range expansion; endemicity; pliocene; pleistocene; insect; species

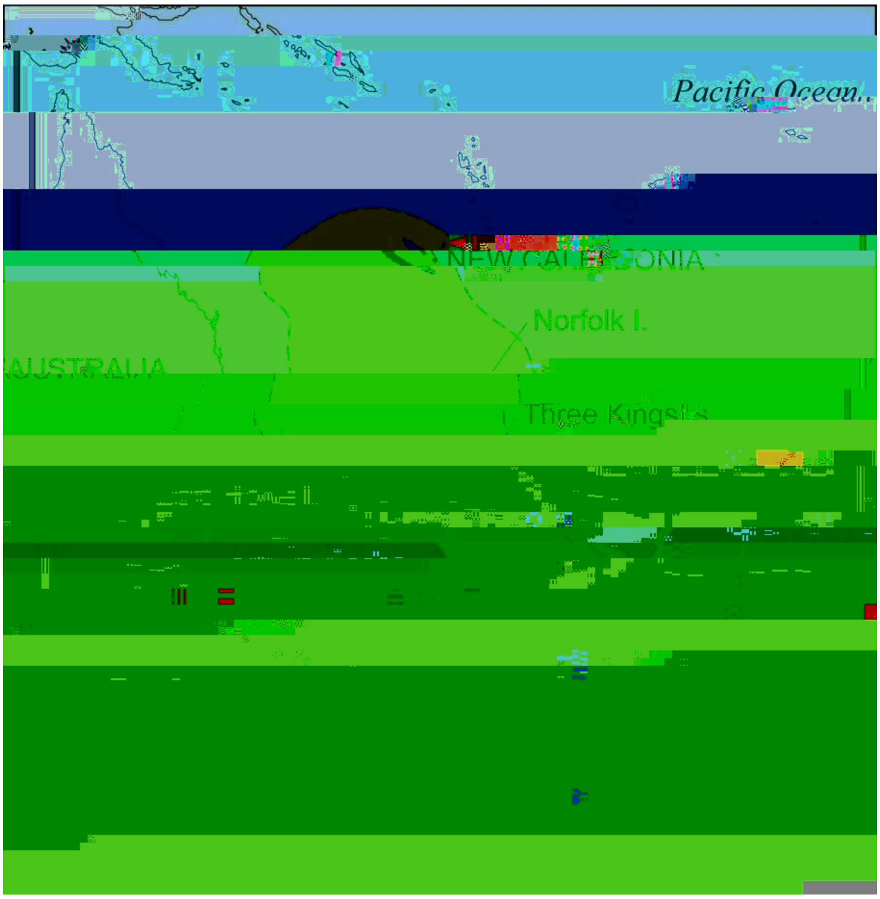
Phylogeography uses the geographic distribution of genetic variants to interpret the role of historical processes in the development of biological distributions. As originally circumscribed, phylogeography deals primarily with the structuring of populations within species [1]. This focus distinguishes it from phylogenetics and the use of species-level phylogenies to infer biogeography [2–5]. However, many of the pitfalls of biogeographic interpretation from species trees apply also to intraspecific phylogeography—there being a natural evolutionary continuum underpinning population genetics, intraspecific phylogeography, interspecific phylogeography and species phylogeny [6].

In its simplest form, two types of information can be gleaned from phylogeographic studies: first, the spatial distribution of genetic variation (e.g., whether the same DNA sequence for a gene is found in individuals from several locations) and second, the extent of differentiation between genetic variants (e.g., the proportion of nucleotide differences among DNA sequences for a given gene). Approaches founded in population genetic theory and latterly statistical phylogeography using coalescent modeling [7,8] allow description and consideration of the amount of variation present and how that variation is partitioned. Thus phylogeographic traits scale from shallow to deep in terms of divergence among sequence variants, with either intense partitioning (heterogeneous) or thorough mixing about which extrinsic factors have influenced gene flow, because: (a) drivers may be contiguous or even coincide in time; and (b) divergence time estimates are imprecise for many reasons at the scale that is relevant in phylogeography [9–11].

1.1. The New Zealand Phylogeographic Context and the Development of the Fauna

New Zealand is an archipelago of nearly 270,000 km^2 situated in the south-western Pacific Ocean [12] (Figure 1). There are two main islands separated by a narrow seaway, Cook Strait, with a much greater distance of ocean to other significant land areas. Australia is a minimum of 1500 km to the west and the island of New Caledonia is 1500 km north. There are a number of small island groups within New Zealand waters including Chatham (east), Three Kings (north) and subantarctic (south).

New Zealand‘s place in the Pacific. The approximate position of the largely submerged continental crust of Zealandia is indicated in yellow.



Uncertainty about the history of the New Zealand landscape (neither certainly continental nor oceanic [13]), and the presence of some peculiar elements in the fauna, have led biologists to view the New formation of New Zealand [17–19]. Most if not all of the pre-existing continent of Zealandia, which is an order of magnitude larger than New Zealand, is today below the sea [21,22] (Figure 1). A more youthful

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Geophysical and biogeographic features of New Zealand past and present. Environmental heterogeneity: , mean annual temperature, , mean annual rainfall, , elevation. Temporal changes: , Pliocene palaeogeography at 3 Ma, , Pleistocene LGM, may yield uneven distribution of biodiversity ( ). , regional insect endemicity in a sample of 1724 species, % of species in a region that are endemic to that region (left), % of all 596 regional endemics that are endemic to a particular region (right). Thus phylogeographic (population) structure is a product of current and past environmental structure. Climate maps (,), courtesy of NIWA [91]. Palaeogeographic reconstructions (,) based on [92] and [93] respectively. Regional insect endemicity ( ) from analysis of data in Fauna of New Zealand series volumes (2,3,12,15, 16,20–21,23,25,27,30,3–36,39–50,53,54,57–59,62,63,65) containing suitable information.

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1.2. Predicting the Past

Spatial variation in climate, topography and vegetation generates fairly steep north-south, and in some places east-west gradients (Figure 2). Spatial variation intersects with temporal variation in these features, as changes in land area have been considerable in New Zealand during and since Pliocene time (Figure 2) [92,94] emerging genome scale data, and coalescent model based approaches promise to enhance the sensitivity of phylogeographic testing [7,97,98].

Phylogeographic outcomes of different geophysical events in North Island New Zealand may be similar. ( ) Taupo volcanic; ( ) LGM forest range; ( ) land emergence since 2 million years ago. Yellow area indicates range of hypothetical taxon. ( ) Black and grey indicate area affected by pyroclastic flow and ash deposits from Taupo eruption. Existing diversity, which may or may not be partitioned in space is extinguished close to centre and subsequently replaced by range expansion. This is expected to result in reduced diversity around the centre; ( ) Climate cooling during glacial events resulted in retraction of forest northwards, and formation of potential refugium. Subsequent expansion of habitat is expected to result in lower diversity in south compared to north through leading-edge re-colonization; ( ) A near identical phylogeographic pattern is expected to result from land formation which resulted in southward extension of North Island, but branch lengths

South Island ( ) Habitat partitioning by glaciation, ( ) Formation of alps, ( ) Alpine fault displacement. On a long narrow island a widely distributed taxon is likely to develop a pattern of isolation by distance, even without any habitat heterogeneity. Geophysical processes may influence the gene genealogy among populations and species that evolve. Yellow area indicates range of hypothetical taxon. ( ) Glaciation (black area) might cause extinction of some populations (and their genetic lineages), and partition residual populations in the north and south. Subsequent retraction of glaciers could allow expansion of forest taxa through leading-edge colonization; ( )

1.3. Pattern and Process

Identifying the pattern of genetic structuring among populations (or other samples) is just a first step in

1.4. Sampling for Phylogeography

The scope of studies of New Zealand invertebrates that involve some spatial and genetic information is enormous, ranging from multispecies to single species, widely sampled to narrowly sampled, with shallow genetic diversity to variation at the informative limits of cytochrom

Variation in the level of mtDNA diversity may by used to infer population expansion

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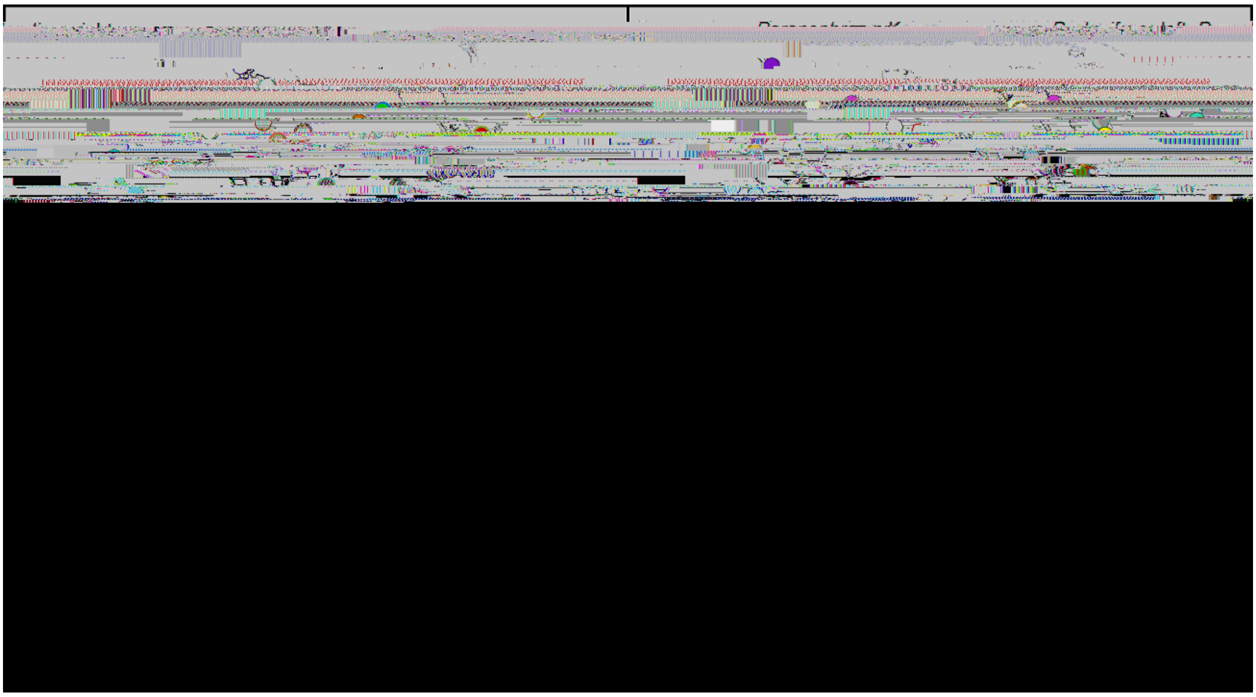

From the 37 putative population-level studies we can conclude that many invertebrates were apparently unaffected by the Pleistocene LGM, as they have widespread, high genetic diversity (e.g., fungus beetles *Epistranus lawsoni* and *Pristoderus bakewelli*, ground weta *Hemiandrus maculifrons* and *H. pallitarsis*, scree weta *Deinacrida connectens*, mite harvestman *Aoraki denticulata*, stick insect *Niveaphasma annulata*, stonefly *Zelandoperla fenestrata*, waterboatman *Sigara potamius*) (Table 3). For example, we see regional diversity and widespread sympatry of divergent haplotype lineages in the forest (fungus beetle Figure 7F). There is clearly differentiated regional diversity in alpine (weta Figure 7B), aquatic (stonefly) and open grass/scrub taxa (cicada Figure 7A). Species that are likely to have extended their ranges during cold glacial cycles, such as alpine, sub-alpine and open-habitat species are well sampled in the New Zealand phylogeographic literature (Table 2). These taxa show regional variation, distinguishing populations that, although currently isolated, could have been connected at lower altitudes during colder times. Alpine environments are thought to have first appeared about five million years ago when fault movement started the formation of the Southern Alps. Evidence of multiple origins of alpine adaptation comes from studies of weta [80] and flightless scarabaeid beetles [65]. The formation of the alpine zone resulted in species radiations (e.g., spiders, moths, cicada, cockroaches, grasshoppers) and the origin of intraspecific diversity (e.g., scree weta,

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