group, which diversified in the Pliocene (Baker *et al.* 2006) and is distributed around the Southern Ocean (Bertelli & Giannini 2005).

Pelecaniformes (gannets & cormorants)

Around 25% of the world's pelecaniforms breed in and around NZ; most are cormorants (shags). Cormorants have colonized NZ several times, in some cases resulting in the evolution of island endemics (Kennedy *et al.* 2000). For example, a group including the Stewart, Chatham and Campbell Island Shags (*Leucocarbo* spp.) are closely related to each other, and among their closest relatives are South American cormorants (Kennedy *et al.* 2000). The Australasian Gannet of NZ and Australia is closely related to the South African Cape Gannet *Morus capensis* and diversification of these

gannets is thought to have occurred in the Plio-Pleistocene (Friesen & Anderson 1997).

Ciconiiformes (herons & storks)

The NZ avifauna includes a few widespread Australasian heron and egret species (*Ardea* spp., *Egretta* spp.). The New Zealand Little Bittern became extinct at human contact. However, the Australasian Bittern *Botaurus poiciloptilus* and Little Bittern *Ixobrychus minutus* are now present. No molecular analyses of the NZ taxa exist but *Ixobrychus* is sister to *Botaurus* (Sheldon *et al.* 2000) and both genera have worldwide distributions.

Falconiformes (falcons) and accipitriformes (hawks & eagles)

Molecular phylogenetics has been instrumental in revealing that the falcons, hawks and eagles are not a monophyletic group (Fain & Houde 2004, Ericson *et al.* 2006, Gibb *et al.* 2007, Hackett *et al.* 2008, Morgan-Richards *et al.* 2008, but see Pratt *et al.* 2009). The most common raptor in NZ is the Australasian Marsh Harrier *Circus approximans*, which probably arrived after the first humans (Worthy & Holdaway 2002). A larger and now extinct endemic species *Circus eylesi* is known only from Holocene fossils. Also represented only by Holocene fossils is Haast's Eagle *Harpagornis moorei*, an unusually large species (wingspan up to 3 m) that survived into Polynesian times and whose talon marks have been found in fossil moa hipbones. However, Haast's Eagle has been shown to be closely related to the Australian Little Eagle *Hieraaetus morphnoides* and appears to have evolved after colonization in the Pleistocene (Bunce *et al.* 2005). Haast's Eagle provides an excellent example of rapid and substantial morphological change that can occur following colonization of an island. If, as has been proposed, *Hieraaetus* is reclassified with *Aquila*, then Haast's Eagle should be *Aquila moorei* (Lerner & Mindell 2005). The New Zealand Falcon *Falco novaeseelandiae*, which also reached the Chatham Islands (Worthy & Holdaway 2002), is a member of a genus with worldwide distribution and relatively shallow phylogenetic history (Griffiths 1999). Six species of *Falco* occur in Australia, and the Nankeen Kestrel *Falco cenchroides* has also reached NZ at various times (Falla 1953), although perversely the globally distributed and habitat-tolerant Peregrine

Falcon *Falco peregrinus* has never been recorded (Caughley 1964).

Gruiformes (rails & cranes)

Rails are an important component of the NZ avifauna, as they are on many islands in the Pacific (Steadman 2006). In all cases, close allies of NZ taxa are known in Australia and the western Pacific. Crakes (*Porzana*) are represented on the mainland and offshore islands by two species that are also found in Australia. Coots (*Fulica*), swampheens (*Porphyrio*), brown rails (*Gallirallus*) and moorhens (*Gallinula*) are represented by recently dispersed and vagrant species (e.g. *Fulica atra*, *Porphyrio porphyrio*, *Gallirallus philippensis*) in addition to endemic and often flightless derivatives of earlier but not ancient colonizations (Trewick 1996, 1997a,b). Strikingly, although they are often skulking and secretive ground birds, many volant rails are very effective dispersers, such that most Pacific islands have or had prior to arrival of humans one or more endemic rail species (Steadman 2006). Although these birds are effective at moving between islands (e.g. Kirchman 2009), natural selection and/or isolation has been sufficient to yield morphologically distinct endemics. In rails, flight is primarily a predator escape response, so on many oceanic islands that lack mammalian predators, flight appears to be less beneficial (Livezey 2003). Rails demonstrate an important feature in the assembly of the NZ avifauna, whereby repeated colonization rather than insular radiation is responsible for the accumulation of species diversity. Indeed, flying species of *Fulica*, *Gallirallus* and *Porphyrio* appear to be recent colonists of NZ.

The genus *Gallinula* is represented by two species shared with Australia and also an extinct endemic *Gallinula hodgenorum*. The Coot *Fulica atra australis* arrived in NZ in the 1950s almost certainly from Australia, but at least one earlier colonization yielded large endemic species. The extant population of the flying Purple Swamphean is not separable genetically from populations elsewhere in the region, and judging by fossils and midden remains appears to have arrived after Polynesian colonization (Trewick & Worthy 2001). However, earlier and separate colonizations resulted in the evolution of two large flightless species (*Porphyrio hochstetteri* and *Porphyrio manteli*; Trewick 1996), and morphologically similar species are evident in fossil remains on other islands (Steadman 2006).

An analogous history explains the (extinct) flightless relatives of the cosmopolitan Banded Rail *Gallirallus philippensis*. Although data for the NZ endemic *Capellirallus karamu* (= *Gallirallus karamu*) are not yet available, other species including *Gallirallus australis* (NZ), *Gallirallus dieffenbachii* (Chatham), *Gallirallus modestus* (Chatham) and *Diaphorapteryx hawkinsi* (= *Gallinula hawkinsi*) (Chatham) are evidently products of separate colonizations by flying ancestors most probably similar to *G. philippensis* (Trewick 1997a, S. Trewick unpubl. data). The widespread and flying Banded Rail has low genetic diversity with shallow ancestry consistent with recent range expansion across Oceania including NZ. In contrast, flightless island endemics including the Weka *Gallirallus australis* arise from older nodes in the *Gallirallus* tree (Trewick 1997a, Kirchman 2009).

The extinct, robust and flightless adzebills *Aptornis* are thought to be gruiforms and are sometimes interpreted as relatives of the Rallidae. Adaptations to terrestrial habitats and putatively predatory feeding make placement of *Aptornis* difficult on the basis of morphological evidence. Analysis of a small amount of molecular data (Houde *et al.* 1997) indicates that *Aptornis* is closer to the rails than to a group of taxa including the New Caledonian Kagu *Rhynochetos jubata* with which it has also been allied from bone characters (Livezey 1998).

Charadriiformes (shorebirds)

The second largest order in NZ comprise shorebirds, although a large proportion are non-breeding migrant or vagrant species. The shorebirds may have started diversifying in the Cretaceous, with an estimated 14 modern lineages extending to before the K/T boundary (Baker *et al.* 2007). Nevertheless, genus-level diversification is much more recent, indicating that native shorebirds must have colonized the NZ archipelago in the Tertiary or later. Oystercatchers *Haematopus* and stilts *Himantopus* both have global distributions, although genus-level molecular analyses are not yet available. Banks and Paterson (2007) found low levels of sequence variation among three NZ species of *Haematopus*, including a form on the Chatham Islands. *Himantopus* in NZ appear to have resulted from two separate arrivals but the taxa are so closely related that they hybridize (Wallis 1999). Speciation of both these genera in the Australia–NZ

region might be, at most, Miocene in age (Thomas *et al.* 2004). The genus *Charadrius*, which may have originated in South America (Joseph *et al.* 1999) and diversified in the early Miocene (Thomas *et al.* 2004), has a global distribution and includes a number of Australasian species. However, the Australasian taxa do not appear to be monophyletic, indicating more than one colonization. In addition to vagrants, the NZ fauna includes four endemic *Charadrius* species allied to Australian taxa. The distinctive Wrybill *Anarhynchus frontalis* is the sole member of an endemic NZ genus, which is sister to an Australian species (*Peltahyas australis* = *Charadrius australis*). Despite current taxonomic distinction, the *Anarhynchus/Peltahyas* clade originated as recently as the mid-Pliocene (Thomas *et al.* 2004).

A number of gulls and terns are rare visitors to NZ. However, the masked gulls are an Australasian clade (*Chroicocephalus*) with Black-billed Gull *Chroicocephalus bulleri* sister to the Red-billed Gull *Chroicocephalus scopulinus* and the Silver Gull *Chroicocephalus novaehollandiae* of Australia. This is consistent with two colonization events: either both to NZ or one each way (Given *et al.* 2005, Pons *et al.* 2005). The masked gull group appears to have radiated in the Pleistocene and much of the taxonomic diversity may have emerged in the last 600 kyr (Thomas *et al.* 2004, Given *et al.* 2005). The terns are also a young radiation and the *Chlidonias* group, which includes the NZ endemic Black-fronted Tern *Chlidonias albobristatus*, probably radiated during the Pliocene (Bridge *et al.* 2005).

Snipe (*Coenocorypha*) have reached NZ and offshore islands (two taxa seem to have existed on the Chatham Islands; Tennyson & Martinson 2006), and vagrants of the Japanese species (*Gallinago* spp.) also reach NZ. NZ snipe show a strong population genetic structure among islands (Baker *et al.* 2009). The relationship between these two genera is not well resolved but the clade that includes *Gallinago* and *Coenocorypha* may be early Miocene in age (Thomas *et al.* 2004).

Psittaciformes (parrots)

Three species (two genera) are endemic to NZ; the forest Kaka *Nestor meridionalis*, alpine Kea *Nestor notabilis*, and flightless, lek-breeding Kakapo *Strigops habroptilus*. A third species of *Nestor* (*Nestor productus*) is extinct on Norfolk Island (750 km northwest of NZ), and a fourth may have existed

on the Chatham Islands (800 km east; Millener 1999). Strikingly, *Strigops* and *Nestor* appear to form a clade that is sister to all other extant parrots (de Kloet & de Kloet 2005) and this has been used to calibrate parrot phylogenies on the assumption of vicariant origin of the NZ lineage (Tavares *et al.* 2006, Tokita *et al.* 2007, Wright *et al.* 2008). Wright *et al.* (2008) also found substantial genetic divergence between *Nestor* and *Strigops*, implying an early separation of these two lineages. Although the sister relationship of large NZ parrots to other parrots may be consistent with a vicariant history, molecular phylogenetics of Neoaves dated using penguin and galliform fossils (Pratt *et al.* 2009) found that *Strigops* probably arose after the K/T boundary (i.e. < 65 Ma). The use of an 82 Ma age for the common ancestor of all parrots needs to be reassessed (see Discussion).

The *Cyanoramphus* parakeet radiation has most of its diversity in the NZ region with lineages on the main islands, the Chatham Islands, sub-Antarctic islands, Norfolk Island and New Caledonia. The New Caledonian lineage appears to be sister to a group including those in NZ and Norfolk Island (Boon *et al.* 2001a, Chambers *et al.* 2001). Molecular analysis with other representatives of the platycercine parakeets including the New Caledonian *Eunymphicus* supports the NZ/New Caledonia relationship (Boon *et al.* 2008). Genetic exchange among *Cyanoramphus* populations is problematic for taxonomy and conservation, but is evidence of a youthful radiation associated with allopatry on islands (Chan *et al.* 2006). Boon *et al.* (2001a) estimated the split between NZ and New Caledonian *Cyanoramphus* as mid- to late Pleistocene in age. A clade including *Cyanoramphus*, *Eunymphicus* and other Australasian Platycercini started diversifying in the early Miocene, assuming that a Gondwanan calibration for the divergence of the *Strigops/Nestor* clade is reliable (Wright *et al.* 2008).

Cuculiformes (cuckoos)

The Long-tailed Cuckoo is not closely related to other *Eudynamis*, but instead may group with another Australasian taxon *Scythrops novaehollandiae* (Sorenson & Payne 2005). The Long-tailed Cuckoo breeds only in NZ but winters on islands of the western Pacific. In contrast there is shallow genetic diversity among Bronze Shining-cuckoo populations breeding in Australia, New Caledonia

and NZ, and this species belongs to a radiation distributed from Africa through southern Asia to Australasia. It is sister to a tropical species *Calidris ruficollis* breeding in Papua New Guinea and Indonesia (Sorenson & Payne 2005).

Strigiformes (owls)

Of the two native owls, the extinct monotypic endemic Laughing Owl is of uncertain affinity, although Falla (1953) inferred it to be a close relative of *Ninox*. The extant native Morepork also occurs in Australia, along with three other *Ninox* species. Distributed from Asia to Australia, the species-rich *Ninox* has received little molecular phylogenetic treatment (Norman *et al.* 1998, Olsen *et al.* 2002). Moreporks in NZ are closely related to other populations of this species, although slightly closer to the Norfolk Island than to the Tasmanian population (Norman *et al.* 1998).

Coraciiformes (kingfishers)

The kingfishers are represented in NZ by a single native species, the Sacred Kingfisher *Halcyon sanctus* (*Todiramphus sanctus*). The same species occurs in Indonesia, throughout Australia and on many other Pacific Islands, indicating recent dispersal. Low kingfisher diversity on islands contrasts with the high taxonomic and phylogenetic diversity of the group in the Australian region (Moyle 2006). Phylogeography indicates that this diversity and endemism is not due to an ancient history in the region but rather recent radiation and colonization from Asia (Moyle 2006). Kingfishers therefore provide a nice counterpoint to assumptions about the relationship between centres of diversity and centres of origin.

Passeriformes (perching birds)

The native passerine fauna of NZ and offshore islands comprises between 27 and 38 species (depending on taxonomic treatment; Table 1). These represent 13 families spread across global passerine diversity (Fig. 4). Two of these families are endemic to NZ: Acanthisittidae with six species and Callaeidae with three to five species, and a third (*Notiomystidae*) has been proposed for the monotypic genus *Notiomystis* (Driskell *et al.* 2007). At other taxonomic levels, 13 of 21 genera and 23 of 27 species are endemic to NZ.

The NZ wrens (Acanthisittidae) comprise five genera, of which three are extinct. *Xenicus* is now represented by the Rock Wren *Xenicus gilviventris* with small populations in alpine habitats of South Island, whereas the Rifleman *Acanthisitta chloris* is still relatively abundant in native forests. No thorough analysis of the phylogenetic relationships of the living and extinct species has been completed, although genetic distance data suggest *Xenicus* might belong within *Acanthisitta* (Cooper 1994).

Petroicid robins predominate in the Austral–Papuan region and on Pacific Islands, and include two or three NZ species (*Petroica*). Molecular analysis is consistent with the hypothesis that NZ was colonized twice by *Petroica* (as proposed by Fleming 1950), and populations have managed to reach offshore islands (Miller & Lambert 2006). A melanic robin lineage *Petroica traversi* on the Chatham Islands appears to be sister to mainland Tomtit *Petroica megacephala* rather than to the New Zealand Robin *Petroica australis* (Miller & Lambert 2006). Fine-scale mtDNA sequence variation shows strong spatial partitioning between North Island and South Island *Petroica australis*, but more mixing among *Petroica megacephala* (Miller & Lambert 2006).

The NZ wattlebirds (Callaeatidae) comprise three endemic species in three genera that form a monophyletic group when compared with a range of other passerines (Shepherd & Lambert 2007). The Huia is extinct, as are most populations of Kokako *Callaeas cinerea* and Saddleback *Philesturnus carunculatus*. Wattlebirds appear to share a common ancestor with Australian cnemophiline birds of paradise (Barker *et al.* 2004) around 39–34 Ma (Shepherd & Lambert 2007). The Stitchbird (*Hihi*) *Notiomystis cincta*, formerly placed with the honeyeaters (Meliphagidae), is sister to the NZ wattlebirds (Ewen *et al.* 2006, Driskell *et al.* 2007). The split between Saddleback and Stitchbird is estimated at 39–28 Ma, which could indicate existence of the callaeid/notiomystid lineage in NZ since the Oligocene (Driskell *et al.* 2007). As Driskell *et al.* (2007) and Shepherd & Lambert (2007) used the assumed separation of Acanthisittidae from all other passerines by continental drift at 82 Ma for date calibration, the common ancestor of these lineages might be more recent. A monotypic family has been proposed for Stitchbird mostly on the grounds of missing morphological characteristics typical of wattlebirds (Driskell *et al.* 2007). No near relatives of the

Table 1. New Zealand native passerine diversity and endemism (in bold) across taxonomic levels, based on the NZRBN (Robertson & Medway 2003)

Family	Genus	Species	Subspecies	English name	Location	Status
ACANTHISITTIDAE: New Zealand Wrens	Acanthisitta	chloris	granti	North Island Rifleman	NI, L&GBar	
			chloris	South Island Rifleman	SI, St, Cod	
	Xenicus	longipes	stokesii	North Island Bush Wren	NI	Extinct
			longipes	South Island Wren	SI	Extinct?
			variabilis	Stead's Bush Wren	St	Extinct?
			gilviventris*	Rock Wren	SI	
	Traversia	lyalli		Stephens Island Wren	Step	Extinct
	Pachyplichas	yaldwyni		South Island Stout-legged Wren	SI	Extinct
			jagmi [^]	North Island Stout-legged Wren	NI	Extinct
	Dendroscansor	decurvirostris		Long-billed Wren	SI	Extinct
HIRUNDINIDAE: Swallows and Martins	<i>Hirundo</i>	<i>neoxena</i>		Welcome Swallow	NI, SI, Chat	
MOTACILLIDAE: Wagtails and Pipits	<i>Anthus</i>	<i>novaeseelandiae</i>	novaeseelandiae	New Zealand Pipit	NI, SI	
			chathamensis*	Chatham Island Pipit	Chat	
			aucklandicus*	Auckland Island Pipit	Auk	
			steindachneri	Antipodes Island Pipit	Ant	
SYLVIIDAE: Old World Warblers	¹ <i>Megalurus</i>	punctatus	vealeae	North Island Fernbird	NI	
			punctata	South Island Fernbird	SI	
			stewartiana	Stewart Island Fernbird	St	
			wilsoni	Codfish Island Fernbird	Cod	
			caudata*	Snares Island Fernbird	Snares	
			rufescens	Chatham Island Fernbird	Chat	Extinct
			PACHYCEPHALIDAE: Whistlers and Allies	Mohoua	albicilla	Whitehead Yellowhead
ochrocephala	Brown Creeper	SI, St				
novaeseelandiae	Grey Warbler	SI, St				
ACANTHIZIDAE: Australasian Warblers	<i>Gerygone</i>	igata albofrontata		Chatham Island Warbler	NI, SI, offsh Chat	
MONARCHIDAE: Monarch Flycatchers	<i>Rhipidura</i>	<i>fuliginosa</i>	placabilis	North Island Fantail	NI	
			fuliginosa	South Island Fantail	SI, St	
			penita	Chatham Island Fantail	Chat	
PETROICIDAE: Australasian Robins	<i>Petroica</i>	macrocephala	toitoti*	North Island Tomtit	NI, offsh	
			macrocephala	South Island Tomtit	SI, St	
			chathamensis	Chatham Island Tomtit	Chat	

Table 1. (Continued)

Family	Genus	Species	Subspecies	English name	Location	Status
			<i>dannefaerdi</i> *	Snares Island Tomtit	Snares	
			<i>marrineri</i> *	Auckland Island Tomtit	Auck	
		<i>australis</i>	<i>longipes</i> *	North Island Robin	NI, L&GBar, Kapiti	
			<i>australis</i>	South Island Robin	SI	
			<i>rakiura</i>	Stewart Island Robin	St	
			<i>traversi</i> *	Black Robin	Chat	
ZOSTEROPIDAE: White-eyes	<i>Zosterops</i>	<i>lateralis</i>	<i>lateralis</i>	Silvereye	NI, SI, Chat	
MELIPHAGIDAE: Honeyeaters	² <i>Notiomystis</i> <i>Anthornis</i>	<i>cincta</i> <i>melanura</i>	<i>obscura</i>	Hihi Three Kings Bellbird	LBar Three Kings	
			<i>oneho</i>	Poor Knights Bellbird	Poor Knights	
			<i>melanura</i> <i>melanocephala</i> *	Bellbird Chatham Island Bellbird	NI, SI, St Chat	Extinct
	<i>Prothemadera</i>	<i>novaeseelandiae</i>	<i>novaeseelandiae</i> <i>chathamensis</i>	Tui Chatham Island Tui	NI, SI, St Chat	
CALLAEATIDAE: New Zealand Wattlebirds	<i>Callaeas</i>	<i>cinerea</i>	<i>wilsoni</i> *	North Island Kokako	NI, GBar	
			<i>cinerea</i>	South Island Kokako	SI, St	Extinct?
	<i>Philesturnus</i>	<i>carunculatus</i>	<i>rufusater</i> *	North Island Saddleback	NI, offsh	
			<i>carunculatus</i>	South Island Saddleback	SI, St	
	<i>Heteralocha</i> ³ <i>Turnagra</i>	<i>acutirostris</i> <i>capensis</i>	<i>tanagra</i> *	Huia North Island Piopio	NI	Extinct
PARADISAEIDAE: Birds-of-Paradise, Bower-birds and Piopios			<i>capensis</i>	South Island Piopio	SI, offsh	Extinct?
CORVIDAE: Crows and Jays	<i>Corvus</i>	<i>moriorum</i>	C*	Extinct New Zealand Crow	NI, SI, St, Chat	Extinct

Annotations indicate alternative taxonomic treatment: * and ^ are taxa treated as species or subspecies, respectively, by Worthy and Holdaway (2002), ¹*Megalurus* is otherwise placed in endemic genus *Bowdleria*, ²*Notiomystis* was recently proposed as sole representative of New Zealand family Notiomystidae (Driskell *et al.* 2007), ³*Turnagra* has been placed in Paradisaeidae (Christidis *et al.* 1996) but new data indicate otherwise (G.C.G. in prep.), C *Corvus* from Chathams, but a second undescribed *Corvus* is known from New Zealand mainland. Location codes: NI, North Island; SI, South Island; Cod, Codfish Island; Chat, Chatham Islands; ST, Stewart Islands; off, offshore; Ant, Antipodes Islands; Auck, Auckland Islands; LBar, Little Barrier Islands; GBar, Great Barrier Islands; Step, Stephens Island.

Stitchbird are available for comparison and so far no phylogenetic analysis has included all three NZ wattlebirds and Stitchbird. Recognized forms of the Kokako in North Island and South Island are reciprocally monophyletic in mtDNA, albeit with only a shallow divergence between the clades (Murphy *et al.* 2006).

The diverse Austral–Papuan honeyeaters (Meliphagidae) are represented in NZ by a clade of two species, Tui *Prothemadera novaeseelandiae* and Bellbird *Anthornis melanura*. Tui and Bellbird lie

within one of four large honeyeater clades and may have diverged from other members of the clade *c.* 19–31 Ma, though not necessarily in NZ, and from one another in the late Pliocene (Driskell & Christidis 2004, Driskell *et al.* 2007).

An analysis by Christidis *et al.* (1996) indicated that the New Zealand Thrush, or Piopio, *Turnagra capensis* might be closer to the bowerbirds than birds of paradise, but node support was weak, and taxon sampling was insufficient to test alternative placements.

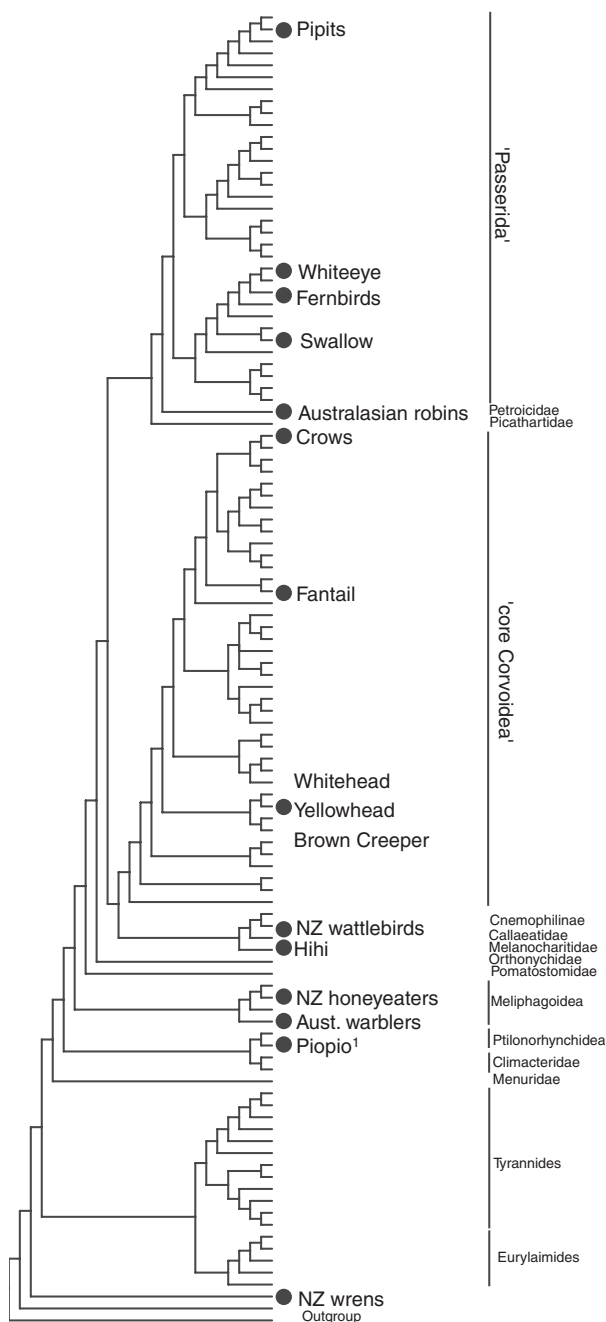


Figure 4. Phylogeny of passerine diversity (from Barker *et al.* 2004), indicating likely placement of native New Zealand taxa. Placements are based either on published molecular phylogenetic data for NZ taxa or close relatives of NZ taxa, or on current taxonomy. ¹Placement of *Piopio* based on Christidis *et al.* (1996) but unpublished data (GCG) indicates this is incorrect.

DNA–DNA hybridization indicates that the New Zealand Fernbird *Bowdleria punctatus* is sister to the Australian Grassbird *Megulurus gramineus* and thus belongs in *Megulurus* (Sibley & Ahlquist

1987), a relationship that had previously been proposed by Oliver (1955), although Olson (1990) has argued for retention of *Bowdleria*. Molecular data for one of the three NZ putative pachycephalines, Yellowhead *Mohoua ochrocephala*, Whitehead *Mohoua albicilla* and Brown Creeper *Mohoua novaeseelandiae*, suggest that these species do not belong to that group but rather represent a distinct lineage within the so-called core Corvoidea that comprises many Austral–Papuan taxa (Norman *et al.* 2009).

Two recent arrivals to NZ have ranges beyond NZ and sister species in the region. The Welcome Swallow *Hirundo neoxena* is closely related to the Pacific Swallow and has been considered a race of this species (Sheldon *et al.* 2005). The Silvereye is one of three Australian races, and a member of a speciose genus distributed in Africa, Asia and Australasia (Clegg *et al.* 2002). Diversity in this genus over this geographical scale reflects dispersal and isolation during and since the Pleistocene (Warren *et al.* 2006). The New Zealand Pipit *Anthus novaeseelandiae* also occurs in Australia and belongs to a clade distributed across Africa, Asia and Australasia (Voelker 1999). Nevertheless, allozyme data suggest that NZ populations are currently reproductively isolated from one another and might constitute distinct species (Foggo *et al.* 1997). The warblers *Gerygone* and fantails *Rhipidura* in NZ belong to speciose groups distributed in Australia and the Pacific, and both have close allies in Australia. Molecular analysis has resolved six main clades among *Rhipidura* species (Nyári *et al.* 2009). Limited genetic divergence in the clade that includes the NZ Fantail *Rhipidura fuliginosa* indicates recent radiation and dispersal (Nyári *et al.* 2009).

DISCUSSION

If NZ had been biologically isolated since the mid/late Cretaceous, when modern birds were first evolving, we might expect it to have a very distinctive avifauna comprising ancient (in a phylogenetic context) endemic radiations of early bird lineages diverged from their cousins elsewhere in Gondwana. In fact, the NZ avifauna is far from monophyletic and few families or genera are endemic (Fig. 3). None of the orders that are reasonably speciose in NZ (e.g. ratites, parrots, shorebirds, passerines) forms monophyletic groups. Evidently, ‘places’ in New Zealand have repeatedly ‘been seized on by intruders’ (Darwin 1859 p81–82).

The NZ avifauna is thus composite in nature; its ancestry is mixed in space and time. As Falla (1953) and others observed, a high proportion of NZ species have their closest relatives in Australia. This is true for shallow species-level (e.g. fantails, robins) and deeper family-level (e.g. kiwi) relationships. Others are associated with Pacific or northern regions (Fleming 1979). This is not to say that the NZ avifauna is Australian in character; it is quite distinct in terms of behavioural, morphological and ecological characteristics, family composition and species diversity, which is generally lower than Australia but notably higher among ratites and penguins (Fig. 3). Falla (1953) thought the composition of the NZ avifauna typical of an oceanic island and this view is largely supported by the molecular phylogenetic evidence reviewed above. In addition, molecular data have demonstrated instances of unexpected taxonomic distinctiveness (e.g. Stitchbird), and shallower than expected connections with non-NZ taxa (e.g. Haast's Eagle), and have opened an important window on recently extinct species and populations (e.g. moa). Finally, molecular evidence has been instrumental in revealing the way that natural selection has yielded, often in a short time frame, extraordinary changes in behaviour and form, producing for example flightless rails, a giant eagle and a nocturnal parrot.

Although the affinity with the avifauna of Australia is consistent with a vicariant history involving Zealandian continental drift, the depth and extent of endemism are not. The phylogenetic composition of the NZ avifauna shows that it is drawn from throughout the diversity of modern birds (Fig. 3) and it has been drawn repeatedly, not at a single event. In this phylogenetic sense, NZ's avifauna is a subset of Australia's, which is in turn a subset of global diversity (Fig. 3). The composite nature of the avifauna is evident at all levels, for instance with representation of multiple families across passerine diversity (Barker *et al.* 2002) (Fig. 4). Some of these passerine families are Australasian (cis-Wallacean of Barker *et al.* 2002), but others are not and occur on both sides of Wallace's Line. The observation that the Australasian passerine lineages tend to arise basally in phylogenetic reconstructions indicates that the Passeriformes might have originated in this part of the world (Barker *et al.* 2002, 2004, Edwards & Boles 2002, Ericson *et al.* 2002). This is supported by the presence in Australia of the oldest known songbird fossils from the Eocene (Boles 1995, 1997),

whereas northern hemisphere songbird fossils are younger (Cooper & Penny 1997).

Accumulation and radiation

Island biogeography theory (MacArthur & Wilson 1967) interprets island biotas as primarily the product of colonization and extinction, but colonizers may modify their environment, influence the evolution of competitors and themselves evolve under natural selection or genetic drift. This combination of processes is evident among the NZ birds, and is exemplified by the rail fauna, which appears to have accumulated sequentially from separate founding populations (Trewick 1997a, Crisp 2008). Rates of dispersal by flying rails are high, but this inference is derived from analysis of current distributions and relationships rather than direct observation of immigration. Similar rates of dispersal may exist in other taxa but be less apparent in the absence of rapid isolation of successive colonizations (e.g. by adaptive shifts associated with flightlessness). The rails also exemplify the influence of directional asymmetry in colonization (Cook & Crisp 2005a). A speciose NZ clade with an Australian or cosmopolitan taxon nested within it might be seen as indicating that NZ is a source of dispersal, as has been suggested for other organisms (e.g. Winkworth *et al.* 2002). However, the same phylogenetic pattern is obtained if the likelihood of dispersal and colonization in different directions is not equal. In the case of rails where NZ endemics are flightless, the likelihood of dispersal out of rather than into NZ is intuitively considerably lower (Crisp 2008).

Flightlessness is not confined to rails, but is a feature of the NZ avifauna and that of many other islands (Roots 2006, Steadman 2006). Rather than a dichotomy in flight ability, flightlessness is a continuum from moa, which lack any wing structure, through kiwi, some rails, and Kakapo, to Kokako, wrens and Owlet-nightjar, which use(d) their wings to varying degrees. NZ birds are generally naive to ground predators, although some show evidence of adaptation to avoid diurnal aerial predators (e.g. nocturnal Kakapo and kiwi). Many lack defensive behaviour against terrestrial predators and are especially susceptible when nesting. Such traits might indicate ancient origins of these taxa, but are in fact common to birds of many islands. Flightlessness, for instance, has evolved independently and sometimes in short geological time in many bird groups on

islands (Roots 2006). Even among ratites, the evidence for multiple, independent evolution of flightlessness is now strong (Harshman *et al.* 2008, Phillips *et al.* 2010). Indeed, these traits are likely to have been derived fairly recently in NZ birds as Zealandia has not always lacked a mammal fauna. Fossils indicate that terrestrial mammals, whether descended from Zealandian stock or from later colonists, were present in Miocene NZ (Worthy *et al.* 2006). Modern experience in conserving NZ birds (King 1985) makes it abundantly clear that species such as the large, flightless, ground-dwelling, strong-smelling and behaviourally defenceless Kakapo are unlikely to have evolved in the presence of ground-hunting mammals.

Similarly, distinctive morphological and behaviour traits (e.g. extreme sexual dimorphism of beak in Huia, small omnivorous kiwi, giant eagle) are common features of island species (Quammen 1997), and phylogenetic topologies alone cannot show whether these are young or old traits.

The capacity for successful colonization in the past can be understood to some degree by scrutiny of recent colonization, which in turn provides some information on dispersal. Long-distance dispersal that fails to result in colonization will usually go unobserved, although the incidence of vagrants may provide some indication of actual dispersal rates in taxa that have not yet successfully colonized (Falla 1953). The ecological characteristics of the birds that have naturally colonized NZ in recent times are varied. Recent dispersal yielding viable populations has occurred in small arboreal (e.g. Silvereyes *c.* 11 g) and large terrestrial species (e.g. Purple Swamphen *c.* 1000 g). Neither the small body mass of Silvereyes nor the ungainly flight and skulking habit of swamphens suggests these species as candidates for distance travel. In contrast, some habitat-tolerant and powerful fliers are notable by their absence (e.g. Peregrine Falcon, Caughley 1964). Thus, dispersal may be largely stochastic, whereas success in colonization may be strongly influenced by availability of niche space (i.e. colonization opportunity).

Few NZ lineages are represented by genuine radiations. Most notable were the moa, which exhibited substantial variation in size within and among species that may have facilitated sympatry (Baker *et al.* 2005, Turvey & Holdaway 2005, Wood *et al.* 2008). Wattlebirds comprised three species, each of which represents different ecotypes, whereas honeyeaters, large parrots and

wrens were represented by two, three and five species, respectively. However, five kiwi species appear to have occupied different geographical areas. Many taxa are represented by North and South Island forms, and sometimes also additional forms on offshore islands. Although the North Island and South Island are close to one another today, in the early Pleistocene and before, they were separated by a larger seaway, which may have contributed to population isolation. Overall diversity is greatest when we consider the islands of the NZ region together, as many small islands provided sufficient isolation to allow the evolution of distinct morphological forms (e.g. *Nestor*, *Hemiphaga*, *Cyanoramphus*, Fleming 1976). Sometimes these island populations are sufficiently distinct to be deemed separate species. In all cases, dispersal has been required to establish island populations and in some instances dispersal has resulted in a reticulate pattern of evolution (e.g. *Cyanoramphus* parakeets on the Chatham Islands, Boon *et al.* 2001b, Chan *et al.* 2006).

A Zealandian element?

NZ is essentially the product of tectonic activity since the Miocene (Fig. 2). It is just one part of a Zealandian system, which had a long 60-Myr biotic history of its own after separation from Gondwana, but before NZ as we know it began to form. Part of the modern NZ fauna could have been derived from the Zealandian biota carried on that continental fragment, as it is not known whether all parts of Zealandia were submerged prior to emergence of the current islands. Evidence for continuous existence of substantial land in NZ's position is equivocal, and current knowledge of Zealandian geology indicates that persistence of terrestrial life may be best envisaged in the context of a largely tectonic, ephemeral archipelago comprising Miocene islands north of NZ (Meffre *et al.* 2006), New Caledonia emergence in the Eocene (Paris 1981), formation of modern NZ during the Miocene, emergence of the Chatham Islands in the late Pliocene plus volcanic edifices including Lord Howe Island and Norfolk Island to the north and west, and the islands on the Campbell Plateau to the south (Campbell & Hutchings 2007) (Figs 1 and 2).

A putative Zealandian element might include currently unplaced lineages (e.g. *Aptornis*), and taxa on long branches with nodes basal to their

respective group (e.g. large parrots, NZ wrens, New Zealand Pigeon). But a paradox exists, as at least some of these lineages include populations on young offshore islands that indicate a retained capacity for dispersal and colonization over substantial areas of ocean. For example, parrots *Nestor* and pigeons *Hemiphaga* are also represented on offshore islands > 600 km away (Norfolk and Chatham islands) that are just a few million years old and were never connected directly to mainland NZ (Fleming 1976). Their ancestors are likely to have been at least as mobile and therefore able to move in or out of Zealandia or NZ in earlier times.

The endemic NZ bird families might represent lineages with old ancestry in the region, although this need not be as old as Zealandia, nor geographically fixed in 'NZ'. Identifying the mechanisms that have resulted in endemism of deep taxonomic lineages in NZ is difficult and perhaps impossible. Absence today of a given lineage (e.g. bird family) outside NZ is not evidence of its absence in the past. Phylogenetically old lineages might not have evolved in the places in which their descendants are found today (Fig. 5). Furthermore, there is less chance of current distribution patterns confounding inference of lineage origin when we are considering those that are speciose (see Cook & Crisp 2005b, Crisp & Cook 2005).

Endemic bird families exist on other landmasses of greater and lesser size and age than NZ, e.g. Caribbean Palmchat *Dulus dominicus*, New Caledonian Kagu, Greater Antilles todies (Todiidae), Hawaiian honeycreepers (Drepanidinae), mesites (Mesitornithidae) and ground-rollers (Brachypteraciidae) of Madagascar, and dodos (Raphidae) of Mascarene Islands. Endemic families might indicate local survival of relatively old lineages, or rapid evolution of novel and unusual traits (resulting in taxonomic splitting). For example, molecular phylogenetics has shown that the distinctive Raphidae are actually embedded within the geographically widespread pigeon family Columbidae (Pereira *et al.* 2007). Estimates using molecular phylogenies of Columbiformes calibrated with multiple fossils indicate the Raphidae lineage originated about 33 Ma, which is some 20 million years before the islands they lived on came into existence. In this case, morphology misleads taxonomy, but the lineage cannot have originated where it was found. The same situation could apply to endemic families in NZ. For example, the monotypic and distinctive

Aptornithidae (*Aptornis*) might be a Zealandian lineage, but unusual morphology, lack of molecular data and apparent lack of any near relatives elsewhere in the world preclude confirmation of this. Even robust phylogenetic placement of the *Aptornis* lineage when sufficient data are available will tell us neither absolutely when the lineage arrived in NZ, nor when its distinctive morphology evolved.

Disharmony and extinction

A striking feature of the avifauna, also seen in the NZ biota as a whole, is its patchiness (Fig. 2), sometimes described as disharmonic (Carlquist 1974) or ill-balanced (Falla 1953). For the birds this is particularly evident in low species diversity, i.e. the tendency for genera and even deeper taxonomic levels to be represented by single or few species. In Carlquist's (1974) terms, the NZ avifauna has a higher representation of dispersing species than would be expected from an old 'harmonic' biota. On human contact, the NZ region including offshore islands had some 245 species (Worthy & Holdaway 2002). The modern list extends to 305 (with introductions), compared with UK (599), New Guinea (764), Hawaii (303) and Galapagos (147) (Clements 2007 with updates from Avibase, 2009). NZ bird diversity is low considering its large area and wide latitudinal range (Neall & Trewick 2008). This condition has frequently been ascribed to a long period of isolation (e.g. Baker 1991). However, whereas geophysical isolation of the land is evident, it is obvious that even the modern NZ biota is not isolated; some species migrate in and out of NZ repeatedly in their lifetimes (e.g. cuckoos, godwits, albatrosses). Regardless, there is no obvious direct correlation between long physical isolation and low species diversity (Goldberg *et al.* 2008). Examples of the reverse are abundant, and are well recognized as having provided a vital stimulus for Darwin's thesis on evolution (Trewick & Cowie 2008). Whereas some islands, especially more distantly isolated ones, may lack some lineages, they often include radiations within the lineages that are present (e.g. Hawaiian honeycreepers, Galapagos finches). Island biogeography theory (MacArthur & Wilson 1967) leads us to predict that low species diversity is best explained by extreme youth of island (insufficient time), small area and/or low habitat diversity (insufficient niche space).

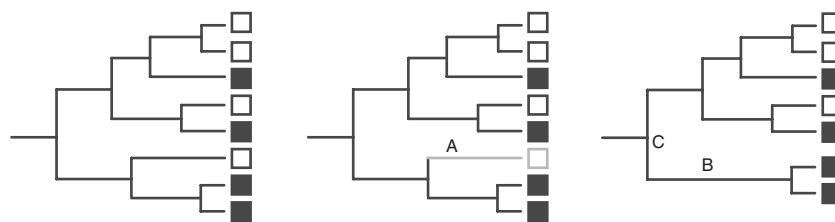


Figure 5. The effect of taxon sampling on tree interpretation. The rooted tree on the left depicts the relationships of a hypothetical set of taxa distributed in two geographical areas (black or white squares). Consider the situation if a single lineage (A) in the tree was missing because it has become extinct or was not sampled for some other reason (grey branch and box in centre tree). On the right is the tree that would in this case be inferred. Notice that branch B now extends to the most basal node (C) in the rooted tree and lineage B now appears to be sister to all other taxa. If the black and white areas had been separated by some vicariant event at a known time, molecular clock calibration that applied this date to node C would overestimate the age of the entire clade. It could also be inferred using parsimony that the geographical area (or morphology or behaviour) depicted by black boxes was the more likely ancestral location (or morphology or behaviour) of the entire group of taxa.

The combination of broad phylogenetic representation (Fig. 3) and low species diversity in the NZ avifauna could be explained by a combination of fairly extensive extinction and stochastic arrival of lineages. Long, naked branches in phylogenetic trees are indicative of extinction, but do not tell us where extinction or survival has taken place in space or time (Fig. 5). Recent colonists may be the sole representatives of lineages that are speciose elsewhere, and are unlikely to have had time to diversify within NZ (e.g. Silvereye). Earlier colonists might have diversified after arrival either by adaptive radiation or allopatric isolation or might have been supplemented by additional colonizations, as in the rails. The modern observation of numerous insular taxa on offshore islands around NZ indicates that we can expect equivalent diversification to have arisen in this manner in the past. However, phylogenetic and taxonomic information shows that, in general, inter-island diversity within lineages is shallow, implying it has been short-lived. In some cases, this is easily understood, as the islands themselves are young, but at least the two main islands of NZ have probably existed in some form since the Miocene.

Substantial climate cooling in the Plio-Pleistocene may also have reduced diversity, but fossils of terrestrial avian taxa that might provide evidence for early Pleistocene extinction are few. In contrast, extinction of Miocene plants and animals is evident from the fossil record (Lee *et al.* 2001, Worthy *et al.* 2006). Oligocene land area in the NZ region was small and possibly negligible. We can therefore infer that only a small fraction of the Zealandian biota could have survived, as the combined effects of small population size and environmental stochasticity on species survival are well recognized

(MacArthur & Wilson 1967, Saether *et al.* 2005). Not only does geology show that most of the terrestrial environment of Zealandia was lost in the Oligocene (Graham 2008, Landis *et al.* 2008), molecular data indicate that only few extant taxa could plausibly represent lineages with long-term existence in the region (Goldberg *et al.* 2008, Wallis & Trewick 2009). In addition, phylogenetic evidence to date fails to show consistent structure indicative of a shared evolutionary history of the avifauna on the remnants of Zealandia (principally NZ and New Caledonia).

Delving further back into the history of Zealandia and its biota, it is recognized that many species and higher taxonomic groups were lost globally around the K/T boundary (Fortey 1999). At that time (65 Ma) Zealandia was already a shrinking and low-lying landmass (Graham 2008) and local extinction of angiosperms and most gymnosperms is evident (Vajda & Hollis 2001). Forests were destroyed globally and any fauna associated with forests must have been similarly devastated (e.g. Labandeira *et al.* 2002). Although it is obvious that globally, many lineages persisted through the K/T, and these include one lineage of dinosaurs (i.e. the birds, Neornithines) (Penny & Phillips 2004, Padian & de Ricqlès 2009), we can assume that many did so only locally and then expanded their ranges to occupy vacant ecological space, rather than surviving in all parts of the globe. Although it is possible that some of these surviving lineages might have been in Zealandia, there is no logical reason to believe the region was especially favoured in this respect. Even in the absence of explicit details about biotic turnover it has to be recognized that, in the long history of Zealandia, extinction must have been a major force in shaping the biota.

Dating diversification

With the application of molecular clocks (Bromham & Penny 2003) it is possible to estimate the timing of lineage formation, although the reliability of this approach is dependent on the consistency of rates of molecular evolution among lineages or the appropriate accommodation of rate variation, and the suitability and reliability of clock calibrations. In studies of bird evolution, molecular clock calibrations have used two main tools: fossils and vicariant events. The value of fossils is dependent on their accurate dating, correct identification as representing an ancestral taxon of a given lineage and completeness of the fossil record. In recent years, some important bird fossils have been found to supplement fossils of other vertebrates in molecular calibrations. Among them, the dating of the stem Anseriform at 66 Ma (*Vegavis* fossil; Clarke *et al.* 2005) and stem penguins (NZ, Waimanu fossils 64–61 Ma; Slack *et al.* 2006) both lie close to the K/T boundary and are useful in dating the diversification of lineages in Neoaves (Ho & Phillips 2009). Fossils usually represent minimum ages for origin of lineages, as they may form any time after but not before a taxon evolves. Similarly, the timing of vicariance events needs to be based on accurate geological data and then combined with a rigorous hypothesis about their influence on the lineages in question. The assumptions made to justify use of vicariance events in clock calculations are rarely well expressed and can lead to circular reasoning; an assumption of vicariance cannot be used to date the origin of a lineage that is then used to demonstrate a role of vicariance in lineage formation (Waters & Craw 2006). Molecular clock analyses should accommodate variation in rates of molecular evolution among lineages and modelling that meaningfully expresses confidence about the age and affinity of fossils or vicariance events used for calibration and their temporal affinity to specific ancestral nodes (Ho & Phillips 2009). Studies that use point calibrations or fixed rates of molecular evolution can yield point estimates of node age lacking confidence intervals, thus giving a false impression of certainty (Ho & Phillips 2009). What are needed when applying molecular clock calibrations are 'rigidly defined areas of doubt and uncertainty' (Adams 1979).

Although vicariance and dispersal are often seen as polar opposites, especially in the context of NZ biogeography, both processes influence population

exchange or gene flow (Trewick & Morgan-Richards 2009a). Principally because of the combination of geological and biological characteristics typical of both islands and continents, neither vicariance (via continental drift) nor long-distance dispersal can be excluded *a priori* as potential influences on NZ biology (Daugherty *et al.* 1993, Goldberg *et al.* 2008, Trewick & Morgan-Richards 2009b). Thus, both biogeographical interpretations have been in favour at one time or another and the conundrum of NZ has been a focus for many biogeographers, leading one to suggest: 'Explain New Zealand and the world falls into place around it' (Nelson 1975). Molecular analyses have contributed to both sides of the debate but, paradoxically, a growing recognition of the considerable importance of dispersal in founding isolated populations of many kinds of organisms and thus biotas (Sanmartin & Ronquist 2004, Cowie & Holland 2006) has occurred at the same time as some phylogeneticists have turned to vicariance events (for want of alternatives) to date speciation and diversification of a variety of different taxa and clades.

Thus, the earliest time of separation of Zealandia from Gondwana has been used as a calibration point for avian phylogeny. A date of 82 Ma is widely applied in studies of birds including parrots (Tavares *et al.* 2006, Wright *et al.* 2008), passerines (Barker *et al.* 2002, Ericson *et al.* 2002, Irested *et al.* 2008), moa (Cooper *et al.* 2001, Baker *et al.* 2005) and honeyeaters (Driskell *et al.* 2007). This is despite the fact that many of these same analyses have needed to invoke dispersal events to reconcile phylogeny and geography. For example, Barker *et al.* (2004) infer and date 10 major dispersal events for passerine taxa largely on the assumption that one group, ancestors of the NZ wrens, never dispersed. Similarly, Tavares *et al.* (2006) note the value of an independent geological calibration point in allowing rates of molecular evolution to be estimated in parrots. While true in concept, this approach relies on an assumption that the geological event is both correctly dated and correctly inferred as the cause of vicariance. Again, confidence in the correctness of this assumption is undermined because the same study infers dispersal for other parrots (Tavares *et al.* 2006).

If dispersal happens sometimes, or at least has to be inferred sometimes, how do we know it did not happen following the vicariant event in question? A case in point is that of the NZ wrens (represented by the extant Rifleman). Analyses of DNA

sequences indicate that *Acanthisitta* might be the phylogenetic sister of all other living passerines (Barker *et al.* 2002, 2004, Ericson *et al.* 2002, 2003, Slack *et al.* 2007, Hackett *et al.* 2008). Because the Acanthisittidae are endemic to NZ, *Acanthisitta* potentially provides a useful tool for dating the evolutionary history of the largest living bird radiation (Passeriformes), but only if there is confidence in the history of the *Acanthisitta* lineage.

The NZ wren lineage (1) evolved in Gondwana before separation of Zealandia, (2) evolved in Zealandia NZ following separation, or (3) arrived in Zealandia/NZ after separation. As scenarios 1 and 3 both require subsequent extinction of the lineage everywhere else except NZ, they appear to be equally plausible. Only scenario 2 provides a strong evolutionary basis for using the vicariance event to date evolution; in this scenario vicariance is the driver of evolution so that phylogenetic and geographical splitting were contemporaneous. Thus, in the absence of any independent evidence for scenario 2, the use of *Acanthisitta* is reliant on circular reasoning (Waters & Craw 2006) and could easily result in underestimation (scenario 1) or overestimation (scenario 3) of the timing of avian diversification.

It is increasingly evident that modern birds have a history dating at least to the late Cretaceous, prior to the K/T boundary (Cooper & Penny 1997, Penny & Phillips 2004). Just how far back remains unresolved and is dependent on the quality of fossils and stringency of molecular calibration studies (for a discussion of the avian fossil record see Padian & de Ricqlès 2009). When considering the assembly of the NZ avifauna, where there exists the possibility of long isolation, the earlier diversification of modern birds opens the possibility that a number of distinct lineages were isolated by Zealandian vicariance. If we accept a stronger influence of vicariance in the past and dispersal more recently, then we are assuming that birds of that early period had different dispersal capacities than today. Indeed, Ericson *et al.* (2003) suggest that 'the basal members of the major clades of passerines are feeble[sic]-winged groups' and thus less capable of the type of dispersal that would result in significant biogeographical change. But there appears to be no strong evidence that ancestral passerines were less capable fliers than modern ones. There is little logic in inferring weak flight as a condition among passerines or other modern birds, when it is likely or at least arguable that the achievement of effective

flight was one of the key innovations enabling their success and radiation. In some cases at least, inference of feeble flight in 'old' lineages is confounded by what is probably the secondary evolution of that condition in a number of Zealandian lineages (e.g. NZ moa, wattlebirds, wrens and New Caledonian Kagu), as reduction in flight capability is well documented in a broad diversity of avian lineages, especially on islands (Roots 2006). As already noted, large skulking rails and small passerines alike have shown themselves equal to the challenge of transoceanic dispersal.

CONCLUSION

Falla's proposal in 1953 of a series of invasions assumed dispersal was the driver of regional diversity. However, the radical shift in understanding of the geophysical history of the earth that took place soon after introduced a very plausible alternative. Continental drift provided a mechanism to sunder populations and migrate entire biotas, which led to the proposal of a vicariant origin of NZ's biota. The development even more recently of molecular phylogenetic tools provided the means to test the relative importance of these processes. The result has been confirmation of dispersal as dominant in the assembly of the avifauna and the biota in general (Wallis & Trewick 2009). However, the story is not simple and its interpretation is hindered by gaps in our understanding of the geological history of the Zealandian islands, including NZ.

The NZ avifauna is most closely related to that of Australia, in terms of both phylogenetic relationships and overall composition. Many taxa are recent arrivals, whilst others appear to have evolved from lineages reaching NZ earlier in its history. Disharmony appears to reflect both extinction and stochastic colonization, with most diversity derived by accumulation, sometimes accompanied by evolution of flightlessness and other distinctive adaptations, rather than *in situ* radiation. Some species found today only in NZ appear to represent lineages that originated quite early in the evolution of modern birds. Some of these lineages might be remnants of a Zealandian avifauna isolated by vicariance, but might equally have arrived in Zealandia (and latterly NZ) after geological separation from Gondwana. What is striking and very clear is that the vast majority of NZ bird lineages do not owe their presence merely to ancient vicariant isolation. Instead the development

of the avifauna reflects a much more convoluted, dynamic and interesting evolutionary odyssey.

In addition to filling in missing phylogenetic information on placement of NZ species among the extant global avifauna and promoting efforts to conserve NZ's distinctive taxa and assemblages, we predict that fruitful research about the way biotas develop and how susceptible they are to environmental change will come from the application of combined ecological and genomic methods to the evolution of NZ's birds, old and new.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Peer-reviewed publications reporting application of molecular data to New Zealand birds, categorized by taxonomic depth of study.

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