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ORIGINAL ARTICLE

Population structure and biogeography of *Hemiphaga* pigeons (Aves: Columbidae) on islands in the New Zealand region

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ABSTRACT

Aim The New Zealand avifauna includes lineages that lack close relatives elsewhere and have low diversity, characteristics sometimes ascribed to long geographic isolation. However, extinction at the population and species levels could yield the same pattern. A prominent example is the ecologically important pigeon genus *Hemiphaga*. In this study, we examined the population structure and phylogeography of *Hemiphaga* across islands in the region.

Location New Zealand, Chatham Islands and Norfolk Island.

Methods Mitochondrial DNA was sequenced for all species of the genus *Hemiphaga*. Sixty-seven individuals from mainland New Zealand (*Hemiphaga novaeseelandiae novaeseelandiae*), six of the Chatham Islands sister species (*Hemiphaga chathamensis*), and three of the extinct Norfolk Island subspecies (*Hemiphaga novaeseelandiae spadicea*) were included in this study. Novel D-loop and cytochrome *b* primers were designed to amplify DNA from museum samples. Additionally, five other mitochondrial genes were used to examine placement of the phylogenetic root.

Results Analyses of mitochondrial DNA sequences revealed three *Hemiphaga* clades, consistent with the allopatric populations of recognized (sub)species on oceanic islands. Of the 23 D-loop haplotypes among 67 New Zealand pigeons (*Hemiphaga n. novaeseelandiae*), 19 haplotypes were singletons and one haplotype was common and widespread. Population genetic diversity was shallow within and between New Zealand populations, indicating range expansion with high inter-population exchange. Tentative rooting of the *Hemiphaga* clade with cyt *b* data indicates exchange between mainland New Zealand and the Chatham Islands prior to colonization of Norfolk Island. We found low genetic divergence between populations on New Zealand, the Chatham Islands and Norfolk Island, but deep phylogenetic divergence from the closest living relatives of *Hemiphaga*.

Main conclusions The data are consistent with the hypothesis of population reduction during the Pleistocene and subsequent expansion from forest refugia. Observed mobility of *Hemiphaga* when feeding helps explain the shallow diversity among populations on islands separated by many hundreds of kilometres of ocean. Together with comparison of distribution patterns observed among birds of the New Zealand region, these data suggest that endemicity might represent not long occupancy of an area, but descent from geologically recent colonizations. We consider the role of lineage pruning in creating the impression of old endemicity.

Keywords

Chatham Islands, dispersal, *Hemiphaga*, mitochondrial DNA, New Zealand, Norfolk Island, population structure, phylogeography.

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INTRODUCTION

One of the reasons New Zealand intrigues evolutionary biologists is that it displays biological characteristics of both oceanic islands and continental land masses (Daugherty *et al.*, 1993; Trewick & Morgan-Richards, 2009). It is continental in stratigraphic composition and origin (founded on a tectonic fragment, Zealandia, separated from Gondwanaland *c.* 83 Ma) and is often viewed as continental in its biology (Cowie & Holland, 2006). However, it is increasingly apparent that the New Zealand biota is a dynamic and relatively young evolutionary system (McGlone, 2005; Goldberg *et al.*, 2008; Wallis & Trewick, 2009). Following its separation from Gondwanaland starting 83 Ma, most if not all of the continent of Zealandia submerged beneath the sea (Pole, 1994; Waters & Craw, 2006; Trewick *et al.*, 2007; Landis *et al.*, 2008). The main islands of New Zealand, which are a small emergent part of Zealandia, are primarily the product of tectonic activity initiated *c.* 25 Ma (Trewick *et al.*, 2007; Landis *et al.*, 2008; Neall & Trewick, 2008). Other emergent parts of Zealandia include New Caledonia, Norfolk Island and the Chatham Islands (Fig. 1), all of which appear to be the products of volcanic or tectonic activity. If any land persisted from Zealandia through to modern New Zealand, it was at its smallest towards the end of the Oligocene and is likely to have resulted in population bottlenecks and lineage extinction (Cooper & Cooper, 1995). Tectonic activity in the Miocene and Pliocene resulted in substantial remodelling of the archipelago and culminated in crustal uplift and orogenesis since the Pliocene (Kamp, 1992). Furthermore, substantial biotic turnover occurred during the early Miocene (as evident from the fossil record; Lee *et al.*, 2001) and Plio-Pleistocene time, when the forest habitats repeatedly retreated and expanded during climate cycling (McGlone *et al.*, 2001). During glacial phases, forests appear to have been restricted to small areas mostly in northern North Island and north-western South Island of New Zealand, with the remaining vegetation being dominated by shrub and grassland (McGlone, 1985; Alloway *et al.*, 2007). How the biota of the New Zealand region has responded to the geophysical history is of particular interest to biologists attempting to reconcile the region's old continental geological history with the observation of a more island-like biotic composition (e.g. Falla, 1953).

Figure 1 The New Zealand region with an approximation of Zealandia indicated in grey.

In the face of such intense climatic and geological activity, it is not surprising that phylogeographic studies of New Zealand's fauna have suggested that Pleistocene climate cycling had an important influence on the distribution and divergence of several taxa (Buckley *et al.*, 2001; Trewick & Wallis, 2001; Neiman & Lively, 2004; Hill *et al.*, 2009; for a review see Wallis & Trewick, 2009), although other lineages appear to have retained diversity that dates to earlier climatic and geophysical changes of the late Pliocene (Trewick *et al.*, 2000; Trewick & Wallis, 2001; Buckley & Simon, 2007). Among phylogeographic studies of New Zealand vertebrates, some reveal patterns consistent with habitat fragmentation during glacial periods of the Pleistocene (e.g. short-tailed bat, *Mystacina tuberculata* – Lloyd, 2003; brown kiwi, *Apteryx* spp. – Baker *et al.*, 1995), whereas recent speciation in Plio-Pleistocene time is evident in a number of New Zealand forest birds (e.g. kokako, *Callaeas cinerea* – Murphy *et al.*, 2006; parakeets – Boon *et al.*, 2001a; kiwi – Baker *et al.*, 1995; Burbidge *et al.*, 2003; moa – Baker *et al.*, 2005; Bunce *et al.*, 2009; robins, *Petroica* spp. – Miller & Lambert, 2006) (for further discussion see Goldberg *et al.*, 2008; Wallis & Trewick, 2009).

A key observation from the study of New Zealand birds is that the assemblage, while relatively small, is drawn from the range of global phylogenetic diversity, rather than being a monophyletic group (Trewick & Gibb, 2010). There is endemicity, which is suggestive of isolation, but this is at many taxonomic levels from family to subspecies, and so it could be inferred that different elements of the avifauna have experienced different degrees of isolation (Trewick & Gibb, 2010). The geographic ranges and taxonomic distinctiveness of forest birds in the wider New Zealand (Zealandian) region are similarly diverse (Fig. 2). For example, *Hemiphaga* pigeons occur on mainland New Zealand, the Chatham Islands and Norfolk Island (Fig. 2a), whereas *Cyanoramphus* parakeets occur on mainland New Zealand, the Chatham Islands, Norfolk Island and New Caledonia, which also harbours the sister genus (Fig. 2b); New Zealand has some endemic petroicid robins, but the main diversity is in Australia, with evidence for separate exchanges between Australia and other islands (Fig. 2c); and one species of *Ninox* owl is found in New Zealand and also on Norfolk Island, New Caledonia (extinct) and Australia, but most species richness is in Australia and Asia (Fig. 2d).

One inference from genera that are restricted to the New Zealand region, such as *Hemiphaga* pigeons, is that they have

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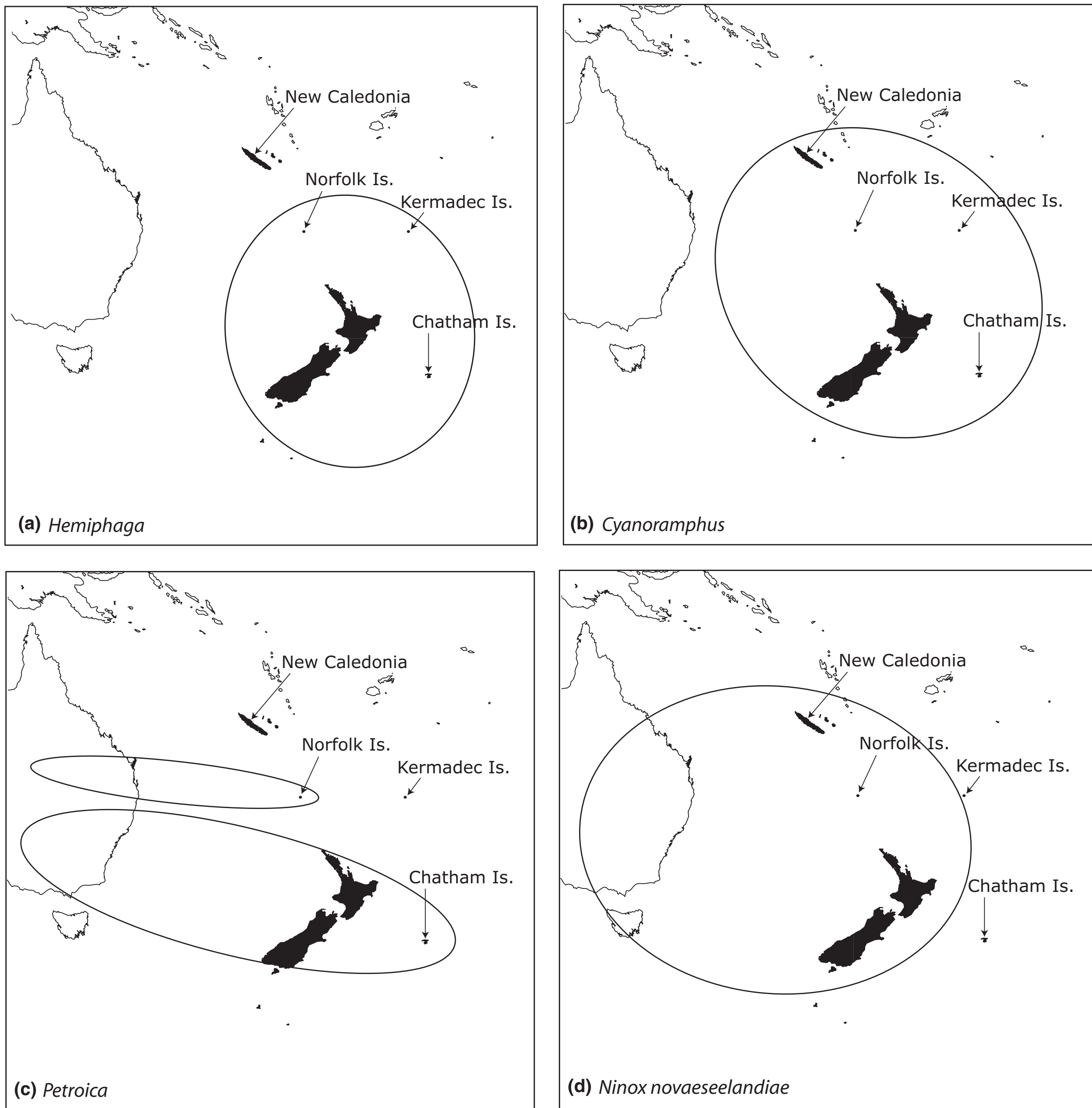

Figure 2 Four paradigms of forest bird distributions among islands, focusing on the New Zealand region: (a) pigeon (*Hemiphaga* spp.), (b) parakeet (*Cyanoramphus* spp.), (c) robin (*Petroica* spp.), (d) owl (*Ninox novaeseelandiae*). Ellipses encompass land areas from where representatives of each taxon have been recorded either in the extant native avifauna or in Holocene fossils (Worthy & Holdaway, 2002; Clements, 2007). *Hemiphaga* (a) and *Cyanoramphus* (b) are endemic to islands in the areas indicated, whereas *Petroica* (c) has additional diversity in Australia, and *N. novaeseelandiae* (d) has most diversity in Australia and Asia.

been isolated there for a comparatively long time, but an alternative explanation is that they arrived more recently and have since been extirpated elsewhere. For example, if *Cyanoramphus* was extinguished in New Caledonia, the genus would be rendered endemic to the New Zealand region (Fig. 2b). Such an inference might be considered less parsimonious because dispersal is often considered to be an unlikely phenomenon (for discussion see Cook & Crisp, 2005). One way to explore the plausibility of this alternative is to examine the population genetic structure of New Zealand taxa to see if they have retained the capacity for recent exchange. If they do, we cannot exclude the possibility that deeper-level endemicity in New Zealand is a result of recent extinction elsewhere.

Therefore, in this study we examined the phylogeography of *Hemiphaga* pigeons, which are ecologically important forest birds and endemic to the New Zealand region. The

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genus *Hemiphaga* is considered to be part of the radiation of Southeast Asian pigeons and doves (Gibbs *et al.*, 2001; Johnson, 2004). It belongs to a small group of four species-poor genera (*Hemiphaga*, two species; *Lopholaimus*, one species; *Cryptophaps*, one species; *Gymnophaps*, three species) that might be remnants of an earlier higher species diversity (Gibbs *et al.*, 2001). Species of *Gymnophaps* occur on the Moluccas, New Guinea and the Solomon Islands, and *Cryptophaps poecilorrhoa* (Brüggemann, 1876) is endemic to Sulawesi (Gibbs *et al.*, 2001). *Lopholaimus antarcticus* (Shaw, 1794) is endemic to the east coast of Australia, and based on morphology it has been suggested that it is the closest living relative of *Hemiphaga* (Gibbs *et al.*, 2001). However, using molecular data, Pereira *et al.* (2007) showed that *Lopholaimus* grouped with *Gymnophaps*, with *Hemiphaga* being sister to these, and new molecular results corroborate this (Gibb & Penny, 2010). In contrast, other genera in the Pacific fruit pigeon clade are both species-rich and widely distributed through northern Oceania (Gibbs *et al.*, 2001). The known distribution of the genus *Hemiphaga* includes mainland New Zealand, the Chatham Islands and formerly Norfolk Island and Kermadec Islands (Worthy & Brassey, 2000). Two extant species of *Hemiphaga* are generally recognized. *Hemiphaga novaeseelandiae* (Gmelin, 1789) consists of two subspecies. *Hemiphaga novaeseelandiae novaeseelandiae* (Gmelin, 1789) is found throughout mainland New Zealand (locally called kereru) and formerly the Kermadec Islands, but is known from there by only a single subfossil bone (Worthy & Brassey, 2000). *Hemiphaga novaeseelandiae spadicea* (Latham, 1802) was described from Norfolk Island (Fig. 1), where it became extinct in the mid 1800s (Tennyson & Martinson, 2006). The sister species, *H. chathamensis* (Rothschild, 1891) (locally known as parea), occurs in the Chatham Islands and was recently attributed species status based on morphometric evidence (Millener & Powlesland, 2001).

The New Zealand woodpigeon (*Hemiphaga n. novaeseelandiae*) is a large (510–850 g) forest bird (Clout, 1990; Higgins & Davies, 1996) that feeds on buds, leaves, flowers and fruits from a wide variety of forest tree and shrub species (McEwen, 1978; Higgins & Davies, 1996). It is the only extant and widespread disperser of fruits with large seeds in the New Zealand islands (Clout & Hay, 1989; Lee *et al.*, 1991; Kelly *et al.*, 2006). Individual pigeons occupy small home ranges (*c*. 1 ha) for short periods when food is readily available (Clout & Hay, 1989), but also travel tens of kilometres between seasonal feeding sites (Clout *et al.*, 1986, 1991; Millener & Powlesland, 2001; Harper, 2003; Powlesland *et al.*, 2007). Little is known about the ecology and behaviour of the extinct Norfolk Island pigeon (*H. n. spadicea*), but it is assumed that it exhibited traits similar to the mainland New Zealand and Chatham Islands pigeons (Tennyson & Martinson, 2006). All three taxa were once numerous in forested areas (Atkinson & Millener, 1991; Worthy & Holdaway, 2002), but were reduced drastically in the 18th and 19th centuries by hunting, deforestation and introduced mammalian predators, which ultimately resulted in the extinction of the Norfolk Island subspecies (Tennyson & Martinson, 2006).

Subfossil bones and fossils of pigeons in the New Zealand region include a small ground dove (*Gallicolumba norfolciensis*) native to Norfolk Island, which became extinct in the late 1800s after human contact (Worthy & Holdaway, 2002; Tennyson & Martinson, 2006), and at least two taxa from mainland New Zealand in Miocene time (Worthy *et al.*, 2009), but there are no other taxa known in the recent avifauna. The low representation of the Columbiformes in modern (and Holocene) New Zealand is in stark contrast with the diversity of Australia and New Caledonia, which possess 27 species in 11 genera and six species in five genera, respectively. A similar pattern of contrasting diversity among these areas is seen in many other bird groups, including kingfishers and raptors (Trewick & Gibb, 2010).

In this study, we generated mitochondrial sequence data in order to examine the population structure of *Hemiphaga*, to measure the scale of diversity within this small genus that is distributed among quite widely spaced oceanic islands, and to place the exchange between island populations in context alongside the evolutionary history of these birds in mainland New Zealand. We consider the scale of genetic diversity and spatial structuring of *Hemiphaga* and other flying birds in the New Zealand region with respect to biotic assembly.

MATERIALS AND METHODS

Sampling

The threat status of *H. n. novaeseelandiae* was recently reassessed and, although it has been changed from 'declining' in 2005 (Hitchmough *et al.*, 2007) to 'not threatened' in 2008 (Miskelly *et al.*, 2008) as a result of the national population increasing mostly due to intensive predator control (Clout *et al.*, 1995; Innes *et al.*, 2004), these birds are protected by law. They are also sensitive to disturbance as a result of capture and manipulations, so we avoided sampling live birds. However, *Hemiphaga* are prone to collision with vehicles and windows in urban areas and, due to their protected status, dead birds are routinely submitted to Department of Conservation (DoC) offices, where they are held in freezers. Our New Zealand sampling therefore reflects the relatively high densities of *Hemiphaga* in several urban areas and the proximity of DoC offices. Accordingly, these samples have little locality data associated with them, but they originated from within about 50 km of the DoC office from which they were sourced.

In this study, we used muscle tissue from frozen birds. For the population studies, 67 *H. n. novaeseelandiae* samples from mainland New Zealand were made available. Six tissue samples of *H. chathamensis* used in this study, which also originated from accidental deaths, were provided by the DoC Chatham Islands area office. Three toepad samples of the extinct Norfolk Island pigeon (*H. n. spadicea*) were kindly provided by the World Museum, Liverpool (D3544) and the Natural History Museum, New York (AMNH 268826 & AMNH 611718).

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These originated from aviary birds collected in the 1800s. Because *Hemiphaga* on the Kermadec Islands is represented by only a single subfossil bone, we were not able to include this extinct species in our study. The *L. antarcticus* (EBU45523M) tissue sample came from the Australian Museum, Sydney.

DNA extraction

For DNA extraction of the modern *Hemiphaga* and *Lopholaimus* samples, the GenElute Mammalian Genomic DNA kit (Sigma, Auckland, New Zealand) was used following the manufacturer's protocol. The DNA extractions of the extinct Norfolk Island pigeon samples were undertaken in a dedicated ancient DNA laboratory, remote from modern DNA facilities, using the Qiagen QiAMP DNA Minikit (Qiagen, Auckland, New Zealand), following standard procedures for ancient DNA (Willerslev & Cooper, 2005).

Polymerase chain reaction and sequencing

We used data from seven mitochondrial genes. Our primary data consisted of DNA sequences from cytochrome *b* (cyt *b*) and the D-loop region, which have both been shown to provide sufficient sequence variation to resolve population structure in pigeons and other birds (e.g. Wenink *et al.*, 1994; Johnson & Clayton, 2000; Butkauskas *et al.*, 2008; Zino *et al.*, 2008). D-loop sequences were then employed for our analyses of the radiation within *H. n. novaeseelandiae* and the genus *Hemiphaga*. Initially we amplified a 1291 bp fragment (for details of these and other primers see Appendix S1 in the Supporting Information), but excluded approximately 492 bp adjacent to the 12S rRNA gene because it could not be sequenced reliably due to the presence of five or more 52 bp tandem repeats. We also sequenced a 978 bp cyt *b* DNA region. In order to amplify and sequence the D-loop and cyt *b* fragments from DNA extractions of the extinct Norfolk Island pigeon samples, we designed *Hemiphaga*-specific primers using the program Oligo4 (Molecular Biology Insights, Inc., Cascade, CO, USA) to generate a series of short (*c.* 130–200 bp) overlapping fragments. For additional comparison of the different species of *Hemiphaga*, and to assess placement of the root using an outgroup, we obtained data from 12S, 16S, ND1, ND2 and cytochrome *c* oxidase subunit I (COI) for *H. chathamensis* using a combination of PCR primers. These data supplemented published sequences for the near relatives *H. n. novaeseelandiae*, *Gymnophaps albertisii* and *L. antarcticus* and further outgroup representatives *Ducula melanochroa* and *Ptilinopus luteovirens* (Gibb & Penny, 2010) (see Appendix S2 for GenBank accession numbers).

PCR amplifications for all samples were carried out in 20 μL volumes, using RedHot Taq (AbGene; ThermoScientific, Epsom, UK). The PCR thermal profile for the D-loop started with 94 °C for 2 min followed by 25 cycles of: 94 °C for 45 s, 50 °C for 30 s, and 72 °C for 30 s for all reactions. Cyt *b* reactions were run with 35 cycles and 2 min extension at 72 °C. The PCR thermal profile of ancient DNA samples for D-loop and cyt *b* was 94 °C for 2 min followed by 38 cycles of 94 °C for 30 s, 50 °C for 45 s, and 72 °C for 2 min for all reactions. PCR reactions using DNA of the extinct Norfolk Island subspecies were prepared in a dedicated ancient DNA laboratory. All PCR products were checked on 1% agarose gels. Each product was sequenced using standard protocols for the ABI Prism BigDye Terminator Ready Reaction Kit (Applied Biosystems, Mulgrave, Australia) and run on an ABI Prism 377 automated sequencer (Applied Biosystems). All sequences were edited using Sequencher software (Gene Codes Corporation, Ann Arbor, MI, USA; http://www.genecodes.com), and aligned using Se-Al v2.0a11 (Rambaut, 1996). All sequences were deposited at GenBank (GQ912532–912619 and HM165267–165270).

Phylogenetic and population analyses

We examined the placement of the root in *Hemiphaga* using combinations of sequence data and taxa. We used cyt *b* data (978 bp fragment) for a subset of *Hemiphaga* samples representing mainland New Zealand (six specimens), the Chatham Islands (three) and Norfolk Island (one) populations, plus two of the nearest living relatives as an outgroup (*L. antarcticus* and *G. albertisii*) (Pereira *et al.*, 2007). We ran separate analyses using a combined dataset of cyt *b* and D-loop sequences from *H. n. novaeseelandiae* (six specimens), *H. n. spadicea* (one), *H. chathamensis* (three) and *L. antarcticus* (one), and a six-gene dataset (12S, 16S, ND1, ND2, COI, cyt *b*) with *H. n. novaeseelandiae*, *H. chathamensis*, *D. melanochroa*, *G. albertisii*, *L. antarcticus* and *P. luteovirens* (see Appendix S2). MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) was used to implement Bayesian analyses using models of DNA evolution indicated using jModelTest 3.5 (Guindon & Gascuel, 2003; Posada, 2008). However, we encompassed the different models selected using alternative criteria in jModelTest by repeating the analyses using either GTR+I+Γ or HKY+I. For each dataset, replicate analyses were employed to ensure convergence, each consisting of two independent Markov chain Monte Carlo (MCMC) runs of 6–10 million generations, applying a burn-in of 10–20%, after consideration of output statistics. We referred to the average standard deviation of split frequencies and potential scale-reduction factors, which were accepted if < 0.01 and at or near 1.000, respectively (Gelman & Rubin, 1992; Ronquist *et al.*, 2005). For analysis of multigene data with MrBayes 3.1.2, we partitioned the dataset by gene and unlinked values of model parameters. Tree topologies from alternative methods and models of DNA evolution were scrutinized and node support statistics compared. To further examine node support in the cyt *b* tree, we used maximum parsimony (MP) analysis implemented in paup* (Swofford, 1998) with stepwise addition of the starting tree, tree bisection–reconnection, all characters given equal weights and bootstrapping with 1000 replicates.

Haplotype diversity (*h*), nucleotide diversity (π, Nei, 1987), Tajima's *D* (Tajima, 1989) and the average number of

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nucleotide differences (k) were calculated using DnaSP v.4.0 (Rozas *et al.*, 2003). Tajima's D statistic (Tajima, 1989) was developed to distinguish homologous DNA sequences evolving in a non-random manner (i.e. lack of neutrality). However, it has been shown that for neutral markers such as the mitochondrial DNA (mtDNA) D-loop, the statistic provides a useful indicator of population range expansion and exchange (Ray *et al.*, 2003; Wegmann *et al.*, 2006). We calculated pairwise F_{ST} values for the nine regional populations using Arlequin v.3.0 (Excoffier *et al.*, 2005).

Geographical structure was investigated using a parsimony haplotype network of mainland New Zealand *Hemiphaga* D-loop sequences constructed with the program tcs 1.21 (Clement *et al.*, 2000). For this analysis, New Zealand was divided into three main sampling areas, north, central and southern, each with three subsamples (Fig. 3). More detailed structuring of populations was not possible because of the lack of precise location data of the samples (see Sampling). The analysis was run using a 95% connection limit.

An unrooted neighbour-net network was constructed with D-loop sequences using SplitsTree 4.8 (Huson & Bryant, 2006) with default settings to show the relationships within the genus *Hemiphaga*, and the extent of conflicting signal among these data. In population studies where sequences are naturally very similar to each other, it is necessary to provide evidence that the tree found is the shortest possible under parsimony criteria. We employed the program MinMax Squeeze (Holland *et al.*, 2005), which compares the shortest tree found with the shortest tree possible on the data, to determine this with the *H. n. novaeseelandiae* population dataset.

RESULTS

Preliminary Bayesian analysis using six mitochondrial genes and an outgroup representing four genera confirms the placement of *Hemiphaga* nearer to *Lopholaimus* and *Gymnophaps* than to *Ducula* and *Ptilinopus* (Fig. 4a). A tentative tree hypothesis based on MP and Bayesian analyses returned trees for cyt *b* that

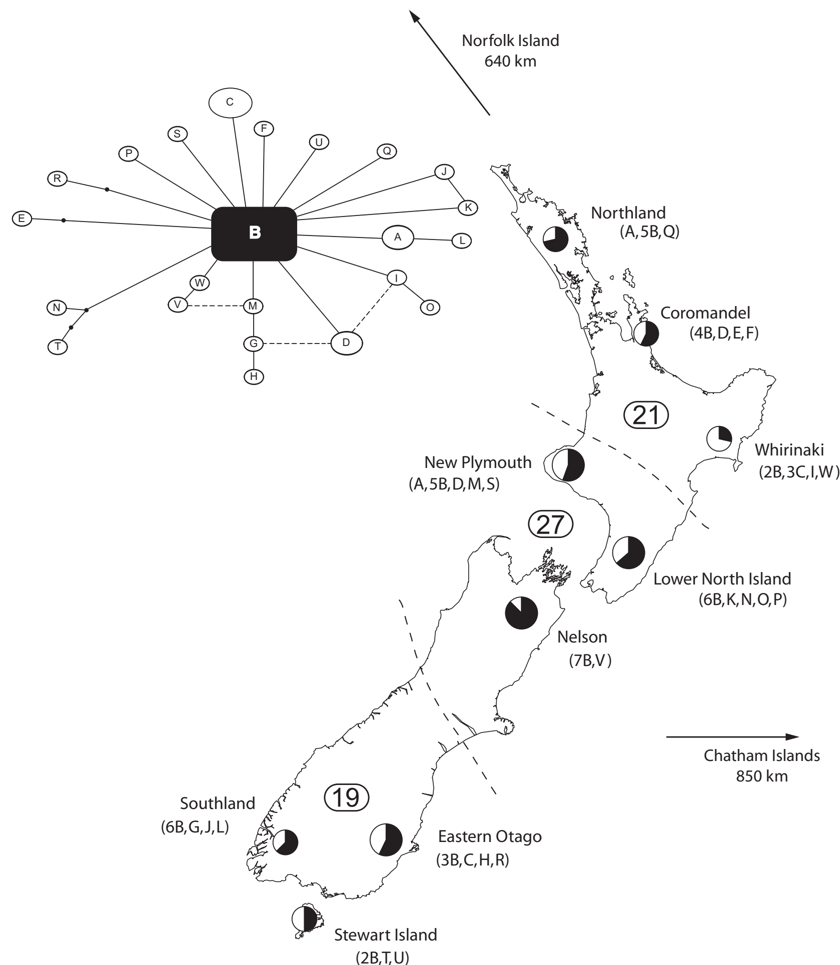

Figure 3 Map of New Zealand showing the three main sampling areas, divided by dotted horizontal lines. Numbers in ovals represent the summed sample size per main sampling area. Letters represent different haplotypes of *Hemiphaga novaeseelandiae novaeseelandiae* within each subpopulation (see inset haplotype network and Table 1). Pie charts depict the frequency of the most common haplotype B (black) per subpopulation in the mainland New Zealand woodpigeon (*H. n. novaeseelandiae)* population.

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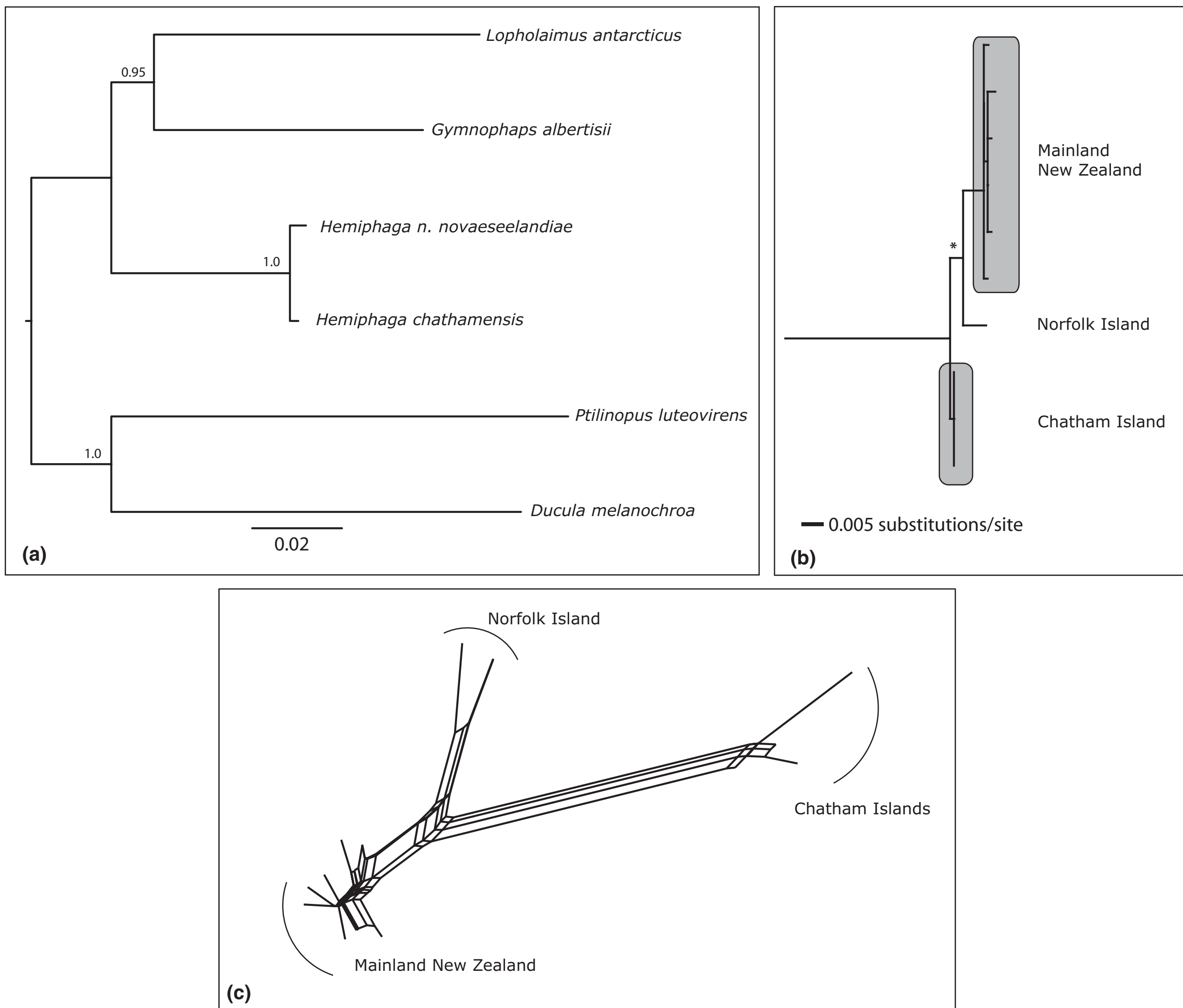

Figure 4 (a) A six-gene Bayesian tree of *Hemiphaga novaeseelandiae novaeseelandiae*, *H. chathamensis* and their closest allies; values on branches are Bayesian posterior probabilities. (b) A cytochrome *b* tree of the genus *Hemiphaga* rooted with closest sister taxon *Lopholaimus* (not shown); the asterisk denotes the node with available values: 0.55 Bayesian posterior probability and 0.75 maximum parsimony bootstrap value (1000 replicates). (c) An unrooted D-loop neighbour-net splitsgraph of the genus *Hemiphaga* depicting the conflict in the dataset.

consistently placed the root between *H. chathamensis* and the two *H. novaeseelandiae* lineages, making New Zealand and Norfolk Island lineages monophyletic (Fig. 4b). A tree of the same topology was obtained using a combined cyt *b*/D-loop dataset (not shown). Not surprisingly, node support for the split between mainland New Zealand and Norfolk Island *Hemiphaga* was intermediate (MP 0.78, MrBayes 0.55) given the disparity between low ingroup diversity and distance to the nearest common ancestor. This tentative rooting is consistent with the current taxonomic treatment of the genus and thus with the current morphological evidence and inference from genetic distance data. An unrooted neighbour-net network (Fig. 4c) of *Hemiphaga* D-loop data revealed a low level of conflicting signal within the ingroup and a relatively long branch between *H. chathamensis* and the pairing of *H. novaeseelandiae* subspecies, and this is consistent with placement of the root between the two species.

We assessed the likely time frame of *Hemiphaga* diversification by comparison of genetic distances with published studies of other birds. All genetic distances among *Hemiphaga* samples were low by comparison with published values for other birds. Indeed, we found no sequence divergence at the COI locus used widely in 'DNA barcoding' studies (e.g. Hebert *et al.*, 2004; Kerr *et al.*, 2007).

The Chatham Islands population shares no haplotypes (D-loop or cyt *b*) with the mainland New Zealand population. With the present sampling, the maximum uncorrected genetic distance in D-loop among the Chatham haplotypes is 0.005, and there is a mean uncorrected genetic distance of 0.028 to the mainland species. Cyt *b* sequences differed between the

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Chatham Islands and mainland New Zealand by 0.012, more or less identical to the *c.* 0.01 difference reported by Millener & Powlesland (2001).

We were also able to obtain D-loop sequences from three specimens of the extinct *H. n. spadicea* from Norfolk Island, which provide valuable comparison with the mainland New Zealand data. Although diversity is not expected to be high on a small island, the Norfolk Island specimens express two different haplotypes in the D-loop fragment. They show mean uncorrected genetic distances of 0.014 to mainland New Zealand specimens and 0.029 to the Chatham Island species, implying a younger split from New Zealand than for the Chathams' population. Additionally, we sequenced the cyt *b* fragment for one Norfolk Island specimen. The mean uncorrected genetic distance to the Chatham Island species was 0.011 and 0.013 to the mainland species.

Comparison of D-loop sequences (733 bp) from 67 specimens of *H. n. novaeseelandiae* revealed 23 different haplotypes within mainland New Zealand, of which 19 were singletons; additionally, four different haplotypes from the Chatham Islands and two from Norfolk Island were found (Table 1). A statistical parsimony network was generated in TCS containing all mainland New Zealand D-loop sequences (inset, Fig. 3). Among the mainland New Zealand samples, the most common haplotype (B) was found at least twice in each of the nine sampled subpopulations, but only three other haplotypes (A, C, D) were found in more than one location (Fig. 3). The relative abundance of the common haplotype B, compared with rare haplotypes in each subpopulation, indicates the dominance of haplotype B. Haplotype C was found four times: three times in a northern (Whirinaki) and once in a southern (Eastern Otago) subpopulation. Haplotypes A and D were found twice each, in northern and central populations. Nineteen other haplotypes were encountered just once each, and most of these differed from the common haplotype B by just one nucleotide substitution (inset, Fig. 3). Even directly connected haplotypes show no spatial distribution (e.g. haplotypes M, G and H occur in New Plymouth, Southland and Eastern Otago; Fig. 3). Coalescent theory predicts that older (interior) haplotypes are likely to be more common than derived (tip) haplotypes. Tip haplotypes are defined as those connected to only one other haplotype, whereas interior haplotypes are connected to multiple haplotypes (Crandall & Templeton, 1993). In the available dataset, the B haplotype is the most common and is connected to multiple haplotypes (inset, Fig. 3).

Populations of *H. n. novaeseelandiae* displayed very low levels of DNA nucleotide diversity within mainland New Zealand (Table 2). The sequences of the northern area had the highest level of haplotype and nucleotide diversity, followed by the southern and central populations (Table 2). Pairwise F_{ST} comparisons (results not shown) revealed no significant difference in the genetic composition of the nine regional sample locations in *Hemiphaga* in mainland New Zealand. Tajima *D* tests (Tajima, 1989) for the three separate mainland New Zealand populations of *H. n. novaeseelandiae* and the complete mainland New Zealand dataset were consistent with range expansion with high levels of migration among demes (Table 2). Negative Tajima's *D* statistics for the different populations indicate an excess of sites with low-frequency polymorphisms, that is, the population has yet to reach equilibrium (Tajima, 1989).

Analyses with MinMax Squeeze (Holland *et al.*, 2005) demonstrated that no shorter tree was possible for the mainland New Zealand D-loop sequence data, or for the data that included sequences from Norfolk Island and the Chatham Islands. For the mainland New Zealand samples, this means that the parsimony tree is almost certainly the maximum

Table 1 D-loop haplotype frequency in *Hemiphaga* populations and regions of mainland New Zealand.

Population	Region	n	N_{haps}	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	a	b	c	d	e	f
Northland	N	7	3	1	5															1												
Coromandel	N	7	4		4		1	1	1																							
Whirinaki	N	7	4		2	3						1														1						
New Plymouth	C	9	5	1	5		1									1						1										
Lower North Island	C	10	5		6									1			1	1	1													
Nelson/Blenheim	C	8	2		7																				1							
Eastern Otago	S	6	4		3	1					1										1											
Southland	S	9	4		6					1			1		1																	
Stewart Island	S	4	3		2																		1	1								
Northern	N	21	9	1	11	3	1	1	1			1								1						1						
Central	C	27	10	1	18		1							1		1	1	1	1			1			1							
Southern	S	19	9		11	1				1	1		1		1						1		1	1								
All New Zealand		67		2	40	4	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1						
Chatham Islands		6	4																								2	2	1	1		
Norfolk Island		3	2																												2	1

n = Number of individuals sequenced per population; N_{haps} = number of different haplotypes within sampled areas; haplotype codes as in Fig. 3. A total of 67 mainland New Zealand (*H. novaeseelandiae novaeseelandiae*), six Chatham Islands (*H. chathamensis*) and three Norfolk Island (*H. novaeseelandiae spadicea*) birds were assessed.

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Table 2 DNA variation and haplotype diversity within and between regional samples of *Hemiphaga novaeseelandiae novaeseelandiae* in New Zealand, with the sample size for each region (n), number of observed haplotypes (N_{haps}), average number of nucleotide differences (k), nucleotide diversity ($\pi \times 10^{-3}$), number of polymorphic sites (S), Tajima's D ($P < 0.05$) and haplotype diversity (h).

Area	n	N_{haps}	k	π (± SD)	S	Tajima's D	h
Northern	21	9	1.011	1.55 (± 0.34)	8	–1.815	0.719
Central	27	10	0.872	1.34 (± 0.35)	9	–1.996	0.564
Southern	19	9	0.936	1.44 (± 0.43)	10	–2.126	0.614
Total population	67	23	0.925	1.42 (± 0.36)	16	–2.141	0.623
Northern/Central			0.934	1.43 (± 0.36)			
Central/Southern			0.973	1.38 (± 0.38)			
Northern/Southern			0.967	1.48 (± 0.39)			

likelihood tree because the tree consists almost entirely of sequences linked by no more than a single change, and in such cases the parsimony tree is the maximum likelihood estimator (Steel & Penny, 2000).

DISCUSSION

The large forest pigeon *H. n. novaeseelandiae* is distributed throughout mainland New Zealand where suitable habitat exists today. We found that genetic diversity at the mtDNA D-loop locus lacks spatial structure. The pattern of low diversity, shallow coalesence and high connectivity among populations of *Hemiphaga* within mainland New Zealand is indicative of a recent bottleneck and rapid recent range expansion. The geophysical phenomenon most likely to have resulted in substantial population reductions and thus genetic bottleneck that could yield this pattern is Pleistocene climate cooling/aridification during global glacial phases. Similar patterns on a larger spatial scale have been identified among birds in Europe (Merilä *et al.*, 1997), North America (Zink, 1996) and Australia (Joseph & Wilke, 2007). In New Zealand, palynological studies indicate that the primary habitat (forest) of *Hemiphaga* was much reduced in total area and distribution during the Last Glacial Maximum, and probably also during prior glaciations (McGlone, 1985; Alloway *et al.*, 2007). The most extensive forest patches are thought to have been in northern New Zealand (McGlone *et al.*, 2001; Alloway *et al.*, 2007), and this might explain the slightly higher haplotype diversity in northern populations apparent in our sample (Table 2). The modern widespread distribution of *Hemiphaga* in mainland New Zealand (despite recent human interference) confirms subsequent range expansion, and the near continuous extent of forest habitat in New Zealand immediately prior to human contact (Trewick & Morgan-Richards, 2009) would have provided ample opportunity for gene flow throughout and among the three main islands, as these birds are not philopatric. Field studies confirm that *Hemiphaga* pigeons are highly effective flyers that regularly travel substantial distances to reach their food resources, including crossing sea straits between islands of mainland New Zealand (Powlesland *et al.*, 2007).

This pattern of population structure is not unique to *Hemiphaga* among New Zealand birds, suggesting a more general response of expansion out of refugia in the wake of expanding forest habitat. Similar low nucleotide diversity combined with high haplotype diversity is documented in the kokako (*Callaeas cinerea*, Murphy *et al.*, 2006) and New Zealand robin (*Petroica australis*, Miller & Lambert, 2006). On the other hand, kiwi (*Apteryx*), a group of ground-dwelling birds, comprises deeper phylogeographic and taxonomic diversity consistent with regional persistence of populations through the Pleistocene (Baker *et al.*, 1995; Burbidge *et al.*, 2003), perhaps explained by a lesser dependence on high forest.

Although the process of population retraction and expansion in New Zealand could have occurred repeatedly throughout the Pleistocene, we see no signature of earlier episodes or survival of multiple mainland lineages or discrete populations through the Pleistocene. There is, however, spatial structuring of genetic diversity among the more widely spaced islands (New Zealand, the Chatham Islands, Norfolk Island) even though total genetic diversity is still very low. Colonization of the Chatham Islands cannot have occurred before 4 Ma, as geological evidence indicates that the Chatham archipelago was completely submerged prior to this time (Campbell *et al.*, 2006; Campbell & Hutching, 2007; Trewick *et al.*, 2007). This nevertheless provides ample time for the morphological and genetic separation of *H. chathamensis*. The D-loop variation we found in a small Chatham Island sample indicates that this species maintained relatively high genetic diversity on this small archipelago (970 km^2 total land area) despite recent population decline. This population went through at least one well documented bottleneck in the 1980s, with a maximum of 50 birds surviving mostly in a small area of southern Chatham Island (Grant *et al.*, 1997). Norfolk Island also formed in the late Pliocene (3.2–2.4 Ma) by intra-plate volcanism (Johnson, 1989), so here, as with the Chatham Islands, the biota must have assembled predominantly through recent colonization over water. The slightly closer affinity of the Norfolk Island pigeon to the New Zealand taxon (compared with the Chatham birds) is consistent with a more recent exchange between mainland New Zealand and Norfolk Island, but it is not possible to determine the direction of exchange with the present data.

Although the Chatham Islands and Norfolk Island are Pliocene in age, colonization of these islands by *Hemiphaga*

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could have occurred at any time after their formation and the establishment of suitable vegetation. These islands are, and have always been, separated from mainland New Zealand by more than 600 km of ocean, yet both have been colonized during their short history by a range of forest birds, including *Cyanoramphus* parakeet, *Nestor* parrot, *Petroica* robin, *Chrysococcyx* cuckoo, *Gerygone* warbler and *Zosterops* silvereyes (Clements, 2007). The Kermadec Islands, which were also once inhabited by *Hemiphaga*, are even further (> 900 km) from New Zealand, and their general lack of bird endemicity has been ascribed to extinction through repeated, violent volcanic eruptions rather than failure of colonization (Worthy & Holdaway, 2002). Each island population represents the descendants of an independent oversea colonization event, replicated by many taxa. Clearly, dispersal over inhospitable habitat is not rare in biogeographic terms.

For *Hemiphaga*, episodes of dispersal between mainland New Zealand, the Chatham Islands and Norfolk Island are likely to have occurred in the Pleistocene rather than earlier in the Pliocene. We found maximum genetic distances among *Hemiphaga* of 1.3% at the cyt *b* locus, which is less than that found in the same region among *Cyanoramphus* parakeets (max. 2.7%, Boon *et al.*, 2001b, 2008) and *Petroica* robins (max. 8.7%, Miller & Lambert, 2006). Even within mainland New Zealand, cyt *b* genetic diversity of *Petroica* robins is higher (2.7%) than that found in all *Hemiphaga* (Miller & Lambert, 2006). By comparison, a study of doves in North America, known to have been influenced by Pleistocene climate cycling, found intraspecific cyt *b* divergence up to 0.1%, and 0.9% between species (Johnson & Clayton, 2000). This has been interpreted as indicating a phylogenetic split within the past 450,000 years (based on a 2% molecular clock calibration; Johnson & Clayton, 2000). Not surprisingly, we found inter- and intra-specific divergences within *Hemiphaga* at the D-loop locus to be slightly higher than for cyt *b*, with a maximum of 2.9% and 1.4%, respectively. Again, *Petroica* robins have a higher genetic diversity in D-loop within New Zealand (max. 6.4%) and much higher (22.6%) between mainland New Zealand and Chatham Island species (Miller & Lambert, 2006). The same is apparent in *Cyanoramphus* parakeets, with an intraspecific divergence in mainland New Zealand of 3.11% and a maximal inter-specific divergence of 9.82% (Boon *et al.*, 2001a,b). Furthermore, at the COI mtDNA locus, where divergence within bird species is documented as ranging from 0.4% to 5.4% (e.g. Aliabadian *et al.*, 2009; Kerr *et al.*, 2009; Johnsen *et al.*, 2010) with a commonly employed threshold for maximum intraspecific divergence of 2.5% (Hebert *et al.*, 2004), we found no differences between the two *Hemiphaga* species. Together with the young age of the islands, our data indicate extensive mixing in New Zealand and very shallow genetic distances overall, and reveal a pattern of recent widespread dispersal.

Although the depth of diversification within *Hemiphaga* does not inform directly on the timing of origin of the lineage in the New Zealand region, the fact that the entire extant diversity is distributed across islands spanning 1200 km of ocean is revealing. Clearly, *Hemiphaga* has retained high mobility even over wide expanses of sea, and has suffered extensive extinction in recent times. The success of *Hemiphaga* in terms of its persistence must rest partly on this ability, so we are left with the conundrum of why the genus is not represented by more and deeper diversity in the New Zealand region and/or further afield in Australia, New Caledonia or other Pacific Islands. Similarly, why has New Zealand no other extant native pigeons, when other genera exist as close as Norfolk Island? The lack of *Hemiphaga* elsewhere might be explained by extinction following human habitat modification or earlier replacement by other dove radiations, including, for example, *Ptilonopus* and *Ducula* (Steadman, 1997, 2006; Gibbs *et al.*, 2001). Molecular phylogenetics indicate that *Hemiphaga* forms a clade with other species-poor genera (*Lopholaimus*, *Gymnophaps*) but is allied to species-rich genera in Melanesia and Polynesia (*Ptilonopus*, *Ducula*) (Goodwin, 1960; Johnson, 2004; Pereira *et al.*, 2007; Gibb & Penny, 2010). The lack of diversity in *Hemiphaga* and allies may be due to lineage pruning, but it is not possible to determine the timing of this process. Any biogeographic inference drawn from the long *Hemiphaga* branch must be tenuous, because it is not possible to exclude (or estimate the likelihood of) a close relative having existed recently outside the region. Even the recent discovery of a pigeon fossil (single humerus) from early-mid Miocene (19–16 Ma) New Zealand, that may be allied to the *Hemiphaga–Lopholaimus* group (Worthy *et al.*, 2009), does not demonstrate continued occupation of New Zealand by the lineage since that time. Instead, along with other fossils from the Miocene representing taxa not present in New Zealand now, it suggests subsequent extinction of many lineages. Given that the New Zealand avifauna (and biota in general) has experienced substantial extinction and has been subjected to many arrivals during that time frame, we cannot exclude the possibility that there have been repeated arrivals and extinctions of pigeons, including members of this lineage. Indeed, this scenario may help reconcile the various patterns of taxon distribution and endemicity observed among the (avi-)fauna (Fig. 2).

It might be expected that, when examining the New Zealand avifauna, some dominant pattern of distribution and endemicity (indicating a dominant process) would emerge, but this is not the case. Overlapping but incongruent distribution patterns in the New Zealand area might be best explained by repeated colonization in concert with extirpation in various areas. Extinction of lineages (phylogenetic relatives) at any time prior to the present tends to yield increasingly narrow endemism of remaining lineages and increasingly lengthy branches in phylogenetic trees (Trewick & Gibb, 2010). This combination of localized taxa and deep-branching phylogenies, especially when the only remaining taxa are found on an island, can lead to an inference of ancient isolation. However, it is obvious that this pattern is deceptive and open to misinterpretation; understanding the evolutionary history of New Zealand's supposedly ancient biota requires a better understanding

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of dispersal, colonization and extinction governing its assembly.

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SUPPORTING INFORMATION

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

Appendix S1 Primers used in this study.
Appendix S2 Additional species and genes included in this study.

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