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ORIGINAL PAPER

What can the geographic distribution of mtDNA haplotypes tell us about the invasion of New Zealand by house mice *Mus musculus*?

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Abstract We mapped the distribution and diversity of mitochondrial D-loop haplotypes among 502 New Zealand house mice (*Mus musculus)*. By widespread sampling from 74 sites, we identified 14 new haplotypes. We used Bayesian phylogenetic reconstructions to estimate the genetic relationships between the New Zealand representatives of *Mus musculus domesticus* (all six known clades) and *M. m. castaneus* (clade HG2), and mice from other locales. We defined four distinct geographic regions of New Zealand with differing haplotype diversity indices. Our Results suggest (a) two independent pre-1840 invasions by mice of different origin (*domesticus* clade E and *castaneus* clade HG2) at opposite ends of the country; (b) multiple later invasions by *domesticus* clades E and F accompanying the post-1840 development of New Zealand port facilities in the central regions, plus limited local incursions by *domesticus* clades A, B, C and D1; (c) a separate invasion of Chatham I. by *castaneus* clade HG2; (d) previously undescribed New Zealand haplotypes, potentially the products of localised indigenous mutation, and (e) hybridisation between different lineages.

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Introduction

The house mouse (*Mus musculus* L. 1758) has been distributed by human activities to islands around the world for thousands of years (Berry and Scriven 2005; Bonhomme and Searle 2012; Searle et al. 2009b), often colonizing the same island more than once from independent sources (Förster et al. 2009; Gray et al. 2014; Hardouin et al. 2010; Jones et al. 2010, 2013).

The first general survey of genetic diversity in New Zealand house mice (Searle et al. 2009a) revealed the diverse geographic origins of house mouse populations in New Zealand, based on analyses of the D-loop region of the maternally-inherited mitochondrial DNA (mtDNA) belonging to three main subspecies. The vast majority of mice in the original 106 specimens sequenced had mtDNA haplotypes of *M. m. domesticus* Schwarz & Schwarz 1943 (now resident in western Europe) or *M. m. castaneus* Waterhouse 1843 (resident in south-east Asia). One sample from Wellington City had a *M. m. musculus* L. haplotype (typical of northern Europe, Russia and China).

Most of the 55 mice checked by Searle et al. (2009a) for the nuclear markers *Abpα*, *Btk*, *D11 cen B2* and *Zfy2* typed as *M. m. domesticus,* regardless of mtDNA haplotype.

Where mice of different origins meet, mice belonging to different lineages may interact, as at the established hybrid zone between *M. m. domesticus* and *M. m. musculus* in Europe (Bonhomme and Searle 2012). The two most obvious contact zones in New Zealand could mark meetings between *M. m. domesticus* and *M. m. castaneus*. Historical patterns of international trading and migration have largely prevented *M. m. domesticus* and *M. m. castaneus* from meeting elsewhere in the world, so the combination of geographic origins of New Zealand mice is of interest (Guénet and Bonhomme 2003). They offer an opportunity to test potential explanations of the mechanism by which *M. m. domesticus* nDNA has come to dominate New Zealand mice, for example, differential fitness of inter-subspecies male hybrids (Jones and Searle 2015; Oka et al. 2004; Terashima et al. 2006).

Chubb (2008) collected 84 mice from 8 sites spread evenly along a 330 km transect from Napier to Wellington. MtDNA analyses (n = 62) suggested no definite contact zone, but a mosaic of apparently co-existing local populations carrying haplotypes from each subspecies. Chubb also typed 33 with *M. m. domesticus* mtDNA and 25 mice with *M. m. castaneus* mtDNA, for the nDNA markers *Abpα* and D11 cenB2. All 58 mice had *M. m. domesticus* alleles at both nDNA loci.

McCormick et al. (2014) documented a clear contact zone between *domesticus* and *castaneus* mtDNA lineages in the South Island. They mapped a boundary covering a short distance between 44.23°S and 44.68°S, extending about 50 km north to south and at least 40 km inland. In 170 mice collected from 20 different sites around the contact zone, McCormick (2011) sequenced four nuclear genes (*Abpα, Apbβ, Btk*, and *Zyf2*). All but two mice carried nuclear alleles typed as *M. m. domesticus.* In seven mice from representative localities from both sides of the contact zone, high-density SNP genotyping, using an Affymetrix 600k array (JAX Mouse Diversity Genotyping Arrays), found very similar and largely (c. 95 %+) *domesticus*-like nuclear genomes in all seven mice (McCormick 2011).

The diversity of mtDNA haplotypes represented in New Zealand house mice offers useful clues to the historical geographic origins of their ancestors. Moreover, because house mice are a major international pest, and genetic data can provide information critical to efficient management of pest rodents on islands (Abdelkrim et al. 2005, 2007), establishing the geographic origins of New Zealand mice could have a conservation management application (e.g. MacKay et al. 2013).

We retrieved mice from previous collections held in storage, and analysed larger numbers of mitochondrial D-loop sequences than had been possible in the past. We added further collections from additional areas of the North, South and Chatham Islands and their inshore islands. To complete the survey of known information, our analysis includes previously published data for mice from the outlying islands of Pitt, Auckland, Macquarie and Antipodes (mapped by Searle et al. 2009a), which were not re-sampled here.

We used these data for three main purposes.

1. We identify haplotypes found in New Zealand that are identical to those found in other worldwide

locations, and search for close phylogenetic relationships between New Zealand-only haplotypes and those from other areas.
2. We present extended maps of the distributions of the mtDNA haplotypes associated with the three house mouse subspecies present in New Zealand (*M. m. domesticus, castaneus, and musculus)*. We then compare geographic variation in haplotype and nucleotide diversity within and between four regions of New Zealand.
3. We use these data, and the geographic links to other areas we identified, to propose a hypothesis of colonisation history consistent with known shipping records. Areas with low diversity typically indicate founder events followed by expansion from limited entry points, the typical island invasion pattern observed in Australia (Gabriel et al. 2011). Areas with multiple unrelated haplotypes suggest sites of later arrivals from different sources.

Materials and methods

Samples

We generated mtDNA haplotypes for 502 mice collected from 74 locations chosen to represent broad sampling of the whole of New Zealand (Table 1). The sampling locations ranged from 35.28°S to 46.43°S on the North and South Islands, plus 14 inshore islands and Chatham Island (mapped in Figs. 1 and 2; details in Supplementary Material Table S1).

DNA extraction and amplification of D-loop mtDNA

A sample of 3 mm^2 from an ear, or 5–20 mm from the tip of the tail, was removed from each carcase and preserved in 70 % ethanol or Longmire buffer. We then extracted DNA from each sample using a Gentra Pure-Gene Tissue kit (Qiagen—Venlo, Netherlands). We used a modified protocol based on the manufacturer's recommendations, with an extra centrifugation and supernatant removal step after protein precipitation required because lipids were present in the samples. DNA was then re-suspended in 50 µl of TE.

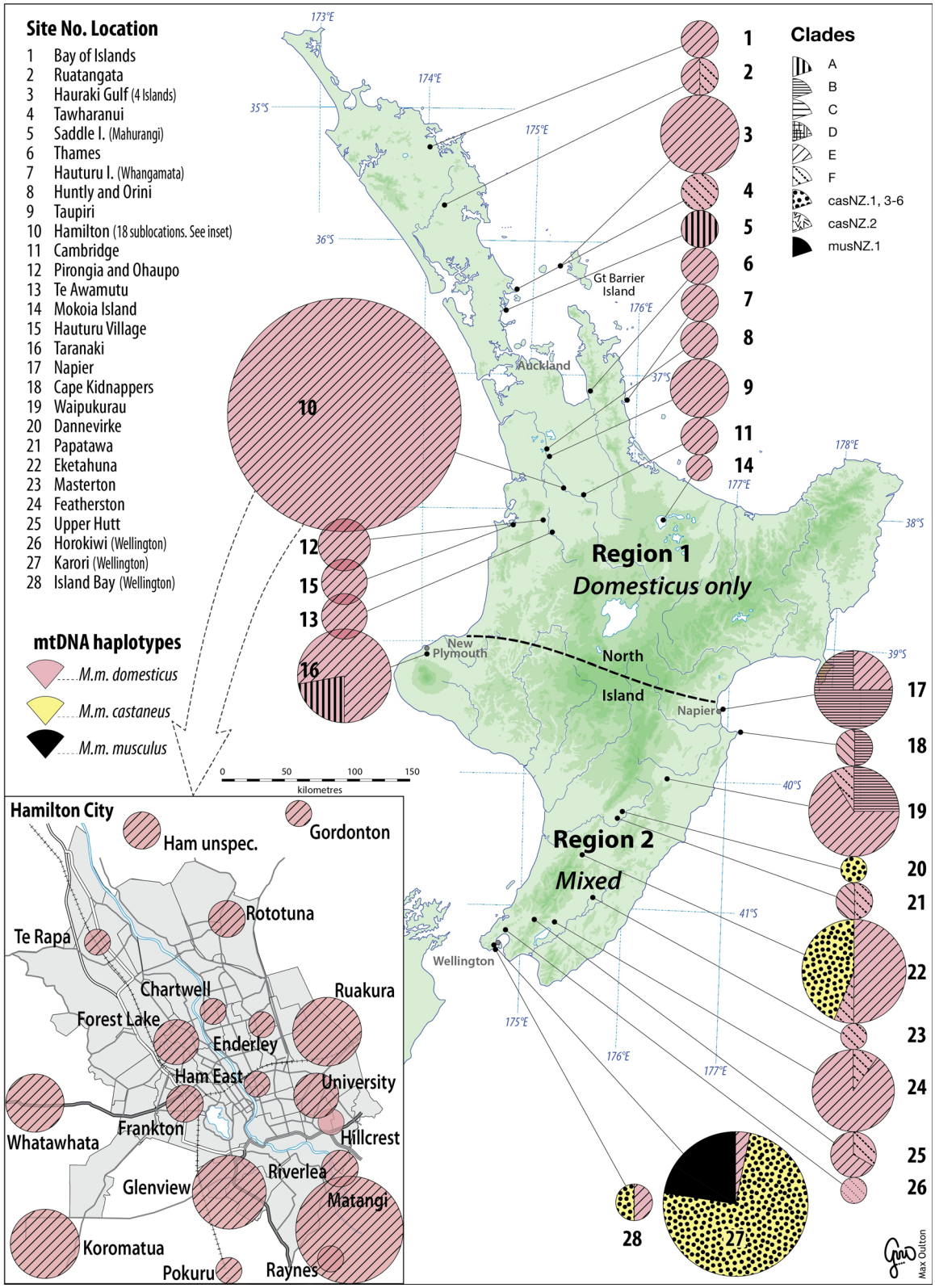
Following extraction, we amplified a 950 base pair (bp) section of the mtDNA D-loop using the primers MouseCRF (MacKay et al. 2013) and H00072 (Prager et al. 1993) in 25 µl reactions, as described in MacKay et al. (2013). The PCR amplicons were sequenced using either the forward or reverse primers by Sanger sequencing, and the resulting sequences were imported into Geneious 7.1.5 (Biomatters, Auckland, New Zealand) for comparative analysis. The sequences were trimmed to the length of *M. m. domesticus* sequences JN091566–JN091568 (MacKay et al.

Table 1 Origins and sizes of collections; number of mice in original papers; number of mice included here

Collector	Jamieson	Chubb	McCormick	MacKay	Murphy	King	Totals
Dates coll.	1999–2000, 2006	2006–2007	2009–2010	2005–2011	2013–2014	2015	
Locations	NZ-wide + 5 islands	NZ-wide + main Chatham I.	Southern SI	Northern NI + 10 islands	Northern SI + 3 islands	Southern SI, Westland	
Total number mice collected	306	248	133	27	43	150	907
N previously published	106	–	–	23	–	–	129
N included in this paper	147	183	62	27	57	26	502
Ref	Searle et al. (2009a) and this study	Chubb (2008)[a]	McCormick et al. (2014)[b]	MacKay et al. (2013) and unpubl.	E. C. Murphy unpubl.	C. M. King (2016)	

[a] Unpublished thesis only, not to be quoted

[b] Published paper does not give haplotype data


Site No. Location
1 Bay of Islands
2 Ruatangata
3 Hauraki Gulf (4 Islands)
4 Tawharanui
5 Saddle I. (Mahurangi)
6 Thames
7 Hauturu I. (Whangamata)
8 Huntly and Orini
9 Taupiri
10 Hamilton (18 sublocations. See inset)
11 Cambridge
12 Pirongia and Ohaupo
13 Te Awamutu
14 Mokoia Island
15 Hauturu Village
16 Taranaki
17 Napier
18 Cape Kidnappers
19 Waipukurau
20 Dannevirke
21 Papatawa
22 Eketahuna
23 Masterton
24 Featherston
25 Upper Hutt
26 Horokiwi (Wellington)
27 Karori (Wellington)
28 Island Bay (Wellington)
mtDNA haplotypes
M.m. domesticus
M.m. castaneus
M.m. musculus
Clades
A
B
C
D
E
F
casNZ.1, 3-6
casNZ.2
musNZ.1
Region 1
Domesticus only
Region 2
Mixed
North Island
New Plymouth
Napier
Wellington
Auckland
Gt Barrier Island
kilometres
Hamilton City
Ham unspec.
Gordonton
Rototuna
Te Rapa
Chartwell
Ruakura
Forest Lake
Enderley
Ham East
University
Whatawhata
Frankton
Hillcrest
Riverlea
Glenview
Matangi
Koromatua
Pokuru
Raynes
Max Outton

◀**Fig. 1** Distribution of sample locations in the North Island. *Numbers associated with circles* represent the site number location; *size of circle* represents relative sample size. Key to sample size given in Fig. 2. *Dotted black line* indicates demarcation between northern North Island (Region 1) and southern North Island (Region 2). For lists of mtDNA haplotypes represented at each location, see Supplementary Table S1

2013), and haplotyped by comparing against previously published *M. m. domesticus* and *castaneus* New Zealand haplotypes. Any sequences not matching known New Zealand haplotypes (domNZ.1–domNZ.10, Mac.domNZ.1–2, casNZ.1–3: Searle et al. 2009a, b; MacKay et al. 2013) were considered to be new haplotypes and named according to the conventions established by Searle et al. (2009a, b), as subspNZ.[number].

Identifying genetic links between New Zealand and other locations

We downloaded all *M. m. domesticus* and *M. m. castaneus* mtDNA D-loop haplotypes available on NCBI nucleotide (GenBank). These sequences were aligned with our New Zealand sequences using Muscle (8 iterations), in Geneious, with the final alignment checked by eye. After alignment, all D-loop sequences were trimmed to the length of the sequences generated in this study, and sequences with more than 20 bp of missing data were discarded. We searched the alignment for haplotypes from other locations identical to those found in New Zealand.

To further establish geographic connections, we conducted a Bayesian phylogenetic reconstruction, separately for *M. m. domesticus* and *M. m. castaneus*, in BEAST v. 2.2.1 (Bouckaert et al. 2014). Only unique haplotypes were included in the phylogenetic reconstructions. For *M. m. domesticus*, we used the following subspecies as outgroups: *M. m. musculus* (AB649750, Suzuki et al. 2013; FM211645, Searle et al. 2009a) and *M. m. castaneus* (casNZ.4, casNZ.5, KP455666, KP455667: this study). For the *M. m. castaneus* phylogenetic reconstruction, we used *M. m. domesticus* (JN091566–JN091568: MacKay et al. 2013) and *M. m. musculus* (AB649750, Suzuki et al. 2013; FM211645, Searle et al. 2009a, b) as outgroups.

Following MacKay et al. (2013) and Searle et al. (2009a, b) for our phylogenetic reconstructions, we implemented the GTR + Γ model of nucleotide substitution, and estimated base frequencies. Unlike previous studies (MacKay et al. 2013; Searle et al. 2009a, b), invariant sites were not included in the model of nucleotide substitution, as interactions between the four gamma rate categories and invariant sites (Sullivan et al. 1999) prevented analyses from reaching convergence (as judged by low equivalent sample sizes: ESS scores).

We completed two independent runs of 90,000,000 states, sampling every 1500 states for each analysis, using a strict clock, and a constant population size coalescent tree prior (as an exponential growth coalescent tree prior over-parameterized the model leading to low ESS values). We checked the two independent runs for adequate ESS values and convergence of posterior values in Tracer v 1.6 (Rambaut et al. 2013). We checked for convergence of tree topologies using AWTY (Nylander et al. 2008; Wilgenbusch et al. 2004). Runs were then combined using LogCombiner v. 2.2.1 (Bouckaert et al. 2014).

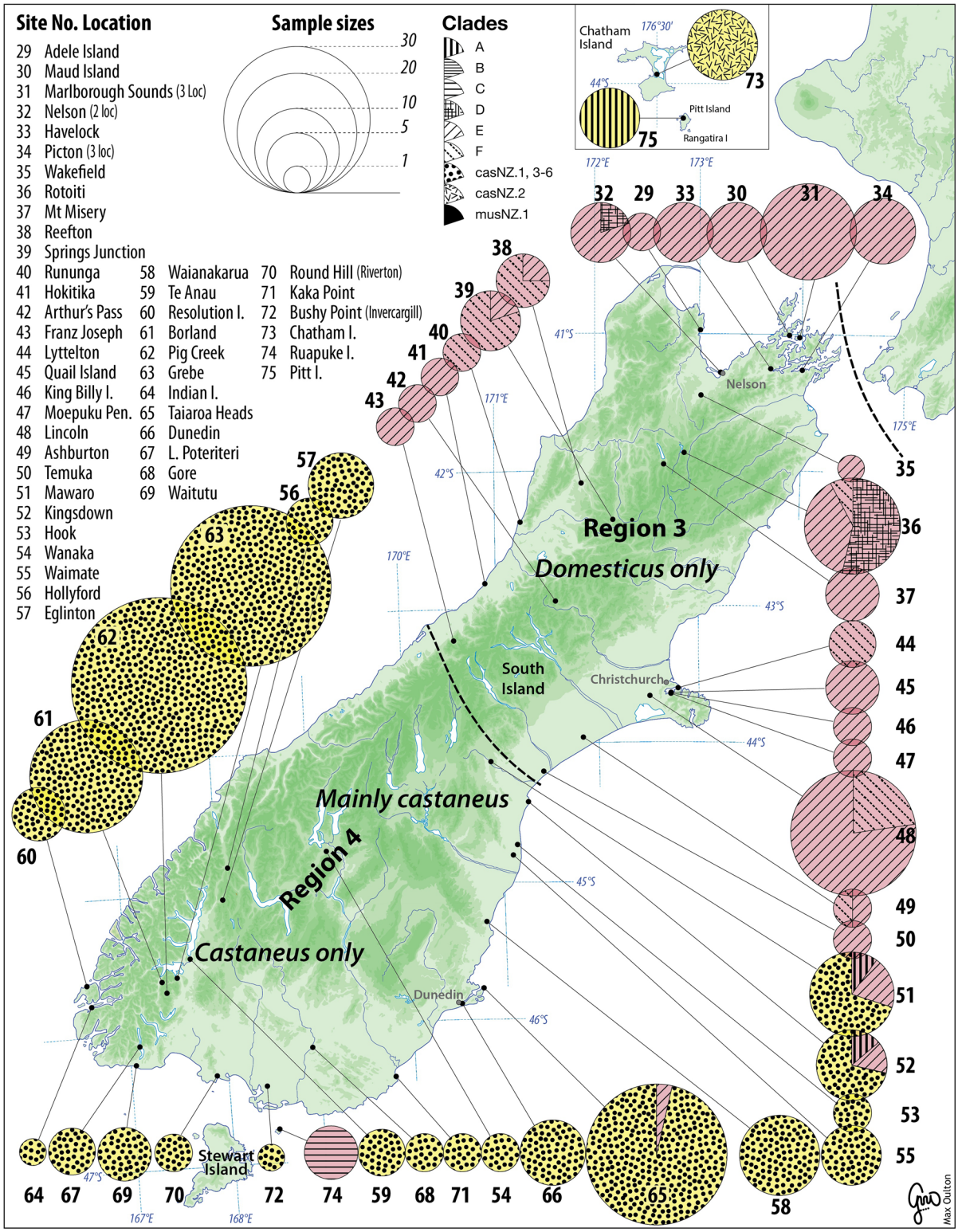
Using trees constructed in Figtree v 1.4.2 (Rambaut 2014) following annotation using TreeAnnotator v. 2.2.1, (Bouckaert et al. 2014), we identified key clades following the naming systems established in previous studies (Gabriel et al. 2011; Jones et al. 2010, 2011; Rajabi-Maham et al. 2012). We considered New Zealand haplotypes that showed strongly supported (i.e. >95 % posterior probability), and recent (<0.005 substitutions/site) relationships with haplotypes from other geographic regions, as evidence for a connection (not necessarily direct) between New Zealand and that region.

Haplotype diversity

We used ARLEQUIN 3.5 (Excoffier et al. 2005) to calculate haplotype diversity and nucleotide diversity, using the Tamura and Nei (1993) model of nucleotide substitution. We calculated these indices separately for four regions of the country (two in each of the North and South Islands).

Statement of ethics

No mice were handled alive. Nearly all were sourced by standard snap trapping; a very few were contributed by domestic cats.


Site No. Location
29 Adele Island
30 Maud Island
31 Marlborough Sounds (3 Loc)
32 Nelson (2 loc)
33 Havelock
34 Picton (3 loc)
35 Wakefield
36 Rotoiti
37 Mt Misery
38 Reefton
39 Springs Junction
40 Rununga
41 Hokitika
42 Arthur's Pass
43 Franz Joseph
44 Lyttelton
45 Quail Island
46 King Billy I.
47 Moepuku Pen.
48 Lincoln
49 Ashburton
50 Temuka
51 Mawaro
52 Kingsdown
53 Hook
54 Wanaka
55 Waimate
56 Hollyford
57 Eglinton
58 Waianakarua
59 Te Anau
60 Resolution I.
61 Borland
62 Pig Creek
63 Grebe
64 Indian I.
65 Taiaroa Heads
66 Dunedin
67 L. Poteriteri
68 Gore
69 Waitutu
70 Round Hill (Riverton)
71 Kaka Point
72 Bushy Point (Invercargill)
73 Chatham I.
74 Ruapuke I.
75 Pitt I.
Sample sizes
30
20
10
5
1
Clades
A
B
C
D
E
F
casNZ.1, 3-6
casNZ.2
musNZ.1
Chatham Island
176°30'
44°S
73
75
Pitt Island
Rangatira I
172°E
173°E
Region 3
Domesticus only
Region 4
Mainly castaneus
Castaneus only
South Island
Nelson
Christchurch
Dunedin
Stewart Island
41°S
42°S
43°S
44°S
45°S
46°S
47°S
167°E
168°E
170°E
171°E
175°E
Max Oulton

◀**Fig. 2** Distribution of sample locations in the South Island. *Numbers associated with circles* represent the site number location; *size of circle* represents relative sample size. *Dotted black line* represents demarcation between northern South Island (Region 3) and southern South Island (Region 4). For lists of mtDNA haplotypes represented at each location, see Supplementary Table S1

Results

Numbers of haplotypes

Among the 502 mice that we surveyed, we found 23 mtDNA haplotypes of *M. m. domesticus* among 279 mice, and six *M. m. castaneus* mtDNA haplotypes among 218 mice (Table 2). *M. m. musculus* was present only as a single mtDNA haplotype from one location in 5 mice (location 27 on Fig. 1).

We found eight of the ten *M. m. domesticus* haplotypes (domNZ.1–10) described by Searle et al. (2009a). The other two haplotypes were previously recorded only from isolated islands that we did not resample here (domNZ.2 on Macquarie I. and domNZ.8 on Antipodes I.). The two haplotypes described by MacKay et al. (2013) both reappeared at least once at new locations. All three previously known *M. m. castaneus* haplotypes (casNZ.1–3) reappeared at least once, in all the same locations where they were previously described (Searle et al. 2009a).

In addition, we found eleven new haplotypes of *domesticus* and three of *castaneus*. We named them in series from domNZ.11 to domNZ.21, and from casNZ.4 to casNZ.6 inclusive, and archived them on Genbank with accession numbers as shown in Table 2.

Our replicate BEAST runs within each subspecies converged on the same values for parameters and tree topologies. Given this agreement, after removing 10 % of each run as burn-in, runs were thinned to every second state and combined within subspecies. This gave ESS values over 200 for all parameter estimates.

Identifying genetic links

New Zealand haplotypes of *M. m. domesticus* include representatives of all six European clades A, B, C, D, E and F (Fig. 3; Table 3).

Two clades (E and F) are common in Britain and widespread throughout the North and upper South Islands. Clade E is the dominant lineage in the UK and Australia (Bonhomme and Searle 2012), and was the *M. m. domesticus* clade including 10 of the 23 New Zealand *domesticus* haplotypes. Clade F, with four New Zealand haplotypes is also called the "Orkney" lineage. It has a clearly defined range in northern Europe from coastal Norway and Iceland to northern Scotland and Ireland (Gabriel et al. 2015; Jones et al. 2012; Searle et al. 2009b). Clades E and F are by far the dominant house mouse clades throughout New Zealand from 35°S to 44°S (Figs. 1, 2).

The distribution of mice with haplotypes belonging to the other four *M. m. domesticus* clades (A–D) suggests localised colonisation events and limited dispersal by mice of non-British origin (Figs. 1, 2). Clade A (Fig. 3) is characterized by haplotypes from mice located from Greece through the Middle-East (Jones et al. 2011). There have been at least four geographically separate invasions of New Zealand by mice of Clade A (Table 3).

Clade B is characterized by haplotypes recorded from Portugal, through Greece and Turkey (Jones et al. 2011). Clade B mice appear to have invaded New Zealand at only a single location, southern Hawke's Bay, North Island, where three samples were collected within 70 km of each other (Fig. 1).

Clade C is the most widely distributed clade in central (France, Germany) and southern Europe (Italy, Spain and Portugal) (Gabriel et al. 2015). Within New Zealand, Clade C is represented by domNZ.8 from Antipodes Island (Searle et al. 2009a), and by domNZ.19 on Ruapuke Island in Foveaux Strait (location 74 on Fig. 3), each probably representing an independent island invasion.

Clade D1 (Fig. 3; Table 2) is associated with northern Europe, especially Germany (Jones et al. 2011). DomNZ.11 is the first New Zealand haplotype so far to be located within this clade. A single invasion of the South Island by Clade D1 mice is represented by two samples from the port of Nelson and from Rotoiti, 90 km inland from Nelson (Fig. 2).

In contrast to *M. m. domesticus,* we found no haplotypes anywhere worldwide that were identical to *M. m. castaneus* haplotypes recorded in New Zealand. The only highly supported node including all the New Zealand sequences of *castaneus* united NZ samples with those of haplogroup HG2 (posterior = 1.00), originating in India (Jing et al. 2014; Rajabi-Maham et al. 2012). Within the HG2 clade (Fig. 4), casNZ.1,

Table 2 Complete list of mtDNA haplotypes known to date in New Zealand house mice

Name	Genbank	Reference	Clade	Related haplotypes in
domNZ.1	FM211632	Searle et al. (2009a)	Clade E	UK, Germany, Mauritania, Somalia, Senegal, China
domNZ.2	FM211633	Searle et al. (2009a)	Clade E	None
domNZ.3	FM211634	Searle et al. (2009a)	Clade E	Germany, Shetland Islands
domNZ.4	FM211635	Searle et al. (2009a)	Clade E	UK, Germany, Denmark, Norway, Faroes, France, Germany, Portugal, Canada Morocco
domNZ.5	FM211636	Searle et al. (2009a)	Clade E	UK, Norway, Faroes, France, Canada, Morocco
domNZ.6	FM211637	Searle et al. (2009a)	Clade A	Argentina
domNZ.7	FM211638	Searle et al. (2009a)	Clade A	None
domNZ.8	FM211639	Searle et al. (2009a)	Clade C	Spain
domNZ.9	FM211640	Searle et al. (2009a)	Clade F	Croatia
domNZ.10	FM211641	Searle et al. (2009a)	Clade F	None
domNZ.11	KP455670	This study	Clade D1	None
domNZ.12	KP411761	This study	Clade B	Portugal, other NZ haplotypes
domNZ.13	KP411762	This study	Clade F	None
domNZ.14	KP411763	This study	Clade B	Portugal, other NZ haplotypes
domNZ.15	KP455664	This study	Clade E	UK, Norway, Faroes, France, Canada, Morocco
domNZ.16	KP455665	This study	Clade E	UK, Norway, Faroes, France, Canada, Morocco
domNZ.17	KP455668	This study	Clade F	None
domNZ.18	KP455669	This study	Clade E	UK, Norway, Faroes, France, Canada, Morocco
domNZ.19	KP954688	This study	Clade C	None
domNZ.20	KP455663	This study	Clade E	None
domNZ.21	KR758766	This study	Clade E	None
Mac.domNZ.1	JN091566	MacKay et al. (2013)	Clade A	Iran, Turkey
Mac.domNZ.2	JN091567	MacKay et al. (2013)	Clade B	NZ haplotypes
casNZ.1	FM211642	Searle et al. (2009a)	HG2	None
casNZ.2	FM211643	Searle et al. (2009a)	HG2	None
casNZ.3	FM211644	Searle et al. (2009a)	HG2	None
casNZ.4	KP455666	This study	HG2	None
casNZ.5	KP455667	This study	HG2	None
casNZ.6	KR758765	This study	HG2	None
musNZ.1	FM211645	Searle et al. (2009a)	–	

Clade names of *domesticus* follow Jones et al. (2010, 2011) and Gabriel et al. (2011); and of *castaneus,* follow Rajabi-Maham et al. (2012). "Related haplotypes" are defined as identical haplotypes or haplotypes with close phylogenetic relationships (>0.95 posterior probability support, <0.05 substitutions/site), as summarized in the Supplementary Material. "None" means that this haplotype appears (so far) to show no close relationship to any other haplotypes

.4, .5, and .6 are each others' closest relatives, albeit with posterior support value of only 0.54.

Of the two other *M. m. castaneus* haplotypes found outside the "New Zealand-specific clade": casNZ.3 has a distribution in New Zealand similar to that of casNZ.4–5, while casNZ.2 has been found only on Chatham I.

We re-confirmed the presence of mtDNA of the northern Palaearctic subspecies *M. m. musculus* at Karori, Wellington (location 27 on Fig. 1), as previously reported by Searle et al. (2009a).

Haplotype diversity

The average diversity values for the whole country reported here (Table 4) and previously (Searle et al. 2009a) were very similar, but here we demonstrate substantial regional variation. The two regions at the

Table 3 Original and New Zealand distributions of the major lineages of *Mus musculus* represented in New Zealand

Subspecies	Clade	Haplotypes	Countries within original range occupied by identical or related haplotypes	Distribution in New Zealand (location # or Region, Figs, 1,2)
M. m. domesticus	A	domNZ.6, domNZ.7, mac.domNZ.1	Greece to Turkey, Iran	Saddle I. (5), Taranaki (16), Canterbury (51, 52), Pitt I. (75)
	B	mac.domNZ.2, domNZ.12, domNZ.14	Portugal, to Greece, Turkey	Napier (17), Cape Kidnappers (18), Waipukurau (19)
	C	domNZ.8, **domNZ.19**	France, Germany Italy, Spain, Portugal	Antipodes I. (Searle et al. 2009a), Ruapuke I. (74)
	D1	**domNZ.11**	Central Europe to Spain	Nelson (32), Rotoiti (36)
	E	domNZ.1–**5**, 15, **16, 18, 20–21**	UK, central & northern Europe	Dominant throughout Regions 1–3; isolated on Macquarie, Auckland Is (Searle et al. 2009a); scarce throughout Region 4, absent in far south
	F	domNZ.9–10, 13, **17**	UK, central & northern Europe	Frequent throughout Regions 1–3
M. m castaneus	HG2	**casNZ.1**	SE Asia, India to China	Dannevirke (20), Eketahuna (22), Wellington (27, 28); dominant throughout Region 4; absent Regions 1,3
		casNZ.2		Chatham I. (73); absent Regions 1–4
		casNZ.3–6		Wanaka (54), Waianakarua (58), Grebe (63), Dunedin (66)
M. m. musculus	*NA*	**musNZ.1**	*NA*	Wellington (27)

Haplotypes that might reflect in situ evolution of haplotypes endemic to New Zealand are shown in bold type

opposite ends of the country are both dominated by single haplotypes. In Region 1, the northern half of the North Island (latitude range and approximate area defined in Table 4), 98 of 107 mice carried domNZ.4. Within this large region, we sampled one sub-area of roughly 2500 km^2 of the central Waikato especially intensively (numbers 8–13 and 15 on Fig. 1; location 10 included 18 different sub-locations within and around the city of Hamilton). Of the 85 mice collected from this sub-area, all but four belonged to domNZ.4.

In Region 4, the southern half of the South Island, 170 of 185 mice carried casNZ.1. At Taiaroa Heads, at the entrance of Dunedin Harbour (location 65, Fig. 2), we sampled 24 mice, of which all but one were casNZ.1. In the Borland valley (location 61, n = 15) and in one of its tributaries, Pig Creek (location 62, n = 43), both at the southern end of Fiordland National Park, we found only casNZ.1. CasNZ.3 had been recorded only once before, in southern Fiordland, so we searched a large sample from the Grebe valley in southern Fiordland (location 63, n = 33), and found 32 casNZ.1 plus a single casNZ.3. Eight mice carrying three previously unreported haplotypes (casNZ.4–6) came from Otago locations not previously sampled, all surrounded by casNZ.1.

Neither domNZ.4 nor casNZ.1 has spread far enough to reach the opposite end of the country. Despite extensive sampling effort, we have so far found no domNZ.4 further south than a line between Franz Josef (43.38°S, location 43) in the west and Temuka (44.23°S, location 50) in the east, and no casNZ.1 north of Dannevirke (40.21°S, location 20). These distributions make the local diversity indices at each end of the country extremely low (Table 4).

In contrast, Region 2 (Fig. 2) supported a fine-scale mosaic of multiple mtDNA lineages of European *M. m domesticus* with various geographic affinities, coexisting in different proportions with both the haplotypes dominant elsewhere, and with other less common haplotypes. The population at Karori (location 27) included 26 mice carrying mtDNA of *M. m. castaneus,* 1 with *M. m. domesticus* clade E, and 5 with *M. m.*

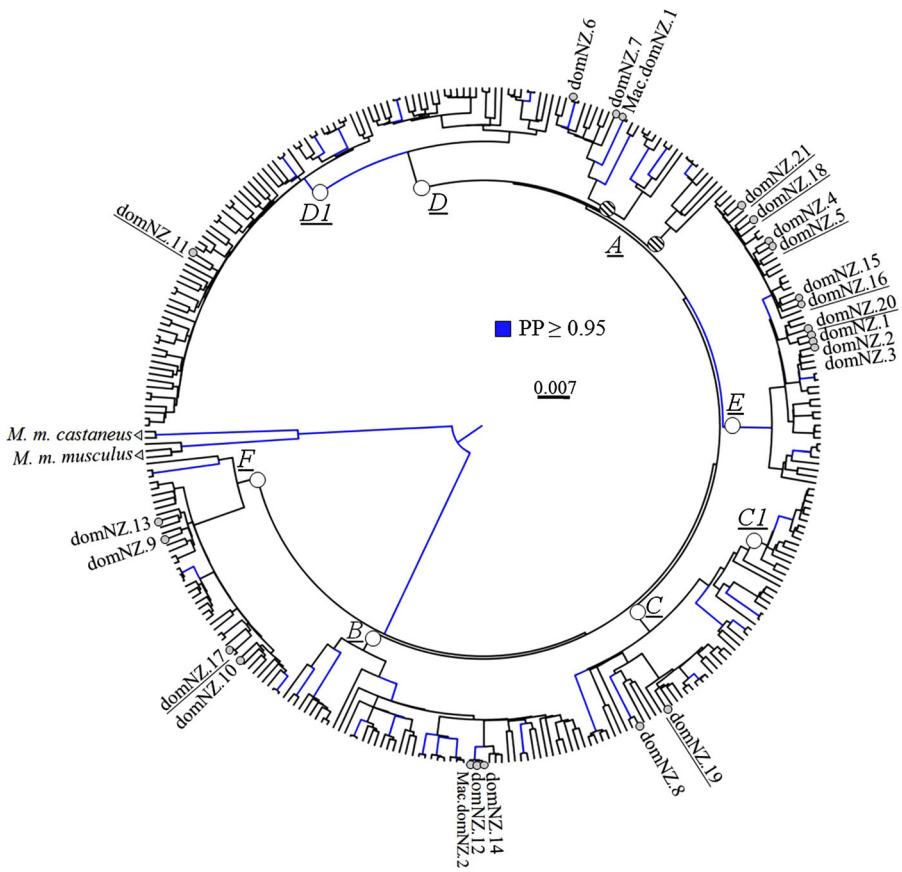


Fig. 3 Bayesian phylogenetic reconstruction for *Mus musculus domesticus*. Branches leading to clades with posterior probabilities greater than or equal to 0.95 are coloured in blue. The *scale bar* gives the number of substitutions per nucleotide site. Outgroup subspecies are indicated by *gray triangles*, and the presence of New Zealand haplotypes by *gray circles*. Haplotypes found in New Zealand and not present in any other area are underlined. *Underlined italic labels* indicate clades names given by Jones et al. (2011) and Gabriel et al. (2011, 2015). The paraphyletic Clade A is distinguished by *striped circles*. Supplementary Fig S1 shows the same tree, but with the Genbank Accession codes for each tip position

musculus. At nearby location 28 we found one each of *M. m. castaneus* and *M. m. domesticus* clade E; at location 22 (136 km north), we found 7 with mtDNA of *castaneus* plus 8 with *domesticus* clade E and 1 with clade F. The presence of mtDNA signatures of all three subspecies in the southern North Island gives that area a higher level of diversity than the country as a whole (Tables 4, 5).

Contact zones

The South Island contact zone described by McCormick et al. (2014), between locations 51 and 52 on Fig. 2, is marked by a short transition between the diversity of 12 haplotypes of *M. m. domesticus* in Region 3, and the near-total dominance of casNZ.1 in Region 4 (Table 4; Fig. 2).

Along the 330 km transect across the lower North Island, between locations 17 and 27 on Fig. 1, we calculated haplotype diversity indices separately for the four largest samples (all with $n > 5$) (Table 5), in comparison with the equivalent indices from the whole country ($n = 502$) and for the southern North Island in general ($n = 93$). At the northern end of the transect (locations 19–22), we found seven different haplotypes in 28 mice, all belonging to one subspecies, *M. m. domesticus.* At the southern end around Wellington city, we found six haplotypes in 34 mice, representing all three subspecies. Most (26 of 34) mice from Wellington carried only cas.NZ.1, and the other eight included three haplotypes of *M. m. domesticus* and one of *M. m. musculus.* Haplotype diversity indices tended to decline southwards along the transect (Table 5).

In places we found a mosaic of apparently coexisting local breeding populations of both subspecies. Haplotype diversity in these areas can be very fine-scaled. For example, at Eketahuna (location 22 on Fig. 1) we found nine mice carrying four different haplotypes of *domesticus* (domNZ.1, .3, .4 and .13, belonging to two clades of *domesticus* (E,F), coexisting in a single calving shed with seven mice

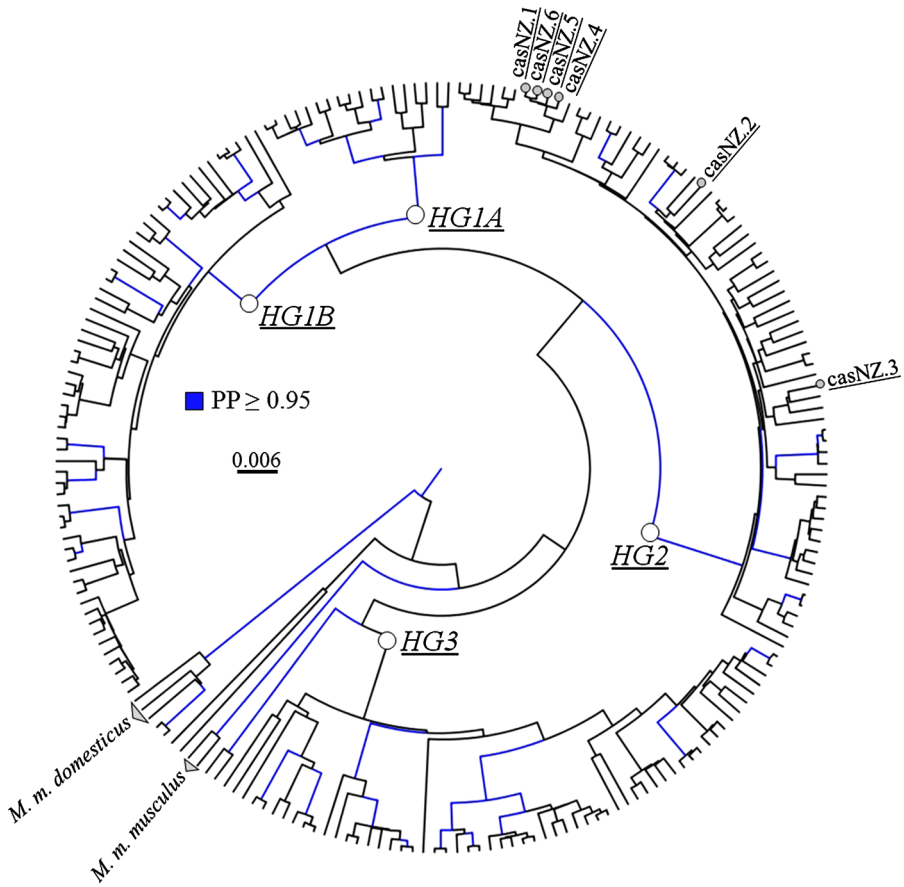


Fig. 4 Bayesian phylogenetic reconstruction for *Mus musculus castaneus,* with the same conventions, *colour coding* and *scale bar* definition as for Fig. 3. Underlined italic labels indicate clades named following Rajabi-Maham et al. (2012). Supplementary Fig S2 shows the same tree, with the Genbank Accession codes for each tip position

Table 4 Genetic diversity indices (all subspecies) by regional distribution in New Zealand, estimated from the 502 mice included drawn from the collections summarized in Table 1

	Area (km^2)	n	Haplotype diversity	SD	Nucleotide diversity	SD
NZ general	268,000	502	0.6756[a]	0.0137	0.019617	0.009656
Northern North Island, Region 1 (35.66–38.10°S)	78,000	107	0.1610	0.0481	0.000984	0.000775
Southern North Island, Region 2 (39.26–41.34°S)	37,000	93	0.7892	0.0292	0.020994	0.010403
Northern South Island, Region 3 (40.98–44.23°S)	74,000	108	0.5758	0.0507	0.004067	0.002302
Southern South Island, Region 4 (44.27–46.10°S)	79,000	185	0.1553	0.0364	0.002438	0.001506

Areas of regions approximate only

[a] Searle et al. (2009a) reported $h = 0.66$

carrying *castaneus* casNZ.1 (clade HG2), and surrounded by neighbouring locations supporting a variety of *domesticus* haplotypes (Supplementary Material Table S1).

This great diversity and fine-scale local variation of haplotypes found across short distances in Region 2 contrasts with the landscape-scale dominance of domNZ.4, in Region 1, and of casNZ.1 in Region 4.

Table 5 Haplotype and nucleotide diversity indices for the southern North Island and for New Zealand generally, compared with local samples taken at intervals along a transect (the route of State Highway 2) between Napier and Wellington

Location	n	Haplotype diversity	±SE	Nucleotide diversity	±SE
Southern North Island (Region 2)	93	0.7892	0.0292	0.020994	0.010403
NZ general, all subspecies	502	0.6756	0.0137	0.019617	0.009656
Waipukurau	12	0.8182	0.0703	0.007284	0.004180
Eketehuna	16	0.7583	0.0798	0.020210	0.010616
Featherston	10	0.3778	0.1813	0.002077	0.001473
Wellington (3 locations)	34	0.4029	0.0975	0.011509	0.005994

Haplotype diversity indices decline from Waipukurau (location 19) supporting 5 haplotypes among 12 mice of one subspecies, to the Wellington area (locations 26–28) supporting 5 haplotypes among 34 mice of three subspecies (Supplementary Table S1)

Possible indigenous mutations

While some haplotypes we recorded are widely distributed and retain identity with haplotypes found overseas, others found in the current study or by Searle et al. (2009a) are confined to one or a few adjacent locations within New Zealand, so appear endemic. These haplotypes could reflect either relatively recent in situ mutations, or under-sampling of source populations. Potential endemic haplotypes are distinguished in Table 3 and Figs. 3, 4.

Discussion

Distribution and number of haplotypes

This paper offers the most extensive survey of mtDNA genetic diversity in New Zealand mice to date, presented in terms of a novel analysis by clade. The geographic distribution of clades (Figs. 1, 2; Table 3) suggests some interesting inferences about possible connections (not necessarily direct) between the present mouse population and their ancestors. The complex history of mice in New Zealand has features in common with the multiple invasions of house mice in Madeira, the Faroes and Iceland (Jones and Searle 2015). These and many other studies, on taxa ranging from bacteria (Moreira et al. 2015) to plants (Miller et al. 2011), insects (Evans et al. 2003), rats (Robins et al. 2016) and carnivores (Gaubert et al. 2015), illustrate how molecular data can be used to reconstruct the phylogeny and invasion history of introduced species. The rates of invasion and reinvasion in mobile pest species can be very high (King et al. 2011).

In all areas of the country north of about Christchurch, domNZ.4 was the most common *domesticus* haplotype we found, as in the previous survey by Searle et al. (2009a). However, by sampling in areas not previously surveyed, we have compiled a more detailed map of the distribution and diversity of other mtDNA haplotypes of *M. m. domesticus* throughout the North Island and northern South Island. We have considerably extended the distribution of eight of the ten previously known haplotypes, filled in some important gaps in the geographic coverage, and added eleven new *domesticus* haplotypes, further illustrating the close relationship between New Zealand and western Europe.

We have also increased the number of known *M. m. castaneus* mitochondrial haplotypes from three to six, and extended their known distribution to the entire southern South Island south of a contact zone at about 44°S (McCormick et al. 2014). In the North Island we found three new locations for *M. m. castaneus* mtDNA, one in a Wellington suburb, and two in towns along the main highway north of Wellington. These data could provide a baseline for future surveys aiming to estimate whether *M. m. castaneus* haplotypes are expanding their range in either island.

Clues to the progress of invasion of New Zealand by house mice

The chances of a successful invasion depend on the numbers of individuals available at each of three sequential stages (transport, introduction, and establishment) (Blackburn et al. 2015). Because D-loop mtDNA is inherited without recombination and only down the maternal line, it is particularly good at

identifying the original colonisers of an area, and demonstrating the resistance of resident female mice to displacement by incoming females (Gabriel et al. 2015; Hardouin et al. 2010). Areas of very low local haplotype diversity may be associated with rapid population expansion by the first colonist(s) carrying the original haplotype into areas free of conspecifics, surfing the wave of the initial population expansion (Excoffier and Ray 2008). This priority effect (Fraser et al. 2015), whereby founders can exclude latecoming immigrants, is suggested when the genetic signature of the primary colonisers appears to be retained in the extant mouse population, barely affected by subsequent introductions, as in Australia (Gabriel et al. 2011).

This logic suggests that the earliest mice to arrive in the north of the North Island belonged to the *Mus musculus domesticus* haplotype domNZ.4, now the dominant haplotype from the Bay of Islands to the Waikato province (locations 1 to 13 on Fig. 1, 380 km). DomNZ.4 is identical to BritIsl.5 and AUSTRALIA.01, the most common haplotypes in Britain and Australia (Gabriel et al. 2011; Searle et al. 2009b), and Sydney was the earliest source of trading goods imported via Sydney to the Bay of Islands, a historically important port since the 1820s (Gabriel et al. 2011; Searle et al. 2009a). The predominance of domNZ.4 in the North Island is therefore entirely as expected from the long history of repeated immigration and wide dispersal of British and Irish settlers in New Zealand (King 2003).

Likewise, casNZ.1 is almost the only maternal haplotype to be found in the entire southern South Island (Fig. 2), even in very large local samples. One explanation for the predominance of the *M. m. castaneus* casNZ.1 haplotype in that area is that mice belonging to this haplotype arrived first in the southern South Island, long enough ago to give their descendants time to spread throughout Otago and Southland (locations 51–70 on Fig. 2, 320 km).

CasNZ.1 belongs to clade HG2, the only one of four divergent haplogroups of *M. m. castaneus* to have been exported to all the other locations around the Indo-Pacific where that subspecies is found, ranging from Pakistan and Myanmar to Taiwan, China and Thailand (Jing et al. 2014; Suzuki et al. 2013). *Mus musculus castaneus* could have colonised the southern South Island between 1792 and 1810, with sealers returning from the Canton fur market (McCormick et al. 2014), although other explanations are possible (King 2016).

The dominance of different haplotypes in the far north and far south are consistent with historical data showing that the northern and southern trade routes to pre-colonial New Zealand (1792–1840) were quite separate at that time (Church 2002).

The ports of Napier, Whanganui, New Plymouth, Wellington, Nelson, Hokitika and Lyttelton were all developed later (after the Treaty of Waitangi established British colonial rule in 1840). Mapping the haplotype distributions by clade (Figs. 1, 2) has demonstrated a greater diversity of *domesticus* haplotypes in the central regions of the country (from Napier to Christchurch), attributable to multiple invasions of different haplotypes of *M. m. domesticus* with European settlers.

Mitochondrial DNA data demonstrate two clear cases of separate colonisations followed by limited dispersal inland. Mice of the south European clade B are confined to the port of Napier and two locations within 68 km of it. Mice of the north-central European clade D1 common in Germany have so far been found only at the port of Nelson and at one location 90 km inland. The Nelson province was colonised by many German settlers (King 2003).

Four island populations of mice represent independent colonisations from which no further dispersal has been possible. Searle et al. (2009a) found domNZ.2 only on Macquarie I., and domNZ.8 only on Antipodes I. Here we report domNZ.19 only on Ruapuke I., in Foveaux Strait (location 74 in Fig. 2). None of these three haplotypes have yet been found anywhere else. The arrival of mice on Ruapuke in 1824 was documented at the time, but in the almost 200 years since then it has not spread across the strait to the southern South Island, 15 km away. DomNZ.8 has been present on the Antipodes since at least 1909, probably earlier (Russell 2012). In the fourth case, the isolation of casNZ.2 both on Chatham Island and in phylogenetic reconstructions in this paper (Fig. 4) and by Jing et al. (2014) suggest an independent colonisation by stock of southeast Asian ancestors different from those that reached the North and South Islands.

On the other hand, Searle et al. (2009a) found domNZ.7 only on Pitt Island, whereas our extended sampling found the same haplotype only at two locations in Canterbury near Timaru, the South Island home port of the Chatham Islands Shipping Co.

Further detailed sampling might well find more links between the main (North and South) and other islands like that of domNZ.7.

The isolated record of *M. m. musculus* at Karori (MusNZ.1, location 27 on Fig. 1) suggests that this subspecies arrived at the Port of Wellington later than the other subspecies. In Nelson Lakes National park (locations 36 and 37 on Fig. 2), Searle et al. (2009a) found mixed evidence of nDNA input from *castaneus* and/or *musculus* in six of 17 mice with *domesticus* mtDNA haplotypes, implying an additional limited input from this subspecies in the northern South Island.

Our results are relevant, not only to further understanding of the invasion history of mice in New Zealand, but also to the ongoing task of monitoring biosecurity. Mice continue to invade New Zealand's islands—or to reinvade islands from which they have been eradicated (Russell et al. 2008). When new mouse incursions are detected, our extensive geographical genetic sampling could help identify the probable source population, and potentially also the invasion route. Such information may be important to planning improved biosecurity measures to prevent future incursions, or expansions of existing ranges.

The long term result of the multiple repeated invasions of New Zealand by house mice of different origins has been to produce a melting pot pattern within contemporary populations. In addition, the genetic diversity of New Zealand could potentially have been enhanced by indigenous mutations since the introduction of the mice, given the presence of local haplotypes apparently endemic to New Zealand and the close similarities between known and new haplotypes (Figs. 3, 4). Future analyses might now concentrate less on where these mice came from, and more on the movements of genetic variants inside the species gene pool (Bonhomme and Searle 2012: 291–292). As Suzuki et al. (2013) point out, genetic introgression may now be shaping the future evolution of the house mouse.

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