Complete genomes of two extinct New Zealand passerines show responses to climate fluctuations but no evidence for genomic erosion prior to extinction

Nicolas Dussex[1,2], Johanna von Seth[1,3], Michael Knapp[2], Olga Kardailsky[2], Bruce C. Robertson[4] and Love Dalén[1]

[1]Department of Bioinformatics and Genetics, Swedish Museum of Natural History, Box 50007, Stockholm 10405, Sweden
[2]Department of Anatomy, University of Otago, PO Box 913, Dunedin 9016, New Zealand
[3]Department of Zoology, Stockholm University, Stockholm 10691, Sweden
[4]Department of Zoology, University of Otago, PO Box 56, Dunedin 9016, New Zealand

ND, 0000-0002-9179-8593; MK, 0000-0002-0937-5664; LD, 0000-0001-8270-7613

Human intervention, pre-human climate change (or a combination of both), as well as genetic effects, contribute to species extinctions. While many species from oceanic islands have gone extinct due to direct human impacts, the effects of pre-human climate change and human settlement on the genomic diversity of insular species and the role that loss of genomic diversity played in their extinctions remains largely unexplored. To address this question, we sequenced whole genomes of two extinct New Zealand passerines, the huia (*Heteralocha acutirostris*) and South Island kōkako (*Callaeas cinereus*). Both species showed similar demographic trajectories throughout the Pleistocene. However, the South Island kōkako continued to decline after the last glaciation, while the huia experienced some recovery. Moreover, there was no indication of inbreeding resulting from recent mating among closely related individuals in either species. This latter result indicates that population fragmentation associated with forest clearing by Maōri may not have been strong enough to lead to an increase in inbreeding and exposure to genomic erosion. While genomic erosion may not have directly contributed to their extinctions, further habitat fragmentation and the introduction of mammalian predators by Europeans may have been an important driver of extinction in huia and South Island kōkako.

1. Introduction

Species declines and extinctions are complex and multifactorial [1,2]. Two paradigms have been proposed in conservation biology [3]. The first paradigm focuses on how extrinsic factors, such as climate fluctuations or human activities, contribute to population decline and extinction. While the role of humans in the extinction of species over the past 500 years is well recognized [4], past climate changes were also major drivers of population declines and extinctions [5,6]. However, the relative impact of human activities and climate on biodiversity are still intensely debated and these impacts may well vary among species [1,2].

As a consequence of declines in population size and geographical distribution from these extrinsic factors, small and isolated populations can then be exposed to intrinsic threats. This is why a second paradigm, which instead focuses on intrinsic demographic and genetic effects, is also central to conservation biology [3]. The role that detrimental genetic effects play in the long-term persistence of populations is well known [7,8]. Such detrimental effects can be

referred to as genomic erosion, which reduces species viability through drift, inbreeding and increase in genetic load [7,9]. Recent empirical data on extinct woolly mammoths (*Mammuthus primigenius*; [10,11]), endangered gorilla (*Gorilla beringei* sp.; [12]) and crested ibis (*Nipponia nippon*; [13]) have shown that severe population declines expose populations to genomic erosion. Moreover, species that have experienced long-term, pre-human decline in effective population size (N_e) may be more vulnerable to human-induced declines and to genomic erosion as was suggested for the critically endangered Sumatran rhinoceros (*Dicerorhinus sumatrensis*; [14]). Similarly, several avian species on the IUCN Red List of Threatened Species have experienced long-term, pre-human population reductions N_e [15], further highlighting the link between long-term population decline and higher exposure to genomic erosion.

Species from oceanic islands recently colonized by humans are particularly vulnerable to human disturbance due to their small census size and N_e and their limited ability to alter their range in response to anthropogenic pressures [9]. Moreover, island populations have experienced higher extinction rates compared with mainland species [16]. In fact, even though islands represent only 5.3% of the surface of the earth, they have hosted 75% of the known vertebrate extinctions over the past 500 years [17] due to both habitat modification, over-hunting and the introduction of non-native mammalian predators [18].

As a case in point, New Zealand endemic fauna has experienced two major extinction events in association with Maōri (*ca* 1360 CE; [19]) and European settlement (*ca* 1800 CE; [20]). These extinctions have been attributed to direct human interference such as habitat destruction [18] or hunting (e.g. moa, [21]; *Megadyptes waitaha* [22]). Moreover, because New Zealand endemics evolved in the absence of mammalian predators and because a large proportion of its avifauna is flightless, the accidental or deliberate introduction of mammals has been an important driver of species decline [20]. The colonization of New Zealand by the ancestors of its endemic species from a small number of founders, their evolution in a confined geographical area as well as pre-human climate fluctuations may have reduced the genetic diversity of species well before human settlement (e.g. kea, *Nestor notabilis*; [15,23]). It is thus possible that New Zealand avian species characterized by historically low genetic diversity may have been more easily exposed to genomic erosion following the human-induced declines of the last 800 years [24]. Yet, to date, the effect of pre-human climate fluctuations and of Maōri settlement on the genome-wide diversity of insular avian species in New Zealand remains largely unexplored. Understanding these effects would allow us to determine whether genomic erosion contributed to their extinction.

Here, we examine the long-term response to climate change and the recent effects of human settlement on the genome-wide diversity of two extinct forest passerines from the Callaeidae family or New Zealand wattlebirds [25,26], the huia (*Heteralocha acutirostris*) and South Island kōkako (*Callaeas cinereus*). Huia were common throughout the North Island but went extinct in 1907, whereas South Island kōkako were only found in the South Island and were declared extinct in the 1960s [27]. Using demographic reconstructions, we show that these species had similar responses to habitat change during the last glaciation.

Moreover, inbreeding coefficients were not consistent with genomic erosion close to the time of extinction. Our data thus suggest that further habitat fragmentation and the introduction of mammalian predators by Europeans may have been the main drivers of the extinction of these two species.

2. Material and methods

(a) DNA extraction, library preparation and sequencing
We extracted DNA from toepads for one huia (*Heteralocha acutirostris*) and one South Island kōkako (*Callaeas cinereus*) collected in 1886 and 1849, respectively (electronic supplementary material, table S1). We built one deep-sequencing library per bird following Meyer & Kircher [28] and sequenced them on HiseqX lanes (see electronic supplementary material). All laboratory procedures were conducted in a dedicated historical DNA laboratory. We took appropriate precautions to minimize the risk of contamination of historical samples [29].

(b) Data processing
After trimming adapters, we mapped the raw genomic data to a de novo assembly for the North Island kōkako (*Callaeas wilsoni*; https://b10k.genomics.cn/) using BWA 0.7.13 aln [30]. We removed duplicates, realigned bam files around indels and filtered them for mapping quality. We then called variants, filtered them for base quality, depth and proximity to indels. Finally, we masked repeats and CpG sites from bam and vcf files to limit possible biases from DNA damage (see electronic supplementary material).

(c) Data analysis
We first used the Pairwise Sequentially Markovian Coalescent (PSMC 0.6.5) [31] to infer temporal changes in the effective population sizes (N_e) of huia and South Island kōkako. Secondly, we used mlRho v.2.7 [32] to estimate population mutation rates (θ), which approximates expected heterozygosity under the infinite sites model. Finally, we identified runs of homozygosity (ROH) and estimated individual inbreeding coefficients (F_{ROH}) using a sliding-window approach [33] (see electronic supplementary material).

3. Results

Demographic reconstruction based on 10× and 14× coverage genomes in huia and South Island kōkako, respectively (electronic supplementary material, figure S1 and table S1) and corrected for low coverage showed broadly similar N_e trajectories (figure 1; electronic supplementary material, figures S2 and S3). However, while huia showed a nearly stable N_e between 1 Myr and 100 kyr BP, South Island kōkako experienced a severe decline dating back to approximately 700 kyr BP. Both species experienced a 2- to 10-fold decline in N_e coinciding with the last glaciation approximately 60–70 kyr BP (figure 1). While the N_e of both species was estimated at approximately 6000 at the Last Glacial Maximum (LGM) approximately 20 kyr BP, huia N_e seems to have increased slightly to approximately 8000 after the LGM, whereas South Island kōkako N_e declined to less than 2000 (figure 1).

Both species showed similar levels of genome-wide heterozygosity, estimated at 0.94–1 SNPs per thousand base pairs (table 1). While the inbreeding coefficient was higher
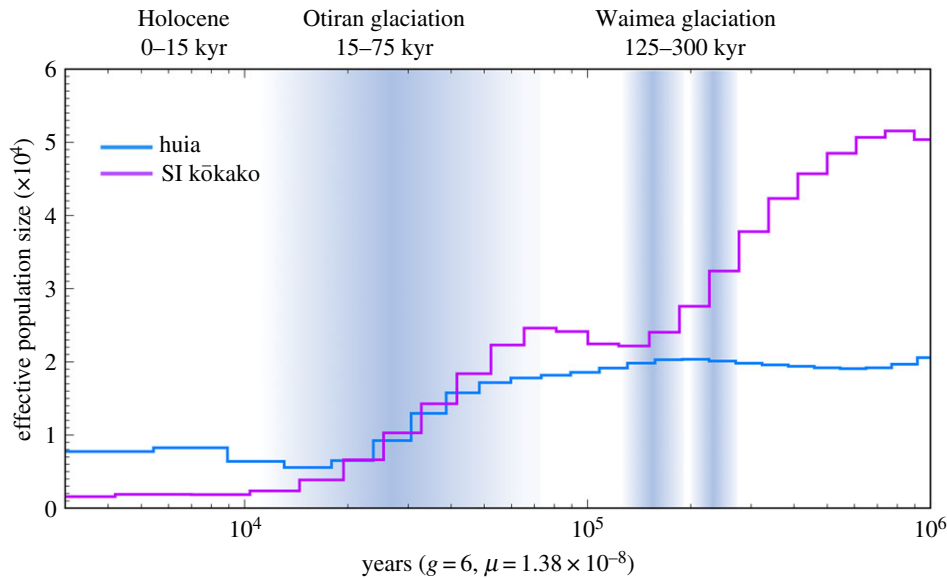
Figure 1. PSMC for huia and South Island kōkako scaled using a generation time of 6 years [34,35], a substitution rate of 1.38×10^{-8} substitution/site/generation inferred from [36] and a uniform false negative rate (uFNR) of 40%. (Online version in colour.)

Table 1. Heterozygosity per 1000 bp (θ) and inbreeding estimates (F_{ROH}). θ = population mutation rate which approximates heterozygosity under the infinite sites model.

species	θ	θ (95% CI)	$F_{ROH} >$ 100 kb	$F_{ROH} >$ 1 Mb
huia	0.944	0.942–0.947	0.187	0
South Island kōkako	1	0.998–1	0.319	0
rifleman	1.67[a]	n.a.	n.a.	n.a.

[a]Estimated as SNP rate per 10^3 bases [37].

in South Island kōkako ($F_{ROH} = 0.32$) compared to huia ($F_{ROH} = 0.19$), the majority of the ROH identified were less than 1 Mb in both species (figure 2).

4. Discussion

Using complete genomes, we examined the long-term response to climate change and tested the hypothesis that habitat modification associated with Māori settlement impacted the genome-wide diversity of huia and South Island kōkako prior to their extinction.

Demographic reconstructions indicated very similar responses to glaciations between species with a reduction in N_e shortly after the onset of the last glaciation and little to no recovery at the end of the LGM approximately 14–22 kyr BP [38]. This pattern is very similar to another forest passerine, the rifleman (*Acanthisitta chloris*; [15]). However, the rifleman had a much higher $N_e > 20\,000$ at the end of the LGM [15]. While the signal of long-term population decline could indicate limited migration between subpopulations [39], this decline in N_e is consistent with a severe reduction in forest cover in the southern North Island and the South Island [40,41]. With the exception of extensive forest tracts mostly confined to the northern parts of the North Island and some isolated forest patches in the South Island (figure 2; [38,42]), most of New Zealand's vegetation was characterized by extensive grassland and shrublands at

the LGM [38,40,41]. Being both forest species, huia and South Island kōkako were thus most likely restricted to such forest refugia, as was the case for other forest species [43–45]. Yet, it is unclear why both species had a similar N_e at the LGM while the forest refugium was smaller in the South Island compared with the North Island [40] and why South Island kōkako had a lower N_e compared to huia after the LGM when both species should have experienced a similar population expansion. However, this latter difference in N_e may be due to the limitation of the PSMC to estimate recent N_e (less than 10 000 BP) [31,46].

While fossil preservation can be affected by temperature, humidity or acidity, an abundance of fossils from the Early to Late Holocene deposits of forest species (e.g. kaka, *N. meridionalis*; pigeon, *Hemiphaga novaeseelandiae*; parakeets, *Cyanoramphus* sp.; [47,48]) suggests that demographic expansion occurred as species tracked their habitat after the LGM [40,41]. Conversely, open-habitat species like the alpine kea (*N. notabilis*) seem to have experienced a decline in N_e or at least lack of post-glacial demographic recovery, as their range became restricted to alpine areas [15,23]. Because both huia and South Island kōkako were forest dwellers, they should have also experienced population expansion after the LGM. In fact, N_e estimates of approximately 30–90 000 huia prior to human arrival in New Zealand based on rapidly evolving mitochondrial sequences suggest that post-glacial recovery could have occurred in these species [49]. However, because the number of recombination events is limited over the recent past and because of the lag time between demographic expansion and increase in N_e, PSMC lacks the power to detect recent population fluctuations (less than 10 000 BP) [31,46]. Moreover, the reliability of N_e estimates can be affected by coverage, the proportion of missing data and the uncertainty about substitution rates (electronic supplementary material, figures S2 and S3; [31,46]). These estimates should be thus interpreted with caution. Nevertheless, in spite of these limitations, the overall long-term decrease in N_e in both species is consistent with that of extant species classified as endangered on the IUCN Red List of Threatened Species [15,50]. Conversely, the rifleman
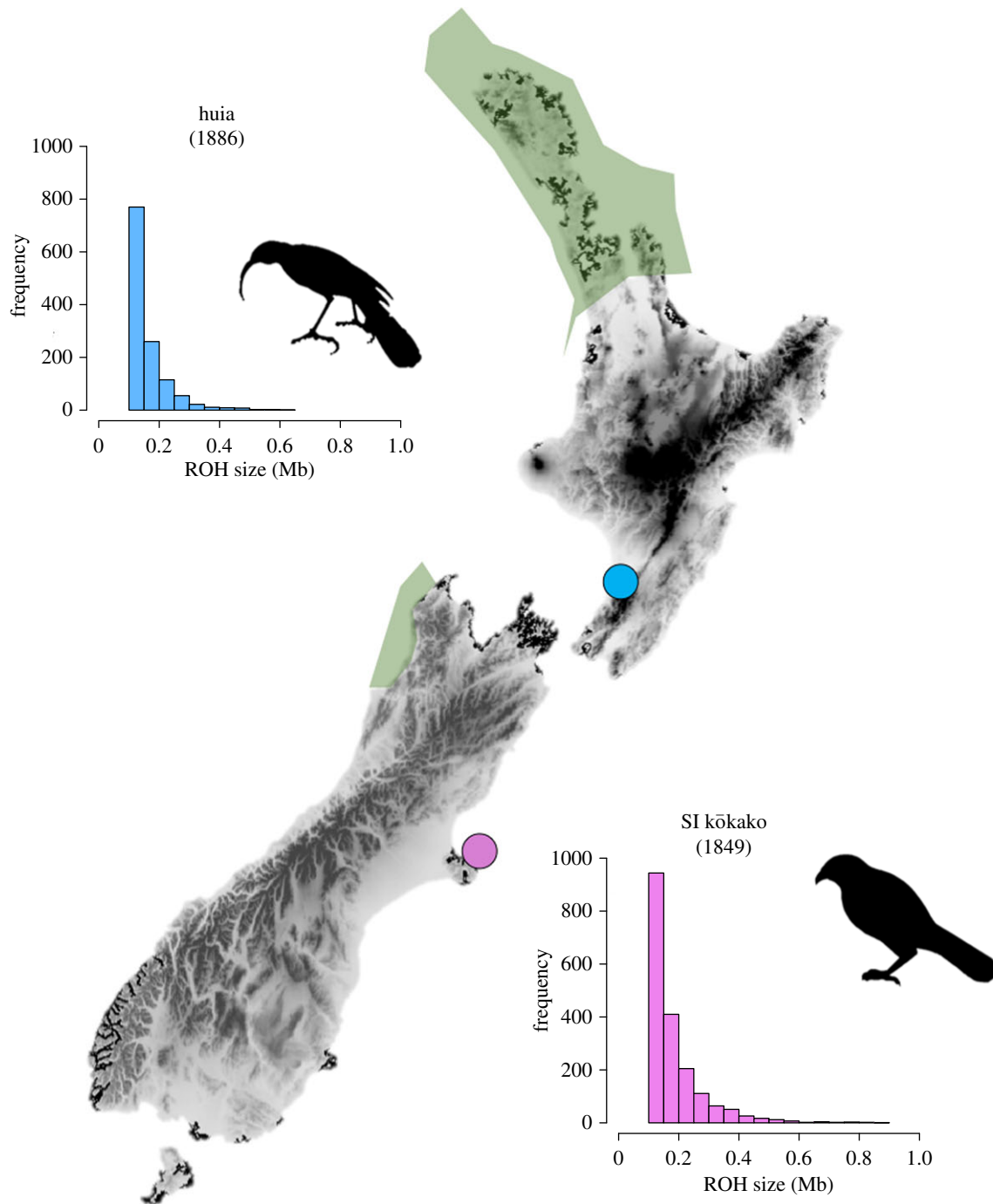
Figure 2. Sampling locations of huia and South Island kōkako museum skins. Green-shaded areas depict forest refugia during the LGM *ca* 22 000 years BP, after Alloway *et al*. [38]. Bar plots depict the distribution of ROHs > 100 kb. (Online version in colour.)

had a higher heterozygosity [37] and N_e, which is consistent with their least concern conservation status [50].

While the relatively important declines in N_e through time in both species could have made them more vulnerable to genomic erosion, inbreeding (F_{ROH}) was low in both species and mostly comprised fragments less than 1 Mb. This indicates that the observed inbreeding was the result of background relatedness (i.e. short ROH caused by random mating in a large population that results in pairing of distant relatives) and not of recent mating among related individuals [51]. While 40% of forest had been cleared by Maōri between the thirteenth and nineteenth centuries [52–54], this result suggests that habitat fragmentation prior to the 1850s may not have been severe enough to reduce gene flow among populations and to increase inbreeding in huia and South Island kōkako populations. Because European settlement

had just started at the time of sampling of these museum skins *ca* 1860–1880 [53], forest habitat may still have allowed large populations to thrive. In fact, previous results based on historical microsatellite data from the same period did not show evidence for population subdivision in huia [49].

Although our data do not show evidence for genomic erosion, future temporal comparison of historical genomes spanning the time of European settlement to the extinction of these species (i.e. huia: 1907; South Island kōkako: 1960s) could indicate whether genomic erosion associated with human-induced bottlenecks contributed to their extinction [55]. This may be especially relevant to South Island kōkako, which went extinct in the 1960s. Assuming a generation time of 6 years [34,35], a period of 100 years corresponds to 17 kōkako generations, which may have been enough for small and fragmented populations to accumulate genetic

load. For instance, a population decline dating back to 20 and 100 years ago for the gorilla [12] and crested ibis [13], respectively, led to increases in inbreeding and genetic load. Moreover, numerous extant avian species in New Zealand have lost a large proportion of their historical genetic diversity and may also have accumulated genetic load, with severe consequences for their viability (e.g. kākāpō, *Strigops habroptilus*; [56,57]; saddleback, *Philesturnus* sp.; South Island robin, *Petroica australis* [58,59]). Conversely, huia went extinct in 1907 [27], 21 years after the study skin was sampled, which corresponds to around three generations [35,49]. It is thus likely that huia experienced a rapid decline and extinction resulting mostly from further forest clearance and the introduction of mammalian predators by Europeans, without genetic erosion contributing markedly to their extinction [60].

In conclusion, our results indicate a severe reduction in huia and South Island kōkako N_e as a result of long-term climate change. However, while our data do not allow us to detect very recent bottlenecks associated with human activities, the low inbreeding coefficients close to extinction of these species suggest that Maōri settlement did not lead to an increase in inbreeding in huia and South Island kōkako. Consequently, neither species seems to have been exposed to genomic erosion at the time of European arrival. While temporal comparison of historical genomes in South Island kōkako are required to properly examine the role of genomic erosion in the extinction of the species, it seems likely that huia went extinct rapidly through the combined effects of forest clearance and mammalian predation.

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