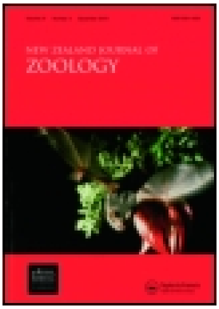

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Scree weta phylogeography: Surviving glaciation and implications for Pleistocene biogeography in New Zealand

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Scree weta phylogeography: surviving glaciation and implications for Pleistocene biogeography in New Zealand

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Abstract The Pleistocene glaciation is thought to have had a profound impact on the distribution of endemic biota. The intraspecific phylogeography of the alpine-adapted scree weta, *Deinacrida connectens* Ander, was surveyed throughout its range in the South Island, New Zealand using mitochondrial cytochrome oxidase I DNA sequence data. Seven distinct genetic lineages were evident from mtDNA haplotypes, with each occupying mountain ranges in discrete geographic regions. Genetic distances among lineages were up to 8.2%, whereas within-lineage distances reached only 2.8%. The inferred age of lineages and the striking phylogeographic structure exhibited by *D. connectens* indicates that it radiated in response to Pliocene mountain building. Maintenance of this structure is likely to relate to the combined effects of mountain-top isolation during Pleistocene interglacials and ice barriers to dispersal during glacials. Two lineages are endemic to the central South Island, an area regarded as species poor due to glacial-extirpation of much of the biota. It appears that *D. connectens* survived across much of the South Island in a mosaic of ecological, rather than one or few, regional refugia. The Pleistocene biogeography of New Zealand in general is discussed in the light of this hypothesis.

Keywords alpine; mitochondrial DNA; COI; phylogeography; Pleistocene glaciation

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INTRODUCTION

Pleistocene climate change and glaciation have been advanced to explain distribution patterns among many New Zealand organisms. Two types of effect are postulated. The first comprises essentially ecological responses to extreme climatic conditions (low temperature and aridity), and the extension of glaciers, whereby species ranges shifted or fluctuated in size in response to changing conditions. The second type includes evolutionary responses (adaptation/speciation) to the new alpine habitat. Paleovegetational studies provide clear evidence of vegetation changes during the Pleistocene (McGlone et al. 1993; Newnham et al. 1999) and the ranges of fauna are expected to have been similar. It has been inferred that broad assemblages were locally extirpated by the direct action of glaciers (Cockayne 1926; Willet 1950; Wardle 1963; Burrows 1965; Dumbleton 1969), or were affected by regional variation in conditions (Rogers 1989). There is also evidence that some plant taxa (e.g., *Eucalyptus, Nothofagus brassii*) became extinct in New Zealand as a result of climate change (Mildenhall 1980; Pole 1994). The modern existence of alpine-adapted taxa in New Zealand, despite the short history of this environment, has been attributed either to colonisation of New Zealand by cold adapted taxa from elsewhere (e.g., Australia (Raven 1973), Antarctica (Hooker 1860) or northern boreal habitats), or to radiation and adaptation *in situ* during the Pleistocene (Fleming 1979). Recent molecular evidence from plant taxa indicates that both explanations can apply, as in some cases dispersal of progenitors to New Zealand was recent and resulted in rapid radiation of alpine taxa (Wagstaff & Garnock-Jones 1998; Breitwieser et al. 1999; Wagstaff & Wardle 1999). It has also been argued that the subspecific/species complex diversity of many New Zealand plants resulted from Pleistocene climate cycling (Wardle 1963; Ogden 1989).

The application of phylogeographic methods (Avise et al. 1987; Avise 1998) to New Zealand biota is in its infancy, and molecular studies of invertebrates in New Zealand are few (but see Emerson & Wallis 1995; King et al. 1996; Buckley et al. 1998; Trewick 2000a). Phylogeography has proven effective in revealing the extent to which the Pleistocene impinged upon the evolution of the biota in Northern Hemisphere systems dominated by glaciation (e.g., Zink 1996; Taberlet et al. 1998; Hewitt 1999), and in southern systems where glaciation did not feature (e.g., Joseph et al. 1995, Schneider & Moritz 1999). The alpine scree weta *Deinacrida connectens* Ander (Orthoptera: Anostostomatidae) provides a good opportunity to use phylogeography to assess hypotheses about the origin of New Zealand alpine biota and to explore the impact of glaciation (Trewick et al. 2000). The flightless scree weta is the most widespread and abundant of the endemic giant weta, and is present on most mountain-tops in the South Island east of the Main Divide and in Nelson where it inhabits alpine scree slopes 1200–3600 m above sea level. The broad distribution of scree weta suggests that either it was not extirpated from the central region of the South Island by glaciation, as postulated for many other taxa (Willet 1950; Wardle 1963; Burrows 1965; Dumbleton 1969), or that it was successful in recolonising after the last glacial maximum (15 000 years ago). Post-Pleistocene dispersal between mountain ranges can be reconciled with the modern absence of scree weta from low altitudes only if this is an artefact of very recent events such as predation by introduced predators. This does not appear to be the case (Trewick et al. 2000).

I present here a revised data set for the scree weta, including individuals and locations additional to those previously reported (Trewick et al. 2000). The results are discussed in the context of the South Island glaciation and New Zealand Pleistocene biogeography in general.

METHODS

Previous studies of morphology, cytogenetics and allozymes (Morgan-Richards & Gibbs 1996) have provided a valuable resource of scree weta specimens (Trewick et al. 2000). These have been supplemented by the collection of small antennal fragments from live individuals in the field, allowing an increase in both the number of individuals and populations analysed. Details of sampling locations are given in Appendix 1.

DNA extraction utilised muscle tissue taken from a femur or antennal fragments, and followed the method of Sunnucks & Hales (1996). Molecular analysis used primers that target part of the mitochondrial DNA (mtDNA) cytochrome oxidase I gene (COI). These primers are known to be highly conserved and applicable to a wide range of invertebrate taxa (Lunt et al. 1996), and COI has been utilised successfully in intra- and interspecific studies (Zhang & Hewitt 1996; Funk 1999). SSCP (single stranded conformation polymorphism) was used to differentiate haplotypes prior to sequencing. Full details of molecular methods, rationale and analyses are given in Trewick et al. (2000). Sequence data are deposited in Genbank (Acc. No.s AF202586–AF202621).

RESULTS AND DISCUSSION

Molecular evidence

Seventy-eight weta from 24 locations were included in the study. Forty different 3′ COI sequence haplotypes were detected ($n = 55$). The 540 bp of aligned sequence contained 100 variable sites, of which 78 were phylogenetically informative. Average Kimura 2 parameter (K2p) (Kimura 1980) genetic distances among the COI haplotypes was 4.8%. The highest genetic distance was 8.2%, and this was between the geographically most distant populations/clades (Eyre mountains and Mt Peel). Genetic distances within clades were comparatively small, up to 2.8%.

The 40 haplotype sequences were analysed using neighbour joining (NJ) and maximum parsimony (MP) as implemented by PAUP* 4.0b4 (Swofford 1998). Analysis using unweighted MP or with transversions:transitions weighted 5:1 gave 96 equally short trees that differed only with respect to placement of terminal branches within each clade. The internal topology of these trees was identical to that of the NJ tree (Fig. 1). Seven principal lineages (a–g) were well-supported having bootstrap values >70% (Hillis & Bull 1993).

Compared with other insects, the levels of mtDNA variation within the alpine scree weta were high. In fact, the highest genetic distance found between two COI haplotypes (8.2% K2p) is more typical of interspecific divergence in insects (Funk 1999). Studies using COI sequences from beetles (Funk et al. 1995) and moths (Brown et al. 1994) have revealed intraspecific distances as high as 3.8% and 5.7% (K2p) respectively, but values closer to 2% are more typical (Langor & Sperling 1997).

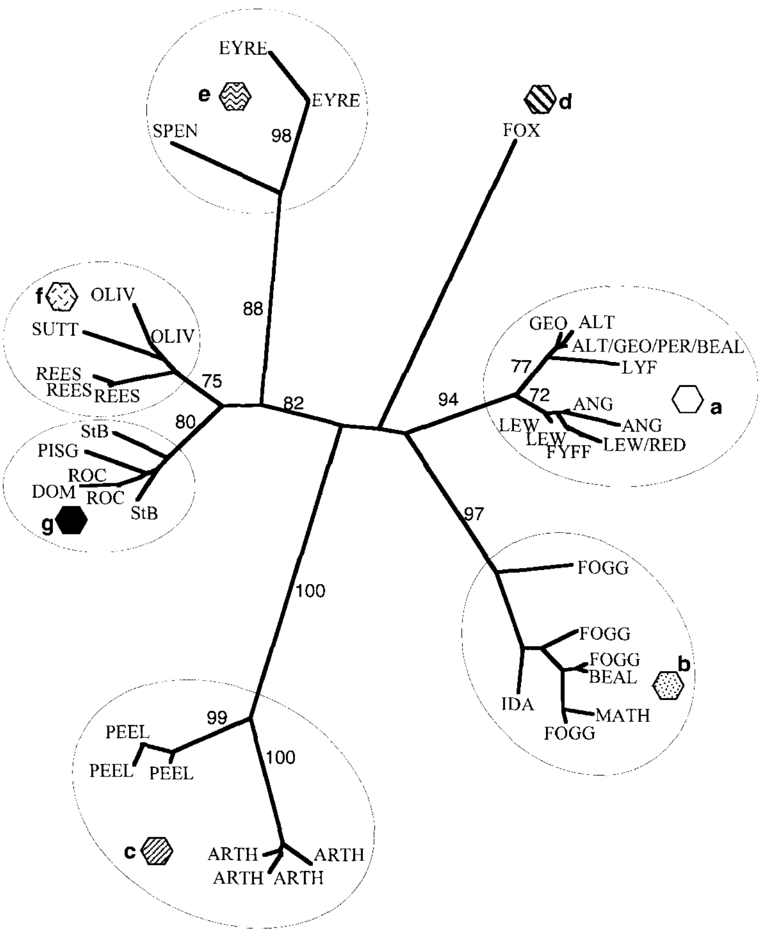

Fig. 1 Unrooted neighbour joining (NJ) network of K2p distances among alpine scree weta COI haplotypes. Principal lineages are coded with a filled hexagon and an alphabetic label (**a**–**g**). Terminal edges (haplotypes) are labelled with location abbreviations (see Appendix 1). Numbers on branches show % support from 500 maximum parsimony (MP) bootstrap replicates with 5:1 TV:TI weighting.

Although COI exhibits a high level of functional constraint (Lunt et al. 1996), and begins to show evidence of saturation beyond 13% sequence divergence in intergeneric studies (Szymura et al. 1996), the present within-species diversity is not expected to result in loss of phylogenetic signal (for more details see Trewick et al. 2000). Despite high mtDNA genetic distances, nuclear markers (morphology, karyology and allozymes) indicate that the scree weta is indeed a single species, as the distributions of regional colour and chromosome variants are not concordant with mtDNA clades, and allozyme distances (mean = 0.12 Nei's D) are typical for intraspecific comparisons of insects (Field 1980; Morgan-Richards & Gibbs 1996).

Using standard mitochondrial DNA evolutionary rate calibrations of 2–2.3% sequence divergence per million years (m.y.) (Brown et al., 1979; DeSalle et al. 1987; Brower, 1994) that are applicable to the COI gene of insects (Juan et al. 1995; Fleischer et al. 1998), the primary, well-supported divisions within scree weta are apparently derived from isolation some 3.3–4.0 m.y. ago (lineages a–g). These old lineages correspond to distinct geographic areas of the South Island (Fig. 2). Shallow divisions are present at the termini of most of these edges but their branching order is generally not well-resolved. Most lineages also have some additional well-supported sub-divisions that generally reflect an intermediate level of geographic structure (e.g., lineage c split into Mt Peel and Mt Arthur haplotypes).

The phylogeographic structure encountered is consistent with an alpine radiation model. It is clearly not associated with recent environmental changes (climate warming and predator introduction)

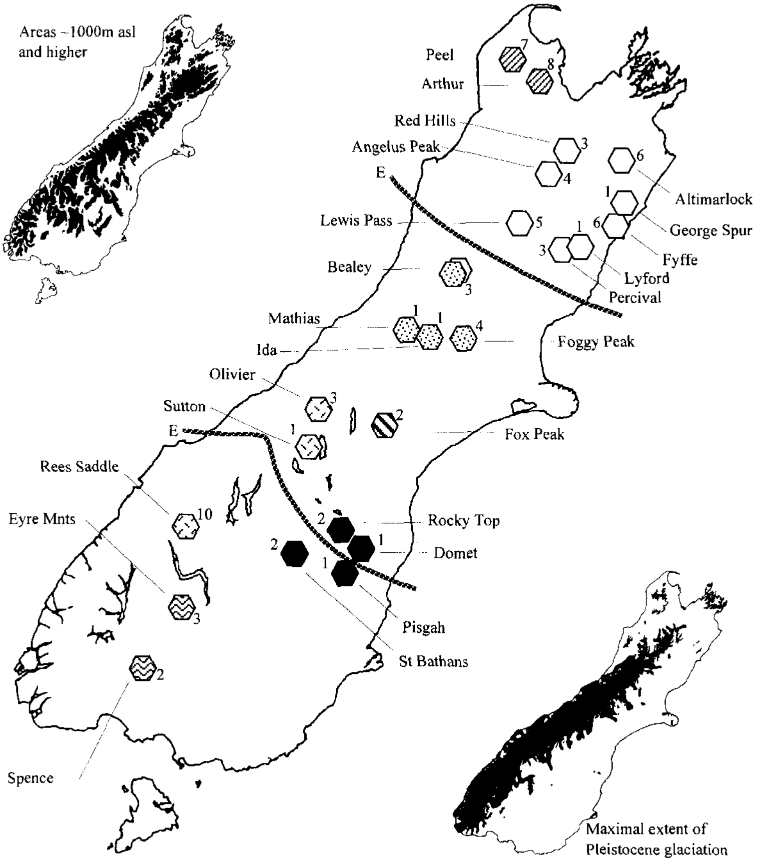

Fig. 2 Map of the South Island, New Zealand, showing sites sampled for scree weta. Filled hexagons correspond with those in Fig. 1. Insert maps indicate: approximate maximal extent of Pleistocene glaciers (re-drawn from Pillans et al. 1992) – bottom right, and extent of mountains above 1000 m (re-drawn from McGlone et al. 1993) – top left. The region of low endemicity in the central South Island is indicated by hatched lines labelled E (after Wardle 1963). Sample sizes are shown.

(Trewick et al. 2000), as the latter would be expected to have resulted in low levels of divergence and/or mixtures of haplotypes in populations. The estimated mean coalescence of ~4 m.y. ago falls within the time range estimated for the emergence of the main axial range of the South Island mountains (Pillans et al. 1992), and the polytomous structure of the gene tree can be explained by isolation of populations on separate mountain ranges. This timing and pattern indicates that the scree weta diverged from other giant weta under the influence of the novel altitudinally-structured habitats generated by Pliocene mountain-building prior to Pleistocene climate cooling.

Refugia

The phylogeographic pattern in the scree weta also indicates that populations survived *in situ* throughout the Pleistocene. Scree weta populations probably expanded and contracted altitudinally to match movement of the alpine zone through glacial-interglacial cycles. However, gene flow among geographic regions was apparently limited, at least in terms of the maternally inherited mitochondrial DNA.

Two different aspects of montane glaciation may explain the persistence of these geographically distinct lineages. A cooling climate will have lowered the alpine zone and allowed scree weta to colonise lower altitudes with potentially greater habitat area. At the same time, glacier extension would have prevented colonisation of many valley systems and maintained lowland barriers between scree populations. For instance, populations in the vicinity of Eyre Peak and Rees Saddle may have been kept apart by the glacier that cut the bed of Lake Wakatipu, thus isolating lineages e and f. Conversely, in Marlborough where the mountain ranges are extensive but ice was scarce during glacials, dispersal across valleys would have been possible when the alpine zone extended more widely than today (McGlone 1988), resulting in the wide distribution of lineage a (Fig. 1). The presence of glaciers at the northern end of the Southern Alps may have prevented gene flow between scree weta populations in Marlborough and Nelson (lineages a and c), as has been proposed for alpine grasshoppers in the region (Peterson 1968). It would certainly have limited exchange between Nelson and populations further south.

The distinctiveness of the Marlborough and Nelson lineages is also superficially consistent with patterns attributed to range displacement by the alpine fault (Heads 1998). However, the extent of genetic divergence (less than would be expected over the time frame of fault movement), and the pattern of relatedness (the Nelson area lineage not being the sister of the Southland/Otago lineages), strongly contradict such an interpretation. During interglacials and the post-glacial optimum at the start of the Holocene, when the climate was warmer than in modern times (Hendy & Wilson 1968; McGlone 1988), the ranges of scree weta populations would have been much reduced, fragmented and restricted to the highest peaks. Such conditions would have resulted in lineage sorting (Avise 1994), local extinction, and isolation of scree weta populations in a mosaic of ecological refugia, as pertains today, through the southern mountains. This is the reverse situation that would have applied to populations of non-alpine taxa (the majority) which had the best opportunities to escape refugia during interglacials and interstadials (e.g., forest species, McGlone 1985).

The species gap

Two scree weta lineages (b and d) appear to be endemic to the mountains within the low endemicity zone of the central South Island (i.e., in the beech-gap), and other lineages (f and g) occur across the boundaries of this area (Fig. 1). This suggests that scree weta survived through the Pleistocene within the beech-gap. Although there was an almost continuous glacier complex along the Southern Alps and down to the sea on parts of the west coast during the last glacial, a non-glaciated alpine zone persisted to the east (Newnham et al. 1999). Wardle (1963, p. 14) suggests that most of the available alpine surfaces in the central South Island probably consisted of scree, and as such could have been inhabited by scree weta. Plant endemicity is comparatively low in the central waist of the South Island, and many of the taxa that are disjunct across this region are alpine specifics (McGlone 1985), but some alpine endemics are present (Cockayne 1917; Wardle 1963; Burrows 1965). The evidence from scree weta contributes directly to our understanding of the biological effects of Pleistocene glaciation in the central South Island, and supports the notion, based on the presence of endemics, that in New Zealand glaciers and glacial outwash did not eradicate all taxa. In addition, it suggests that as well as the alpine plants that are endemic to the central region, others that are now distributed throughout the Southern Alps may, like the scree weta, have survived *in situ* rather than achieving this range by post-Pleistocene colonisation.

New Zealand differs from the Northern Hemisphere pattern

The biological response to the Pleistocene in the Northern Hemisphere was one of continent-wide extirpation from the north by advancing ice sheets and tundra. Warming during interglacials is assumed to have resulted in recolonisation from southern refugia, just as it did following the end of the last glacial (~15 000 y.a.). Distinct patterns of recolonisation have been identified from a variety of taxa (Hewitt 1999). These differ in the number and influence of putative southern European refugia in the history of various taxa, but the consistent signal is one of northward migration in the wake of retreating glaciers. Genetic evidence indicates that this was probably dominated by leading-edge migration (Hewitt 1996, 1999) such that a few genotypes rapidly colonised a large area of virgin habitat.

If Pleistocene climatic conditions in New Zealand had been broadly similar to those in the Northern Hemisphere, an analogous pattern of survival at lowest latitudes and recolonisation would be expected, but with greater overall reduction in biodiversity owing to small land area. However, even in the Southern Alps, where glaciation was extensive because of the high level of precipitation on those ranges (today up to 11 000 mm/year, (Griffiths & McSaveney 1983), it is probable that conditions in New Zealand were not as cold or dry as the northern continents. Distance from the pole, the action of the circumpolar current and lack of sea ice probably ameliorated the impact of Pleistocene cooling and kept New Zealand comparatively warmer and wetter. Permafrost probably extended little beyond the glaciated areas (McGlone 1988).

Modern montane habitats in the South Island are considered to be more similar (more humid and with less extreme seasonal fluctuations in temperature, etc) to those found on oceanic island and tropical alpine systems than to Northern Hemisphere mountains (Mark et al. 2000).

Palynological evidence indicates that during the last (Otiran) glaciation in non-alpine areas, grassland was much more extensive and forest much scarcer than in modern (prehuman) times, with tree species dominating only in Northland (Newnham et al. 1999). However, it is also evident that shifts in vegetation were not dictated solely by latitude (McGlone 1988). The modern vegetation does show an approximate latitudinal gradient in terms of endemism, with more tree species to the north and more grasses/herbs to the south, but this probably reflects broader shifts in climatic conditions since the Miocene (McGlone 1985). The inferred rapid rate of reforestation of most of New Zealand following the last glacial, and during interstadials within it, indicates expansion from many widely distributed ecological refugia, rather than broad geographic migration from a single or few northern refugia (McGlone 1985, 1988; Ogden 1989; Ogden et al. 1992; Newnham et al. 1999). Population genetic methods such as those applied to the scree weta (Trewick et al. 2000) would be informative, as isolation in, and subsequent colonisation from, many small refugia is likely to have resulted in higher diversity than the alternative scenario. Phylogeographic structure would not however be well developed where isolating barriers had not persisted. Existing molecular evidence from a range of invertebrates indicates that intraspecific diversity is higher in New Zealand than across Europe and this is consistent with the existence of a mosaic of ecological refugia (Trewick 2000b; Morgan-Richards et al. 2001; Trewick unpubl. data). To what extent intra- and interspecific genetic diversity in New Zealand can be generally associated with population structuring during the Plio-Pleistocene, and how this relates to species ecology, remains to be tested.

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Appendix 1 Locations sampled for *Deinacrida connectens*–name with abbreviation underlined, longitude/latitude, sample size.

Angelus, 41°54′S, 172°44′E, 4; Mt Altimarlock, 41°45′S, 173°42′E, 6; Mt Arthur, 41°13′S, 172°42′E, 8; Mt Bealey, 42°57′S, 171°33′E, 3; Mt Domet, 44°52′S, 170°22′E, 1; Eyre Peak, 45°18′S, 168°27′E, 3; Foggy Peak, 43°17′S, 171°45′E, 4; Fox Peak, 43°41′S, 170°48′E, 2; Mt Fyffe, 42°19′S, 173°37′E, 6; George Spur, 42°08′S, 173°43′E, 1; Mt Ida, 43°23′S, 171°31′E, 1; Lewis Pass, 42°23′S, 172°21′E, 5; Mt Lyford, 42°27′S, 173°08′E, 1; Mathias, 43°08′S, 171°05′E, 1; Mt Olivier, 43°43′S, 170°04′E, 3; Mt Peel, 41°08′S, 172°35′E, 7; Mt Percival, 42°29′S, 172°56′E, 3; Mt Pisgah, 45°05′S, 170°23′E, 1; Red Hills Ridge, 41°41′S, 173°03′E, 3; Rees Saddle, 44°33′S, 168°34′E, 10; Rocky Top 44°47′S, 170°19′E, 2; Mt St Bathans, 44°46′S, 169°47′E, 2; Spence Peak, 44°52′S, 167°51′E, 2; Mt Sutton, 44°13′S, 169°46′E, 1.