JOURNAL OF THE ROYAL SOCIETY OF NEW ZEALAND
https://doi.org/10.1080/03036758.2022.2079682

REVIEW ARTICLE

Phylogeography reveals the complex impact of the Last Glacial Maximum on New Zealand's terrestrial biota

Katharine A. Marske [a] and Sarah L. Boyer [b]

[a]Department of Biology, University of Oklahoma, Norman, OK, USA; [b]Biology Department, Macalester College, St. Paul, MN, USA

ABSTRACT
We review the major phylogeographic patterns in Aotearoa New Zealand's terrestrial flora and fauna that have been associated with the Ōtira Glaciation of the Pleistocene, the end of which coincides with the global Last Glacial Maximum (LGM). We focus on (1) the complexity of biogeographic histories of New Zealand species, with LGM-driven phenomena overlaying the impacts of mountain-building and other drivers of phylogeographic structure; (2) the locations of glacial refugia and sets of taxa which may have shared refugia; and (3) the role of glaciation in driving diversification. We end with a brief focus on the next directions, including what can we learn about New Zealand's glacial history by expanding our phylogeographic toolbox to include genomic methods and hypothesis-driven inference methods. We provide follow-up questions which take advantage of the wealth of phylogeographic data for New Zealand.

ARTICLE HISTORY
Received 2 April 2022
Accepted 16 May 2022

HANDLING EDITOR
Thomas Buckley

KEYWORDS
Phylogeography; Pleistocene; glacial refugia; biogeographic line; Last Glacial Maximum; Otira glaciation

Introduction

The origin of Aotearoa New Zealand's remarkable fauna and flora has long fascinated naturalists and biogeographers (e.g. Nelson 1975, Diamond 1990). Prior to the widespread use of DNA and phylogeographic methods, the impact of the Pleistocene ice ages and particularly the Last Glacial Maximum (LGM) was considered critical in shaping the distribution of New Zealand's biota, including variation in floral richness patterns (McGlone 1985), the locations of biotic gaps or regions of high species turnover (Wardle 1963), and diversification of endemic New Zealand lineages (Fleming 1979). Thanks to subsequent advances in palaeoecology and phylogeography, we now know that both the LGM in New Zealand, and its impacts on the distributions of species and genetic variation, afford a striking contrast to the 'model' glacial systems of the Northern Hemisphere (Hewitt 2000 and 2004; Wallis and Trewick 2009; Trewick et al. 2011; Wallis et al. 2016). While the extent of glaciation and other climate change impacts were distinctly different from Eurasia and North America, this period also impacted an archipelago which had been reshaping itself since the Miocene (Lu et al. 2005; Bland et al. 2019). In this dynamic landscape, species had to survive the glacial period largely *in situ*, placing an additional survival filter over a biota already shaped

CONTACT Katharine A. Marske ✉ kamarske@ou.edu

by change (e.g. Lee et al. 2001). The result is that many New Zealand lineages show high levels of genetic divergence, often over relatively small geographic space, with each new study adding to a picture of a biota that has assembled over long periods of time and geologically complex conditions (Trewick et al. 2011; Buckley et al. 2015; Wallis and Jorge 2018).

The glacial cycles of the Pleistocene, and particularly the LGM, played a critical role in shaping the modern distributions of species worldwide (Provan and Bennet 2008). While the LGM was a global phenomenon, the precise timing of the coldest period varied at different locations around the planet. In New Zealand, the global LGM coincided with the final advance of the Ōtira Glaciation approximately 20,500–19,000 years ago (Suggate and Almond 2005; Alloway et al. 2007; updated by Newnham et al. 2013); sea level was depressed by ~120–135 m below present level, and colder temperatures and increased aridity during this time resulted in major shifts in the extent and distribution of various biomes across New Zealand (Newnham et al. 2013, Ellis et al. 2015). Today's North and South Islands were connected. In today's South Island, glaciers covered the Southern Alps from Fiordland to north Westland (Vandergoes and Fitzsimons 2003) (Figure 1). As elsewhere, vegetation cover varied significantly between glacials and interglacials: McGlone (1985) has characterised New Zealand as alternating between dominance of two main types of vegetation during Pleistocene glacial cycles: a lowland to montane 'forest flora' during warmer periods, and a montane to alpine 'non-forest flora' during colder periods.

While there is certainly agreement that New Zealand's vegetation cover was drastically altered during the LGM, the past two decades have seen debate concerning the extent to which woody vegetation persisted during this period (Newnham et al. 2013). Some researchers have argued that evidence from the fossil record of beetles suggests much greater extent of woody vegetation than has been inferred from the pollen record (Burge and Shulmeister 2007; Marra and Leschen 2011). In response, McGlone, Newnham, and colleagues re-evaluated New Zealand's LGM pollen record and provided a new reconstruction of vegetation cover (McGlone et al. 2010; Newnham et al. 2013). They describe a North–South cline in forest dominance; in North Island, only Northland and coastlines north of 38° were covered by tall podocarp-broadleaf and beech forest; the abundance of shrubland increased to the south, and dry open grassland dominated the southeast. In South Island, the area with the most significant forest cover would have been along the edge of Nelson, in what is now Karamea Bight, consisting of a shrubland-grassland mosaic with interspersed patches of beech and rare conifer, while in southern South Island glaciers reached the western coastline in most areas, with only a few small patches of shrubland-grassland-forest mosaic persisting on the western shore. To the east of glaciated areas, throughout the great majority of South Island, shrubs, tussock, and herbfield were extensive, with dry open grassland and rare forest patches closer to the coast (Newnham et al. 2013) (Figure 1). The fauna would also have experienced repeated shifts in the sizes and locations of their distributions, periodically persisting in small habitat refugia. Over the past generation, the tools of phylogeography have been used to interrogate the signature that this history has left on the present-day biota of New Zealand.

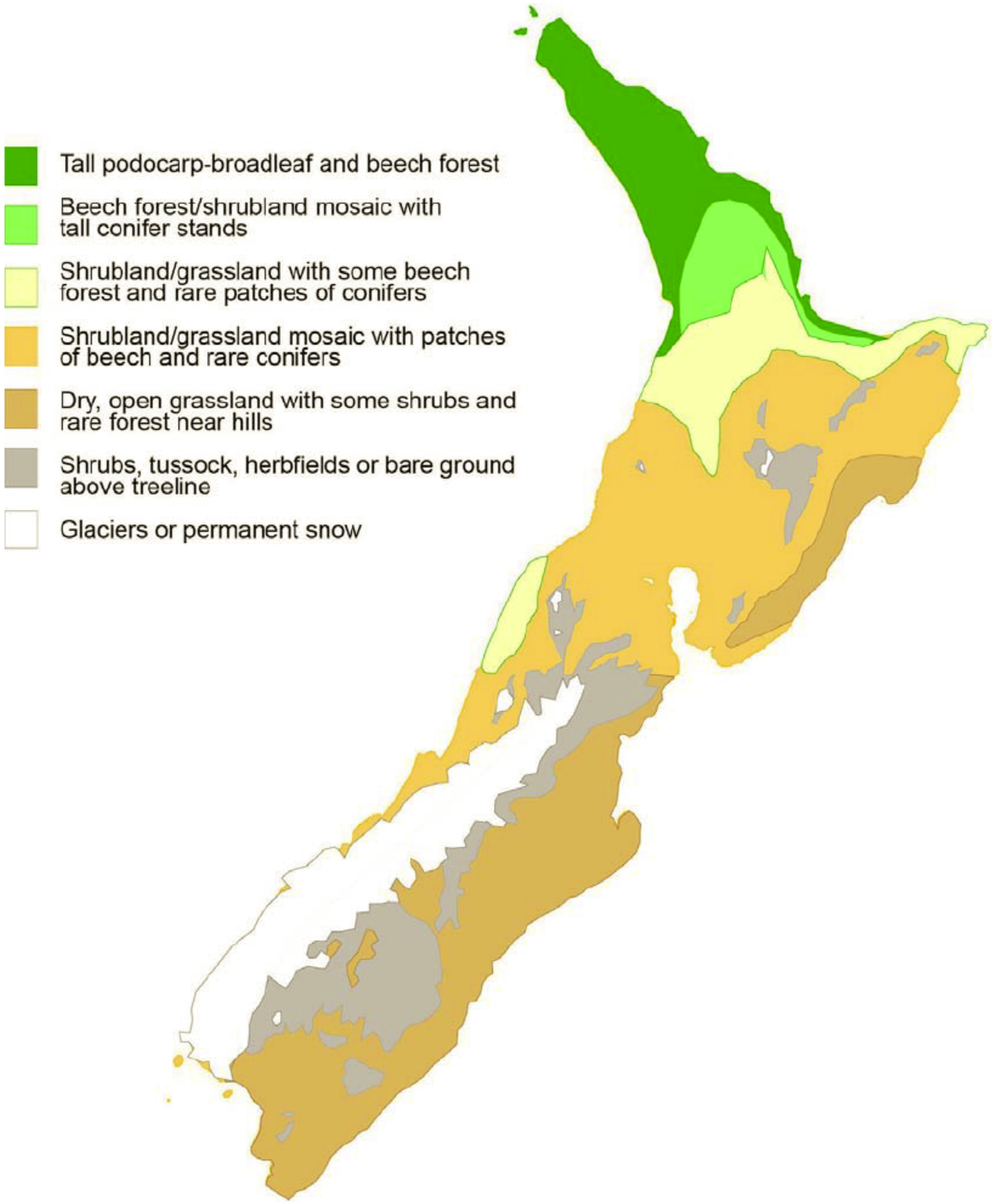

Figure 1. Distribution of major vegetation types during the LGM, adapted with permission from Newnham et al. (2013); see their map for finer spatial resolution of habitat patches and transitions. Despite the restriction of forest habitats relative to their distribution prior to intentional clearing, phylogeographic evidence supports persistence of forest species in scattered refugia throughout North and South Islands. In contrast, species associated with open habitats likely experienced expanded geographic ranges during the glacial period.

Phylogeography in New Zealand

Phylogeography, described as the bridge between population genetics and systematics (Avise et al. 1987), provides a tool for exploring the geography of diversification that is ripe for integration with evidence from other disciplines (Hickerson et al. 2010), such as the timing of geological events (Craw et al. 2016), paleo-records such as subfossils or pollen (Shepherd et al. 2007), or complementary methods such as Ecological Niche Models (ENMs; Marske et al. 2012). While phylogeographic patterns have traditionally ranged from detection of intraspecific genetic lineages to clarifying the evolutionary relationships among recently diverged sister species, an increase in the diversity of genetic/genomic tools is broadening the purview of phylogeography to include features of landscape genetics (Rissler 2016) and phylogenetics (Edwards et al. 2016). Indeed, defining phylogeography as distinct from these other disciplines is particularly complicated for New Zealand, where divergences among sister species (e.g. Baker et al. 2020) and even among intraspecific lineages (Marske et al. 2011; Tardelli Canedo et al. 2021) can exceed millions of years. Here, we largely restrict our focus to the impacts of Pleistocene glaciation on New Zealand's flora and fauna, although that necessarily includes discussion of diversification events initiated before the glacial period.

In a landmark review of New Zealand phylogeography, Wallis and Trewick (2009) identified several widely shared phylogeographic patterns that illuminate the complex impacts of New Zealand's recent geological history. First, many taxa radiated or underwent speciation in association with Pliocene uplift of the Southern Alps and North Island ranges, resulting in diverse lineages that persisted through the Pleistocene. Second, Pleistocene isolation contributed to divergence across the Southern Alps in the South Island and potentially shaped an east–west phylogeographic disjunction in the North Island across the axial mountain range extending from Wellington Harbour to East Cape. Third, despite expectations that southern South Island would have been inhospitable for much of the biota, taxa from a variety of habitats (including forest) show significant phylogeographic structure, including deep lineages, in southern South Island. While this pattern is not universal, it contrasts from the expected 'northern richness, southern purity' pattern hypothesised for lowland temperate habitats based on early Northern Hemisphere phylogeographic studies, where high latitude areas heavily impacted by glaciation harbour lower genetic variation than low latitude areas (Hewitt 2000). Wallis and Trewick's (2009) overarching finding, from their extensive literature review, was that many New Zealand taxa harbour significant phylogeographic structure, much of it predating the Pleistocene, that must have survived all or part of the glacial period in multiple distinct refugia. Given the richness of their review and the wealth of subsequent phylogeographic research, our goal with the current review is to pick up where they left off. We therefore synthesise key findings from the last ~1.5 decades and point to next directions in New Zealand phylogeography.

Phylogeographic patterns and the LGM: North Island (Te Ika-a-Maui)

The histories of North and South Islands are quite different from each other, with one notable contrast being the much more recent widespread marine inundation in North Island. Much of North Island has emerged from marine inundation over the last 1.5 Ma, whereas most of South Island has been above sea level since the late Miocene; consequently, the emergent geomorphological landscape of North Island is effectively much 'younger' than South Island. Substantial geological changes took place in North Island during the late Miocene, including volcanic activity and the creation of mountains and basins. Much of North Island was subsequently inundated during the early Pliocene.

Northern reaches of today's North Island were divided into smaller islands (Morgan-Richards et al. 2001), and most of the southern half was submerged, with the exception of the Wellington area (the far south of today's North Island), which was geographically part of eastern Marlborough (the far north of today's South Island) for several million years prior to the formation of the Cook Strait some 500 Ka (Bunce et al. 2009; Trewick and Bland 2012; Ellis et al. 2015). Mountain-building continued throughout the Pliocene and Pleistocene, with later uplift of the axial ranges in the southern part of North Island occurring approximately 340 ka. During the Pleistocene, in addition to climatic and vegetation changes described earlier, central North Island was affected by major volcanic eruptions that caused habitat destruction and isolation of populations in allopatry (Ellis et al. 2015).

Many studies of North Island's biota have focused on biogeographical boundaries that bisect the landmass either north–south (the Northland Line, the Kauri Line, and the Taupō Line) or east–west (e.g. Cockayne's Line) (Figure 2). Ellis et al. (2015) helpfully contrast two different phenomena that may be described by such biogeographical lines: (1) a division between sister clades isolated by dispersal barriers (ecological or physical), and (2) a boundary between areas of older, genetically diverse populations and newer, less diverse populations. Below, we consider the major biogeographical boundaries identified by previous researchers.

North–south patterning

The Kauri Line, so named because it represents the southern limit of the kauri tree (Wagstaff and Clarkston 2012), marks examples of both divisions between sister clades (e.g. Winterbourn et al. 2017) and a demarcation between areas of relatively lower and higher diversity (e.g. Ellis et al. 2015; Wallis and Trewick 2009). During the LGM, continuous forest habitat in North Island was restricted to areas north of the Kauri Line (Figure 1). Many widespread taxa exhibit the expected pattern of 'northern richness and southern purity'–higher genetic diversity north of the Kauri Line, and higher genetic uniformity to the south–consistent with the expectations of the effect of an LGM refugium in the north (e.g. the Auckland weta *Hemideina thoracica*, Morgan Richards et al. 2001; the stick insect *Clitarchus hookeri,* Buckley et al. 2009, Morgan-Richards et al. 2010; the cicada *Kikihia ochrina,* Ellis et al. 2015; and the giraffe weevil *Lasiorhynchus barbicornis*, Painting et al. 2017). In some cases, researchers have complemented phylogeographic work with ENMs and demonstrated that areas north of the Kauri Line are indeed predicted as a major LGM refugial area for their study taxa (e.g. Buckley et al. 2009, Marske et al. 2011).

Within the northern region bounded by the Kauri Line (Figure 2), land north of the Northland Line is unique, due at least in part to its ultramafic rock soil, rich in iron and magnesium. During the Pliocene, this area was divided into an archipelago of small islands, isolating populations of terrestrial animals and perhaps driving lineage divergence, e.g. leading to the fixation of chromosome rearrangements in different populations in the Auckland weta *Hemideina thoracica* (Morgan-Richards et al. 2001). Today, the Northland peninsula harbours a notably high level of endemism in both plants (McGlone 1985) and insects (Buckley et al. 2015). Ellis et al. (2015) found that nearly every cicada taxon in their study exhibited unique haplotypes north of the

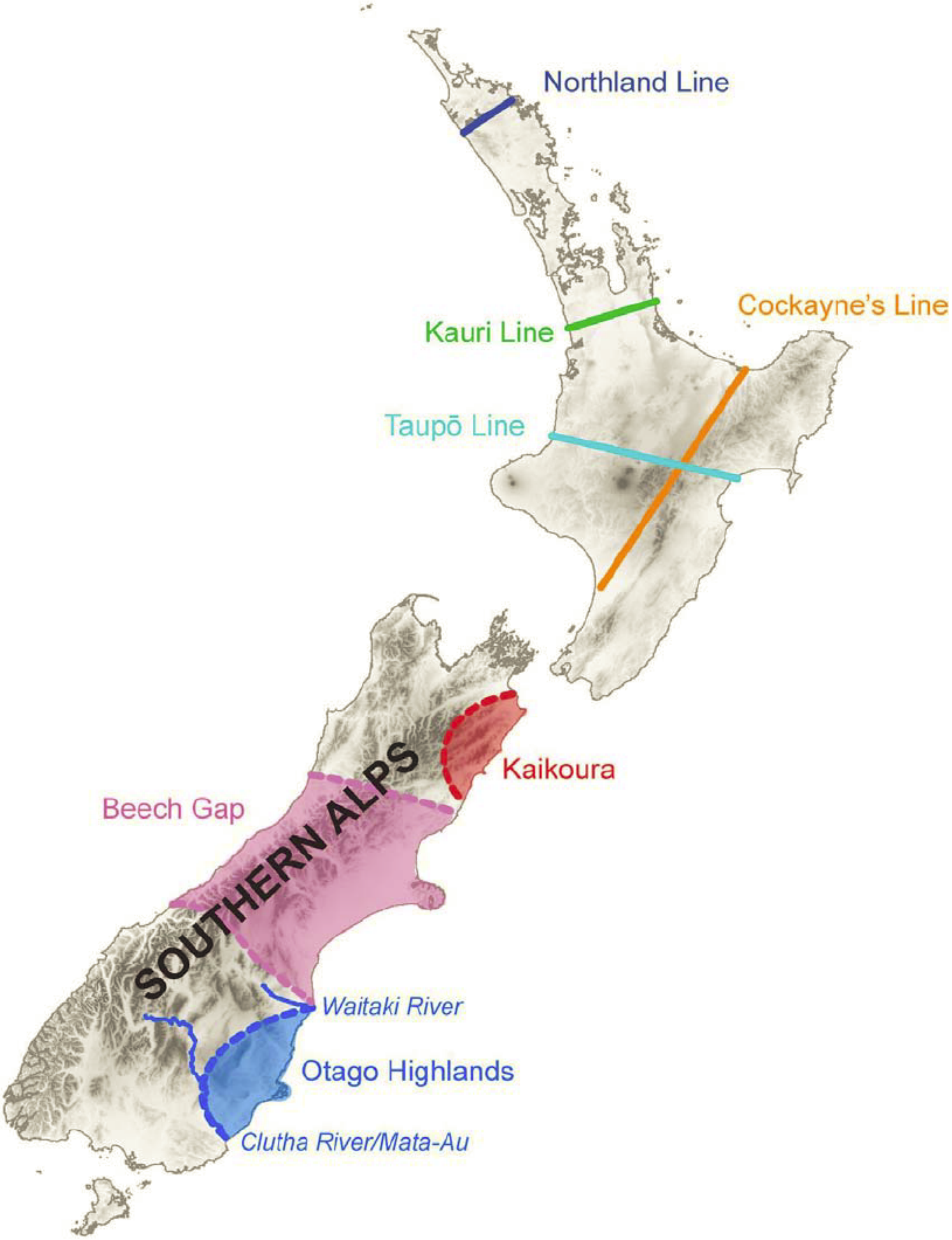

Figure 2. Widely recognised biogeographic lines and other features that recur in the phylogeographic literature. In North Island, the Northland, Kauri, Taupō and Cockayne's Lines define regions of phylogeographic turnover for many species. In South Island, the Southern Alps and Beech Gap are widely recognised geographic features shaping lineage turnover. Less recognised areas of biogeographic interest that appear frequently in the phylogeographic literature are the Central Otago region, including the highlands and major rivers such as the Waitaki and Clutha, and the Kaikoura region. In northeastern South Island, many species either have geographically distinct lineages in the Kaikoura region or experience lineage turnover across the region (e.g. *Kikihia subalpina, Agyrtodes labralis, Brachynopus scutellaris, Pseudopanax ferox*), while in southeastern South Island, many species undergo lineage turnover across the Otago region (e.g. *Agyrtodes labralis, Maoricicada campbelli, Niveaphasma annulata, Pachyornis elephantopus, Dinornys robustus*). (Background digital elevation model from Ollivier & Co, CC-by-3, accessed at koordinates.com)

Northland Line, and Painting et al. (2017) found the same in the giraffe weevil *Lasiorhynchus barbicornis*.

The Taupō Line (Figure 2) was originally discussed as marking a boundary between an area of greater diversity of endemic plants to its north and lower to its south (Wardle 1963); researchers have noted similar patterns in animals (Buckley et al. 2009, 2010, 2015; Marske et al. 2011; Bulgarella et al. 2014; Painting et al. 2017). This line has been drawn at locations between 38.5° and 39.5° by various researchers (see Figure 1 in Ellis et al. 2015). Hypotheses invoked to explain a biogeographic break around this latitude include Pliocene sea-strait flooding and various Pleistocene processes: tectonic uplift, volcanic activity, and glacial cycling. Some animals exhibit divergences around the Taupō Line that predate the Pleistocene: for example, the zopherid beetle *Epistranus lawsoni* (Marske et al. 2011), some native *Oligosoma* skink species (Chapple et al. 2009), and the near-flightless North Island rifleman bird *Acanthisitta chloris granti* (Withers et al. 2021). In other groups, structure associated with the Taupō Line is Pleistocene in origin (e.g. the giraffe weevil *Lasiorhynchus barbicornis*; Painting et al. 2017). In the widespread stick insect *Clitarchus hookeri,* Buckley et al. (2009) found that the lineage that dominates lower North Island and South Island post-dates Pliocene emergence of land from marine inundation, but predates the LGM. They suggest that the species may have colonised areas south of the Taupō Line as marine inundation abated, but endured subsequent near-extirpation from lower North Island.

Of course, the scale on which biogeographic boundaries such as the various named North Island ‘lines’ impact biota depends on the dispersal capabilities of organisms under consideration. For example, the dispersal-limited frog *Leiopelma hochstetteri* is found only north of the Taupo Line (*sensu* Wardle 1963); however, within that range, Fouquet et al. (2010) found strong genetic structure suggestive of multiple species, with divergence times dating back to the Pleistocene. At a much larger geographic scale, in a study of kiwi birds, Weir et al. (2016) found evidence for four genetically distinct lineages of North Island species *Apteryx mantelli,* restricted to Northland, the Coromandel Peninsula, Taranaki, and Gisborne/Hawke’s Bay. For each lineage, they found evidence of a population bottleneck dating to the Pleistocene.

East–west patterning

Ellis et al. (2015) identified a previously unnamed major biogeographic boundary, which they dubbed Cockayne’s Line (Figure 2), following the axial mountain range that extends from Wellington Harbour to East Cape. Elevations are highest in the south and decrease to the north, establishing a gradient proposed to affect the likelihood of dispersal across the range (Cockayne 1911, 1917). Uplift of this range was initiated around 2 Ma, with the most recent mountain-building occurring during the last 500,000 years (Te Punga 1954, Rogers 1989; Bunce et al. 2009). This boundary marks a genetic break in organisms in a wide variety of species, including cicadas, geckos, moas, stick insects, and flightless birds (Ellis et al. 2015; Withers et al. 2021). As with many geographical barriers, Cockayne’s Line reflects processes that operated both long prior to the LGM (e.g. diplodactylid geckos, Nielsen et al. 2011, and certain species of *Kikihia* cicadas, Ellis et al. 2015) as well as in the wake of the LGM (Ellis et al. 2015).

Cockayne's Line is not the only east–west biogeographical boundary in the North Island. McLay et al. (2022) described a division to its west within the parasitic plant *Dactylanthus taylorii,* and noted that it is similar (but not identical) to patterns in the forest fern *Asplenium hookerianum* (Shepherd et al. 2007). The coastal whau tree (*Entelea arborescens*) shows an east–west split dated to the Pleistocene that is unlike patterns seen even in other coastal plants (Shepherd et al. 2019).

Generalizations and exceptions

Within North Island, several major geographic divisions demarcate patterning both in terms of splits between lineages and boundaries between areas of relatively higher and lower genetic diversity in a wide variety of organisms. In some cases, the origin of these patterns can be dated to the LGM; however, in other cases relevant splits predate the LGM (or dates have not been estimated). Finally, some organisms exhibit little-to-no geographic structure or genetic diversity across North Island; e.g. lancewood/ horoeka (Gemmell et al. 2022), and the mite harvester *Aoraki tumidata* (Boyer et al. forthcoming).

Phylogeographic patterns and the LGM: South Island (Te Waipounamu)

South Island landscapes are dominated by the Southern Alps, and the biota is therefore shaped by the joint impacts of Pliocene uplift followed by Pleistocene glaciation. Many species radiated in response to the appearance of novel alpine habitats or to the sundering of populations by new dispersal barriers, (see below), and creation of novel habitats, followed by shifting of these habitats during subsequent glacial cycles, offered opportunities for hybridisation for some taxa (Shepherd et al. 2022, this issue). While the Pleistocene had a profound impact on the distributions of South Island species, Wallis and Trewick (2009) identified multiple South Island taxa with phylogeographic results at odds with a picture of South Island refugia largely restricted to the Nelson region, the region of South Island with the highest density of forest trees during the LGM (e.g. Newnham et al. 2013), instead finding that lineages of diverse taxa emerged from the glacial period without sharp clines in genetic diversity, consistent with survival in multiple habitat refugia, and with high levels of phylogeographic structuring which often predates the Pleistocene period.

Rise of the Southern Alps: setting the stage for glaciation

Uplift of the Southern Alps (Figure 2), which began 8–10 Ma and accelerated around 6 Ma (Lu et al. 2005), radically transformed both South Island and its characteristic biota. Species which colonised and radiated within this new alpine zone include the remarkable alpine flora, in which relatively few colonisers gave rise to a diversity of species and morphologies (reviewed in Heenan and McGlone 2013; Gibbs 2016; and sources therein), and alpine insect radiations among cicadas (*Maoricicada*; Buckley and Simon 2007), wetas (Trewick and Morgan-Richards 2005), cockroaches (*Cellatoblata;* Chinn and Gemmell 2004), stoneflies (McCulloch et al. 2010) and grasshoppers (Koot et al. 2020). For some species, diversification predates the period of orogeny: for example, all of the alpine grasshoppers had speciated well before the origin of their alpine environments (Koot et al. 2020), and divergence among the alpine members of the beetle genus *Syrphetodes* (Ulodidae) predates the origin of the alpine flora (Leschen and Buckley 2015). Likewise, geckos and skinks, which comprise the vast majority of New Zealand's herpetofauna, both experienced their main period of diversification within the Miocene, subsequently radiating into nearly every available habitat type, including the alpine zone (Chapple et al. 2009; Nielsen et al. 2011), and even intraspecific variation among South Island populations often predates the Pleistocene (e.g. Greaves et al. 2007; Chapple et al. 2011; Chapple et al. 2012). Some alpine species may have experienced expanded ranges during the Pleistocene, as suggested by ENMs and high, localised haplotype diversity for the grasshopper *Sigaus australis* (Carmelet-Rescan et al. 2021), high population structure in the cicada *Maoricicada campbelli* (Hill et al. 2009), and the persistence of numerous lineages across diverse taxa that are today characterised by relatively small geographic ranges.

Alpine habitats weren't the only novel opportunities generated by uplift: rather, orogeny resulted in the appearance of diverse habitats at multiple elevations, and many lineages radiated in response, including tiger beetles (*Neocicindella*; Pons et al. 2011); aquatic beetles (Hydrophilidae: *Berosus*; Seidel et al. 2021); the *Kikihia, Maoricicada* and *Amphipsalta-Notopsalta* lineages of cicadas (Buckley and Simon 2007; Marshall et al. 2008, 2012), and New Zealand's iconic moas (Bunce et al. 2009). Evolution of the freshwater fish fauna also reflects the impact of South Island's dynamic geology, beginning in the Miocene and extending through the glacial period. Craw et al. (2016) described 'direct tectonic controls' on evolution of New Zealand's freshwater fish, including radiation within the genus *Galaxias*, speciation within the mudfish genus *Neochanna*, and intraspecific divergence within the upland bully *Gobiomorphus breviceps*. Within the galaxiids, the distributions of different species groups are closely related to the history of the geomorphic zones on which they occur, with lineages sundered by the rise of the Southern Alps and structured by glacial activity (Craw et al. 2016; Waters et al. 2020). Phylogeographic studies have revealed the importance of river capture events in shaping gene flow and isolation among species and lineages (e.g. Waters et al. 2007, Burridge et al. 2008; Waters et al. 2020). In particular, river reversals and capture events across the Pleistocene drove variation within the *Galaxias vulgaris* complex in Otago and Southland, and simultaneous divergence within *Galaxias divergens* and *Gobiomorphus breviceps* in Marlborough (summarised by Waters et al. 2020). Similar geological controls drove the mid-Pleistocene isolation and divergence of three distinct lineages of the stonefly *Zelandoperla maungatuaensis*, whose entire distribution spans four kilometres of the Maungatua Range (McCulloch et al. 2022). Finally, intra- and inter-specific lineages across nearly all groups considered (insects, birds, lizards, fish) have phylogeographic breaks across the Southern Alps, indicating their role as an isolating mechanism as well as a novel habitat (Wallis and Trewick 2009).

The beech gap: separating north and south

While North Island is bisected by numerous biogeographic lines, South Island biogeography has focused on the central waist of South Island, the region most heavily impacted by glaciation, resulting in a region of relatively high biotic turnover (e.g. Wallis et al. 2016), low species richness (Wardle 1963), and disjunct distributions for many species (Leschen et al. 2008). For example, southern beeches, which constitute more than half of New Zealand's standing native forest, are disjunct across central South Island, and this break is widest in the west (Rawlence et al. 2021) The central South Island 'beech gap' (Figure 2) has been hypothesised as glacial in origin, with beech forest expanding across southern South Island from small local refugia rather than dispersing from the north (e.g. Newnham et al. 2013). Rawlence et al. (2021) tested this hypothesis most recently using chloroplast DNA, and despite finding that Silver Beech was most genetically diverse in northern South Island, with only a single (genetically distinct) haplotype south of the beech gap, divergence modelling indicated that this pattern was more consistent with a history of distinct refugia, rather than postglacial expansion across the gap.

Numerous other species from a range of habitats show complex phylogeographic patterns with respect to the beech gap region. Wallis et al. (2016) found evidence for a north–south pattern of lineage divergence coincident with the onset of glaciation (~2 Ma) in alpine genera including rock wrens (*Xenicus*; Weston and Robertson 2015), moas (*Megalopteryx*; Bunce et al. 2009), scree wetas (*Deinacrida connectans*, Trewick 2001); alpine cicadas (*Maoricicada campbelli*; Hill et al. 2009); three genera of grasshopper (Trewick 2001; Trewick and Wallis 2001) and six genera of stonefly, including winged and wingless taxa (McCulloch et al. 2010). Numerous other species also show varying depths of divergence across this region, including among forest leaf litter weevils of the genus *Etheophanus* (Davis et al. 2019) and among intraspecific lineages within two open-habitat tiger beetles of the genus *Neocicindela* (Pons et al. 2011), the saproxylic forest beetle *Agyrtodes labralis* (Leiodidae; Marske et al. 2009, 2012), and the aquatic beetle *Tormus helmsi* (Hydrophilidae; Fikáček et al. 2013).

A few arthropods show phylogeographic patterns that are enigmatic with respect to the beech gap: for example, the saproxylic forest beetle *Brachynopus scutellaris* (Staphylinidae) is either disjunct or occurs at extremely low abundance across the western beech gap, despite occurring in non-beech forests elsewhere, yet divergence across the gap is relatively recent (late Pleistocene; Leschen et al. 2008; Marske et al. 2012, 2020). At the other extreme, two arthropods appear to have persisted in refugia in the heart of the gap region. The forest litter mite harvester *Neopurcellia salmoni*, which occurs only along the west coast from Lake Kaniere through south Fiordland, comprises two clades which likely diverged following the Oligocene Marine Transgression, including a lineage spanning the beech gap region (Tardelli Canedo et al. 2021). Deep divergences within this species, including geographically distinct lineages within these two clades that range from Pliocene to mid-Pleistocene in age, point to a species that is extremely dispersal limited, necessitating survival of each lineage very close to its current distribution (Tardelli Canedo et al. 2021). On the eastern side of the gap, Hill et al. (2009) found two relict populations of *Maoricicada campbelli* that diverged as part of the main species radiation ~1 Ma. Finally, the distribution of the alpine tree weta *Hemideina maori* falls almost entirely within the gap region, and divergence among intraspecific lineages initiated pre-Pleistocene, indicating that this species must have persisted within multiple refugia within the gap itself (King et al. 2020). This suggests that the gap region would likely have been suitable for alpine species, despite the intensity of glaciation in the region (e.g. Hill et al. 2009; Carmelet-Rescan et al. 2021).

Microrefugia and dynamic habitats

The studies above have reinforced the necessity of numerous South Island microrefugia to explain patterns of strong geographic structuring among widely distributed species plus maintenance of a high number of small-range endemic species which radiated prior to the Pleistocene. Some of these refugia likely existed in close proximity to glaciers: for example, Weir et al. (2016) implicated tiny coastal refugia in the Haast region and northern and southern Fiordland in driving Pleistocene diversification within southern brown kiwi/Tokoeka (*Apteryx australis*; larger refugia likely existed in Stewart Island/ Rakiura and Canterbury). These fit with patterns noted for other species: ENMs for the saproxylic beetles *A. labralis, B. scutellaris*, and *E. lawsoni* all indicate a potential refugium in the Haast region, as well as 2–3 refugia in northern South Island. For *A. labralis* and *B. scutellaris*, two dispersal reconstruction methods on different datasets (mitochondrial CO1 and genomic SNPs; Marske et al. 2012, 2020) identified the Haast region as a potential source for colonisation of southern South Island. For *B. scutellaris*, the Haast corridor is also home to a mitochondrial lineage otherwise restricted to North Island (Leschen et al. 2008), while three out of the four mitochondrial lineages within the *Etheophanus optandus/E. nitidellus* complex occur within the Haast region (Davis et al. 2019).

While eastern South Island was mostly open habitats, with smaller, more dispersed patches of forest (Figure 1), some forest species maintained distinct lineages in the east. Microsatellite data for the tree *Pseudopanax ferox* indicate that genetic variation and endemism are widely distributed throughout its range, including in southeastern South Island (Shepherd and Perrie 2011). Distinct genomic clusters were detected within the Nelson-Marlborough region and from Kaikoura to Southland–the first lowland tree for which evidence exists of long-term glacial persistence at high latitudes in southeastern South Island (Shepherd and Perrie 2011). Microsatellite turnover in *P. ferox* is consistent with patterns found in the forest beetles *A. labralis*, which has distinct mitochondrial lineages in Nelson and Marlborough to Kaikoura (Marske et al. 2009), and *B. scutellaris*, which has a distinct genomic cluster which expanded from Kaikoura down eastern South Island (Marske et al. 2020) (Figure 2).

While forest refugia would have been scattered among habitat patches during glacial cycles, eastern South Island species from mixed or open habitats likely benefited from Plio-Pleistocene expansion of dry habitats. For the cicada *Amphipsalta strepitans*, which favours dry slopes and riverbeds, ENMs suggested little range reduction during the LGM, and genetic evidence is consistent with persistence in multiple eastern refugia (Marshall et al. 2012). Several species of *Neocicindella*, which also occupy open habitats, are wholly or mostly distributed in eastern South Island, suggesting histories of persistence (Pons et al. 2011). The stick insect *Niveaphasma annulata,* an ecological generalist, is largely restricted to southern and eastern South Island, with phylogeographic breaks across Otago and the Waitaki River, and persistence of suitable habitats along coastal margins may have facilitated gene flow during the glacial period (O'Neill et al. 2009). A distinct southern South Island gene pool detected for mānuka (*Leptospermum scoparium*) via pooled whole-genome sequencing likely expanded during the Plio-Pleistocene, taking advantage of the extensive distribution of tussock grasslands and shrublands (Koot et al. 2022). Together with southern beech, mānuka are associated with sooty mould fungi, which host multiple endemic beetles (Buckley et al. 2015).

The widespread distribution of mānuka in southern South Island during the LGM may shed light on the puzzling mitochondrial history of the sooty mould feeder *Hisparonia hystrix* (Nitidulidae), which–aside from late Pleistocene divergence of a Stewart Island lineage from all remaining populations–shows little phylogeographic structure across South Island (Marske et al. 2012).

Retreat of forests and expansion of grass-and shrublands also shaped phylogeographic patterns for moas across a variety of habitats in the east and south. The heavy-footed moa (*Pachyornis elephantopus*) occurred mostly in grassland, shrubland and forest margins, and likely experienced significant changes to its distribution during glacial cycles (Rawlence et al. 2012). However, environmental change appears not to have impacted population size for heavy-footed or crested moas (*Pachyornis australis*; Nelson region) (Rawlence et al. 2012), consistent with evidence from four other moa species (Allentoft et al. 2015). Lineage divergence in the heavy-footed moa delimits northeastern and southern/southeastern populations, likely reflecting fluctuations in habitat and connectivity across central Otago and the Clutha River drainage (Rawlence et al. 2012). A haplotype network for South Island giant moa, *Dinornys robustus*, also indicates greater haplotype turnover between southern Canterbury and Otago than within either region (McCallum et al. 2013). This contrasts with phylogeographic patterns for *Emeus crassus*, which is also eastern in distribution, but favoured wet forests; a lack of population structure suggests range restriction to a single glacial refugium, likely in the southeast (Bunce et al. 2009). The coastal moa *Euryapteryx curtis* would have experienced extensive habitat shifts across the Pleistocene, and haplotype variation in this species shows little geographical structure (McCallum et al. 2013).

Shifting habitat mosaics drove population divergence for many species, but for some, they provided opportunities for genetic mixing, resulting in complex phylogeographic patterns. The cicada genus *Kikihia* began to diversify during increased mountain building and appearance of varied habitats, but most lineages appeared in the Pleistocene (Marshall et al. 2008), when the geographic extent of different vegetation types would have been in flux. Several South Island lineages show extensive hybridisation, particularly the *Kikihia 'westlandica'* group, defined using mtDNA, which now appears to be the result of a mitochondrial capture event early in the radiation followed by hybridisation among lineages which now occupy three distinct vegetation types (Banker et al. 2017; see also Shepherd et al. 2022, this issue). As with the alpine grasshoppers, some *Kikihia* lineages diverged prior to the availability of the habitats they now occupy, necessitating habitat-switching, which would have facilitated contact among recently diverged populations (i.e. *Kikihia muta* group; Banker et al. 2017). These South Island histories, which show the effects of glacial cycles, are more difficult to disentangle than relationships among North Island lineages, which experienced more directional environmental change (i.e. continued uplift; Banker et al. 2017).

Cradles and museums

Finally, South Island is characterised by extreme phylogeographic contrasts. On the one hand, the island has served as cradle and museum for deep phylogeographic lineages, including the geckos, skinks, alpine grasshoppers, and mite harvester *Neopurcella*. A second mite harvester, *Aoraki denticulata*, also restricted to native forests, shows similarly deep intraspecific divergence at the mitochondrial CO1 locus (up to 20%; Boyer et al. 2007) and likely began radiating in the proto-Southern Alps (Fernández and Giribet 2014). Two zopherid beetles also show phylogeographic patterns consistent with extreme dispersal limitation: *Epistranus lawsoni* is flightless and less than 2 mm in length, yet is widely distributed across New Zealand, with lineage evolution that reflects both the complex topographic history of North Island and long term persistence in South Island; deep structuring *within* South Island lineages indicates divergence that predates the Pleistocene in the west, and may reach back into the Miocene in the east (Marske et al. 2011, 2012). The larger-bodied *Pristoderus bakewelli* shows a similar pattern of early Pleistocene divergences nested within older, geographically distinct intraspecific lineages, as well as a lineage detected only in Southland and the Chatham Islands which dates to the early Pliocene or late Miocene (Marske et al. 2011). While these scenarios all rely on mitochondrial DNA, which has well-known limitations, these results for disparate species point to a wealth of lineages entering the LGM already highly structured, requiring multiple distinct refugia spread throughout western South Island or populations large enough to retain polymorphism through glacial cycles. Many other litter-dwelling arthropods have complex phylogeographic histories that–while less extreme–point to extensive glacial persistence in multiple refugia throughout South Island (Buckley et al. 2015).

On the other hand, some species do reflect patterns consistent with latitudinal retreat and expansion ('northern richness, southern purity'). For the forest cicada *Kikihia subalpina*, which is distributed in South Island and southern North Island, evidence for up to three refugia were detected in northern South Island (Nelson, Marlborough and Kaikoura), while much less variation was detected in clades occurring farther south (Marshall et al. 2009). The stick insects *Argosarchus horridus* (Buckley et al. 2009) and *Clitarchus hookeri* (Buckley et al. 2010) are also distributed across both islands and have reduced genetic diversity in the south; together with the cicadas, they present an interesting contrast between leaf litter and arboreal arthropods in the impacts of glaciation on species from these highly distinct niches. The distribution of the wētā *Hemideina crassidens* straddles Cook Strait, and reduced nucleotide diversity moving away from the core of its range is consistent with northward expansion during glacials and southern expansion during interglacials (Bulgarella et al. 2014). Similarly, the trees *Pseudopanax crassifolius* (Gemmell et al. 2022) and *Sophora* spp. (Shepherd et al. 2017) have severely reduced genetic diversity in South Island and may have recolonised post-LGM.

Summary and future directions: new data types, analyses and expectations

In the ~1.5 decades since Wallis and Trewick 2009, phylogeographic studies have reinforced their initial portrait of a biota characterised by significant phylogeographic structure, and significant variation in how that structure is geographically partitioned. Phylogeographic patterns across phylogenetically diverse lineages from a variety of habitats together reflect all of the archipelago's dynamic geological history from the late Miocene onward, including glacial histories characterised by persistence in multiple refugia and maintenance of extensive structure. Our review is biased toward species with extensive geographic sampling and strong phylogeographic structure, but there are notable exceptions, including species with comparatively little structure at all (e.g. Kererū, Goldberg et al. 2011; Kākā, Dussex et al. 2015; Kārearea, Trewick and Olley 2016; the cicadas *Amphipsalta zelandica*, *A. cingulata* and *Rhodopsalta leptomera*, Marshall et al. 2011, Bator et al. 2021) or those which show divergence across Cook Strait but little other intraspecific variation (e.g. Whio, Robertson et al. 2007; Weka, Trewick et al. 2017; the cicadas *Rhodopsalta cruentata* and *R. microdora*, Bator et al. 2021; the stonefly *Stenoperla helsoni*, McCulloch et al. 2019). Notably, many birds show relatively little phylogeographic structure, potentially indicating stronger impacts of habitat reductions (compared to arthropods and lizards, which may have maintained higher population sizes and been able to persist in smaller refugia) as well as higher dispersal ability. Striking contrasts in phylogeographic structure exist even within genera (e.g. *Pseudopanax ferox/ P. crassifolius*; Shepherd and Perrie 2011; Gemmel et al. 2022) and among ecotypes within radiations (e.g. mesic- versus dry-habitat cicadas in each of the cicada genera *Kikihia, Rhodopsalta* and *Amphipsalta*; see Bator et al. 2021). Nevertheless, these combined histories point to a biogeography that continues to make the archipelago a rich natural laboratory for all aspects of the evolutionary process.

Over the past decade, new approaches to generating and analyzing large genetic datasets have permitted researchers to expand far beyond single-locus or few-locus approaches. In 2011, Trewick et al. predicted that '[t]he emergence and availability of next generation sequencing will be a boon to phylogeography'. However, aside from those using ancient DNA, New Zealand studies that leverage next-gen technologies remain rare. Weir et al. (2016) use genome-wide SNP data in their phylogeographic analysis of kiwis, Shepherd et al. (2019) use ddRAD-seq in their study of *Dicksonia* tree ferns, Marske et al. (2020) used ddRAD-seq to revisit patterns for two saproxylic beetles, Koot et al. (2020, 2022) used mitochondrial genomes (in grasshoppers) and pooled whole genome resequencing (in mānuka) to ask phylogeographic-scale questions, and McCulloch et al. (2022) used genotyping-by-sequencing to test for spatial structure in a range-restricted stonefly, but to our knowledge, these are the only genome-scale phylogeographic studies of New Zealand biota to date. Target enrichment of ultra-conserved elements permits phylogenomic analysis of non-model organisms on phylogeographic scales of time and taxonomy; for example, this approach has been used in species delimitation of dispersal-limited arachnids (Derkarabetian et al. 2022) and shows promise for resolving long-standing questions in New Zealand's mite harvester fauna, (manuscript in prep, SLB). We urge researchers to adopt these novel approaches widely– while noting a greater preponderance of multi-locus datasets since Wallis and Trewick (2009), with many papers building and deepening existing datasets to include more species and greater geographic coverage.

Given the complex assortment of phylogeographic histories described above, it will be particularly important for researchers to consider multiple working hypotheses and to explicitly compare statistical support for alternative biogeographical scenarios. While there has been progress on this front, many phylogeographic studies continue to base their conclusions largely on phylogenetic and network-based methods, likely due to a lasting emphasis on identifying species boundaries and quantifying the extent of spatial structuring. As has been noted by previous authors, the questions and approaches of phylogeography can lend themselves to biogeographic story-telling (Crisp et al. 2011, Trewick et al. 2011). This is part of the appeal of the discipline; many of us are eager to 'know what happened' and to explain present-day patterns in the distribution of biodiversity in ways that make intuitive sense. However, this aspect of our field can also tempt researchers to look for the patterns they wish to see, and we encourage students of New Zealand's biogeographic history to maintain skepticism of easy explanations.

Researchers have documented high phylogeographic structure in many New Zealand taxa, but pinpointing the causes of that structure has often proved challenging, highlighting the importance of robust dating strategies for identifying key periods of change within and across lineages. For example, Seidel et al. (2021) found that dated phylogenies for the aquatic beetle *Berosus* that were based on widely-used beetle substitution rates significantly underestimated dates of colonisation and divergence compared to analyses based on multiple fossil calibration schemes. While obtaining appropriate fossil calibration points is likely to remain a significant challenge, they will likely be key to deciphering how New Zealand's dynamic landscape has driven evolution of its biota. In systems for which a robust fossil record is not currently available, researchers should continue to interpret molecular clock estimates with caution.

Finally, while the expectation a generation ago may have been that co-distributed organisms would display identical phylogeographic patterns reflecting shared geographic history, it is now clear that idiosyncratic variation across taxa is the rule rather than the exception (e.g. Trewick et al. 2011). This creates opportunities to test new questions about key drivers of this variation, including how variation in species' traits (Zamudio et al. 2016) or the impacts of biotic interactions (Waters et al. 2013) shape differences in the orientation of intraspecific lineages and phylogeographic breaks, or differences in population dynamics within lineages. It also creates opportunities for a consideration of the mechanisms most likely to lead to concordance or discordance, given landscape history and variation in dispersal opportunities among species (e.g. Marske et al. 2020). This may be particularly relevant for North Island, where the same or geographically close biogeographic lines may connect to very different hypotheses on the drivers of genetic variation (e.g. Ellis et al. 2015). Finally, given the richness of phylogeographic datasets of high spatial resolution, predictive phylogeographic methods (Espíndola et al. 2016) could be leveraged to hasten the detection of cryptic lineages, aiding in species discovery and biodiversity conservation.

Acknowledgements

The authors gratefully acknowledge Thomas Buckley and Graham Wallis for the invitation to write this review, and Richard Leschen and Chris Simon for helpful suggestions which significantly improved the manuscript. We also thank Dineesha Premathilake and Phoebe Fu for assistance with the literature search, and Matt McGlone and Rewi Newnham for assistance with Figure 1.

Disclosure statement

No potential conflict of interest was reported by the author(s).

ORCID

Katharine A. Marske http://orcid.org/0000-0002-9837-9367
Sarah Boyer https://orcid.org/0000-0003-1414-4489

References

Allentoft ME, Heller R, Oskam CL, Lorenzen ED, Hale ML, Gilbert MTP, Jacomb C, Holdaway RN, Bunce M. 2015. Extinct New Zealand megafauna were not in decline before human colonization. Proc Natl Acad Sci USA 111(13):4922–4927. doi:10.1073/pnas.1314972111

Alloway BV, Lowe DJ, Barrell DJA, Newnham RM, Almond PC, Augustinus PC, Bertler NAN, Carter L, Litchfield NJ, McGlone MS, et al. 2007. Towards a climate event stratigraphy for New Zealand over the past 30 000 years (NZ-INTIMATE project). Journal of Quaternary Science. 22(1):9–35.

Avise JC, Arnold J, Ball RM, Bermingham E, Lamb T, Neigel JE, Reeb CA, Saunders NC. 1987. Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics. Annual Review of Ecology and Systematics. 18:489–522. doi:10.1146/annurev.es.18.110187.002421

Baker CM, Boyer SL, Giribet G. 2020. A well-resolved transcriptomic phylogeny of the mite harvestman family Pettalidae (Arachnida, Opiliones. Cyphophthalmi) reveals signatures of Gondwanan vicariance. J Biogeogr. 47(6):1345–1361. doi:10.1111/jbi.13828.

Banker SE, Wade EJ, Simon C. 2017. The confounding effects of hybridization on phylogenetic estimation in the New Zealand cicada genus *Kikihia*. Molecular Phylogenetics and Evolution. 116:172–181. doi:10.1016/j.ympev.2017.08.009.

Bator J, Marshall DC, Hill KBR, Cooley JR, Leston A, Simon C. 2021. Phylogeography of the endemic red-tailed cicadas of New Zealand (Hemiptera: Cicadidae: *Rhodopsalta*), and molecular, morphological and bioacoustical confirmation of the existence of Hudson's *Rhodopsalta microdora*. Zoological Journal of the Linnean Society.:zlab065. doi:10.1093/zoolinnean/zlab065.

Bland KJ, Nicol A, Kamp PJJ, Nelson CS. 2019. Stratigraphic constraints on the late Miocene–Pleistocene evolution of the North Island Fault System and axial ranges in the central Hikurangi subduction margin, New Zealand. New Zealand Journal of Geology and Geophysics. 62:248–272. doi:10.1080/00288306.2018.1545675.

Boyer SL, Baker JM, Giribet G. 2007. Deep genetic divergences in *Aoraki denticulata* (Arachnida, Opiliones, Cyphophthalmi): a widespread 'mite harvestman' defies DNA taxonomy. Mol Ecol. 16(23):4999–5016. doi:10.1111/j.1365-294X.2007.03555.x.

Boyer SL, Dohr SR, Tuffield MS, Shu Y, Moore CD, Hahn KM, Ward RS, Nguyen P, Morisawa R. Forthcoming. Diversity and distribution of the New Zealand endemic mite harvestman genus *Aoraki* (Arachnida, Opiliones, Cyphophthalmi, Pettalidae), with the description of two new species. Invertebrate Systematics.

Buckley TR, Krosch M, Leschen RAB. 2015. Evolution of New Zealand insects: summary and prospectus for future research. Austral Entomology. 54(1):1–27. doi:10.1111/aen.12116.

Buckley TR, Marske KA, Attanayake D. 2009. Identifying glacial refugia in a geographic parthenogen using palaeoclimate modelling and phylogeography: the New Zealand stick insect *Argosarchus horridus* (White). Mol Ecol. 18(22):4650–4663. doi:10.1111/j.1365-294X.2009.04396.x.

Buckley TR, Marske K, Attanayake D. 2010. Phylogeography and ecological niche modelling of the New Zealand stick insect *Clitarchus hookeri* (White) support survival in multiple coastal refugia. Journal of Biogeography. 37(4):682–695. doi:10.1111/j.1365-2699.2009.02239.x.

Buckley TR, Simon C. 2007. Evolutionary radiation of the cicada genus *Maoricicada* Dugdale (Hemiptera: Cicadoidea) and the origins of the New Zealand alpine biota. Biol J Linnean Soc. 91(3):419–435. doi:10.1111/j.1095-8312.2007.00807.x.

Bulgarella M, Trewick SA, Minards NA, Jacobson MJ, Morgan-Richards M. 2014. Shifting ranges of two tree weta species (*Hemideina* spp.): competitive exclusion and changing climate. Journal of Biogeography. 41(3):524–535. doi:10.1111/jbi.12224.

Bunce M, Worthy TH, Phillips MJ, Holdaway RN, Willerslev E, Haile J, Shapiro B, Scofield RP, Drummond A, Kamp PJJ, Cooper A. 2009. The evolutionary history of the extinct ratite moa and New Zealand Neogene paleogeography. Proc Natl Acad Sci U S A. 106(49):20646–20651. doi:10.1073/pnas.0906660106.

Burge PI, Shulmeister J. 2007. An MIS 5a to MIS 4 (or early MIS 3) environmental and climatic reconstruction from the Northwest South Island, New Zealand, using beetle fossils. J Quat Sci. 22(5):501–516. doi:10.1002/jqs.1088.

Burridge CP, Craw D, Jack DC, King TM, Waters JM. 2008. Does fish ecology predict dispersal across a river drainage divide? Evolution. 62(6):1484–1499. doi:10.1111/j.1558-5646.2008.00377.x.

Carmelet-Rescan D, Morgan-Richards M, Koot EM, Trewick SA. 2021. Climate and ice in the last glacial maximum explain patterns of isolation by distance inferred for alpine grasshoppers. Insect Conservation and Diversity. 14(5):568–581. doi:10.1111/icad.12488.

Chapple DG, Bell TP, Chapple SNJ, Miller KA, Daugherty CH, Patterson GB. 2011. Phylogeography and taxonomic revision of the New Zealand cryptic skink (*Oligosoma inconspicuum*; Reptilia: Scincidae) species complex. Zootaxa. 2782(1):1. doi:10.11646/zootaxa.2782.1.1.

Chapple DG, Birkett A, Miller KA, Daugherty CH, Gleeson DM. 2012. Phylogeography of the endangered Otago Skink, *Oligosoma otagense*: population structure, hybridisation and genetic diversity in captive populations. PLOS ONE. 7(4):e34599. doi:10.1371/journal.pone.0034599.

Chapple DG, Ritchie PA, Daugherty CH. 2009. Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). Molecular Phylogenetics and Evolution. 52(2):470–487. doi:10.1016/j.ympev.2009.03.021.

Chinn WG, Gemmell NJ. 2004. Adaptive radiation within New Zealand endemic species of the cockroach genus *Celatoblatta* Johns (Blattidae): a response to Plio-Pleistocene mountain building and climate change. Mol Ecol. 13(6):1507–1518. doi:10.1111/j.1365-294X.2004.02160.x.

Cockayne L. 1911. Observations concerning evolution derived from ecological studies in New Zealand. Transactions and Proceedings of the New Zealand Institute. 44:1–50.

Cockayne L. 1917. Notes on New Zealand floristic botany, including descriptions of new species. Transactions and Proceedings of the New Zealand Institute. 49:56–65.

Craw D, Upton P, Burridge CP, Wallis GP, Waters JM. 2016. Rapid biological speciation driven by tectonic evolution in New Zealand. Nature Geoscience. 9(2):140–144. doi:10.1038/ngeo2618.

Crisp MD, Trewick SA, Cook LG. 2011. Hypothesis testing in biogeography. Trends Ecol Evol. 26 (2):66–72. doi:10.1016/j.tree.2010.11.005.

Davis SR, Brav-Cubitt T, Buckley TR, Leschen RAB. 2019. Systematics of the New Zealand Weevil *Etheophanus* Broun (Curculionidae: Molytinae). Zootaxa. 4543(3):341–374. doi:10.11646/zootaxa.4543.3.2.

Derkarabetian S, Starrett J, Hedin M. 2022. Using natural history to guide supervised machine learning for cryptic species delimitation with genetic data. Front Zool. 19(1):8. doi:10.1186/s12983-022-00453-0.

Diamond J. 1990. New Zealand as an archipelago: an international perspective. In: Ecological restoration of New Zealand islands. Wellington: Department of Conservation; p. 3–8.

Dussex N, Sainsbury J, Moorhouse R, Jamieson IG, Robertson BC. 2015. Evidence for Bergmann's rule and not allopatric subspeciation in the threatened Kaka (*Nestor meridionalis*). Journal of Heredity. 106(6):679–691. doi:10.1093/jhered/esv079.

Edwards SV, Potter S, Schmitt CJ, Bragg JG, Moritz C. 2016. Reticulation, divergence, and the phylogeography-phylogenetics continuum. Proc Natl Acad Sci U S A. 113(29):8025–8032. doi:10.1073/pnas.1601066113.

Ellis EA, Marshall DC, Hill KBR, Owen CL, Kamp PJJ, Simon C. 2015. Phylogeography of six codistributed New Zealand cicadas and their relationship to multiple biogeographical boundaries suggest a re-evaluation of the Taupo Line. Journal of Biogeography. 42(9):1761–1775. doi:10.1111/jbi.12532.

Espíndola A, Ruffley M, Smith ML, Carstens BC, Tank DC, Sullivan J. 2016. Identifying cryptic diversity with predictive phylogeography. Proc R Soc B-Biol Sci. 283(1841):20161529. doi:10.1098/rspb.2016.1529.

Fernández R, Giribet G. 2014. Phylogeography and species delimitation in the New Zealand endemic, genetically hypervariable harvestman species, *Aoraki denticulata* (Arachnida, Opiliones, Cyphophthalmi). Invertebrate Systematics. 28(4):401. doi:10.1071/IS14009.

Fikáček M, Minoshima Y, Vondráček D, Gunter N, Leschen RAB. 2013. Morphology of adults and larvae and integrative taxonomy of southern hemisphere genera *Tormus* and *Afrotormus* (Coleoptera: Hydrophilidae). Acta Entomologica Musei Nationalis Pragae. 53:75–156.

Fleming CA. 1979. The geological history of New Zealand and its life. Auckland: Auckland University Press.

Fouquet A, Green DM, Waldman B, Bowsher JH, McBride KP, Gemmell NJ. 2010. Phylogeography of *Leiopelma hochstetteri* reveals strong genetic structure and suggests new conservation priorities. Conserv Genet. 11(3):907–919. doi:10.1007/s10592-009-9935-8.

Gemmell MR, Shepherd LD, Zuccarello GC, Perrie LR. 2022. Phylogeography of the widespread New Zealand tree lancewood/horoeka (*Pseudopanax crassifolius*; Araliaceae). N Z J Bot. doi:10.1080/0028825X.2022.2037670.

Gibbs GW. 2016. Ghosts of Gondwana: the history of life in New Zealand. Nelson: Potton & Burton.

Goldberg J, Trewick SA, Powlesland RG. 2011. Population structure and biogeography of Hemiphaga pigeons (Aves: Columbidae) on islands in the New Zealand region. Journal of Biogeography. 38(2):285–298. doi:10.1111/j.1365-2699.2010.02414.x.

Greaves SNJ, Chapple DG, Gleeson DM, Daugherty CH, Ritchie PA. 2007. Phylogeography of the spotted skink (*Oligosoma lineoocellatum*) and green skink (*O. chloronoton*) species complex (Lacertilia: Scincidae) in New Zealand reveals pre-Pleistocene divergence. Molecular Phylogenetics and Evolution. 45(2):729–739. doi:10.1016/j.ympev.2007.06.008.

Heenan PB, McGlone MS. 2013. Evolution of New Zealand alpine and open-habitat plant species during the late Cenozoic. New Zealand Journal of Ecology. 37(1):105–113.

Hewitt G. 2000. The genetic legacy of the Quaternary ice ages. Nature. 405(6789):907–913. doi:10.1038/35016000.

Hewitt GM. 2004. Genetic consequences of climatic oscillations in the Quaternary. Phil Trans R Soc Lond B. 359(1442):183–195. doi:10.1098/rstb.2003.1388.

Hickerson MJ, Carstens BC, Cavender-Bares J, Crandall KA, Graham CH, Johnson JB, Rissler L, Victoriano PF, Yoder AD. 2010. Phylogeography's past, present, and future: 10 years after Avise, 2000. Mol Phylogenet Evol. 54(1):291–301. doi:10.1016/j.ympev.2009.09.016.

Hill KBR, Simon C, Marshall DC, Chambers GK. 2009. Surviving glacial ages within the Biotic Gap: phylogeography of the New Zealand cicada *Maoricicada campbelli*. J Biogeogr. 36 (4):675–692. doi:10.1111/j.1365-2699.2008.02036.x.

King KJ, Lewis DM, Waters JM, Wallis GP. 2020. Persisting in a glaciated landscape: Pleistocene microrefugia evidenced by the tree wētā *Hemideina maori* in central South Island, New Zealand. Journal of Biogeography. 47(11):2518–2531. doi:10.1111/jbi.13953.

Koot EM, Arnst E, Taane M, Goldsmith K, Thrimawithana A, Reihana K, González-Martínez SC, Goldsmith V, Houliston G, Chagné D. 2022. Genome-wide patterns of genetic diversity, population structure and demographic history in mānuka (*Leptospermum scoparium*) growing on indigenous Māori land. Horticulture Research. 9:uhab012. . doi:10.1093/hr/uhab012.

Koot EM, Morgan-Richards M, Trewick SA. 2020. An alpine grasshopper radiation older than the mountains, on Kā Tiritiri o te Moana (Southern Alps) of Aotearoa (New Zealand). Molecular Phylogenetics and Evolution. 147:106783. doi:10.1016/j.ympev.2020.106783.

Lee DE, Lee WG, Mortimer N. 2001. Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. Australian Journal of Botany. 49:341–356. doi:10.1071/BT00031.

Leschen RAB, Buckley TR, Harman HM, Shulmeister J. 2008. Determining the origin and age of the Westland beech (*Nothofagus*) gap, New Zealand, using fungus beetle genetics. Mol Ecol. 17 (5):1256–1276. doi:10.1111/j.1365-294X.2007.03630.x.

Leschen RAB, Buckley TR. 2015. Revision and phylogeny of *Syrphetodes* (Coleoptera: Ulodidae): implications for biogeography, alpinization and conservation. Systematic Entomology. 40:143–168. doi:10.1111/syen.12094.

Lu HB, Fulthorpe CS, Mann P, Kominz MA. 2005. Miocene–Recent tectonic and climatic controls on sediment supply and sequence stratigraphy: Canterbury basin, New Zealand. Basin Res. 17 (2):311–328. doi:10.1111/j.1365-2117.2005.00266.x.

Marra M, Leschen R. 2011. Persistence of New Zealand Quaternary beetles. New Zealand Journal of Geology and Geophysics. 54(4):403–413. doi:10.1080/00288306.2011.599399.

Marshall DC, Hill KBR, Cooley JR, Simon C. 2011. Hybridization, mitochondrial DNA phylogeography, and prediction of the early stages of reproductive isolation: lessons from New Zealand Cicadas (Genus *Kikihia*). Systematic Biology. 60(4):482–502. doi:10.1093/sysbio/syr017.

Marshall DC, Hill KBR, Fontaine KM, Buckley TR, Simon C. 2009. Glacial refugia in a maritime temperate climate: Cicada (*Kikihia subalpina*) mtDNA phylogeography in New Zealand. Mol Ecol. 18(9):1995–2009. doi:10.1111/j.1365-294X.2009.04155.x.

Marshall DC, Hill KBR, Marske KA, Chambers C, Buckley TR, Simon C. 2012. Limited, episodic diversification and contrasting phylogeography in a New Zealand cicada radiation. BMC Evolutionary Biology. 12(1):177. doi:10.1186/1471-2148-12-177.

Marshall DC, Slon K, Cooley JR, Hill KBR, Simon C. 2008. Steady Plio-Pleistocene diversification and a 2-million-year sympatry threshold in a New Zealand cicada radiation. Molecular Phylogenetics and Evolution. 48(3):1054–1066. doi:10.1016/j.ympev.2008.05.007.

Marske KA, Leschen RAB, Barker GM, Buckley TR. 2009. Phylogeography and ecological niche modelling implicate coastal refugia and trans-alpine dispersal of a New Zealand fungus beetle. Mol Ecol. 18(24):5126–5142. doi:10.1111/j.1365-294X.2009.04418.x.

Marske KA, Leschen RAB, Buckley TR. 2011. Reconciling phylogeography and ecological niche models for New Zealand beetles: looking beyond glacial refugia. Mol Phylogenet Evol. 59 (1):89–102. doi:10.1016/j.ympev.2011.01.005.

Marske KA, Leschen RAB, Buckley TR. 2012. Concerted versus independent evolution and the search for multiple refugia: comparative phylogeography of four forest beetles: Concerted evolution vs. multiple refugia. Evolution. 66(6):1862–1877. doi:10.1111/j.1558-5646.2011.01538.x.

Marske KA, Thomaz AT, Knowles LL. 2020. Dispersal barriers and opportunities drive multiple levels of phylogeographic concordance in the Southern Alps of New Zealand. Mol Ecol. 29 (23):4665–4679. doi:10.1111/mec.15655.

McCallum J, Hall S, Lissone I, Anderson J, Huynen L, Lambert DM. 2013. Highly informative ancient DNA 'Snippets' for New Zealand Moa. PLOS ONE. 8(1):e50732. doi:10.1371/journal.pone.0050732.

McCulloch GA, Foster BJ, Waters JM. 2019. Phylogeography reveals a North Island range extension for New Zealand's only sexually wing-dimorphic stonefly (Stenoperla helsoni). New Zealand Journal of Zoology 46(3):253–260. doi:10.1080/03014223.2018.1527775

McCulloch GA, Dutoit L, Craw D, Kroos GC, Waters JM. 2022. Genomics reveals exceptional phylogenetic diversity within a narrow-range flightless insect. Insect Systematics and Diversity. 6:5. doi:10.1093/isd/ixac009.

McCulloch GA, Wallis GP, Waters JM. 2010. Onset of glaciation drove simultaneous vicariant isolation of Alpine insects in New Zealand. Evolution. 64(7):2033–2043. doi:10.1111/j.1558-5646.2010.00980.x.

McGlone MS. 1985. Plant biogeography and the late Cenozoic history of New Zealand. New Zealand Journal of Botany. 23:723–749.

McGlone MS, Newnham RM, Moar NT. 2010. The vegetation cover of New Zealand during the last glacial maximum: Do pollen records under-represent woody vegetation? In: Altered ecologies: fire, climate and human influence on terrestrial landscapes. Terra Australis. Vol. 32. Canberra: ANU Press; p. 202–214.

McLay TGB, Tate JA, Gemmill CEC, Holzapfel AS, Symonds VV. 2022. Inferring the biogeography of New Zealand's only endemic holoparasitic plant, the threatened *Dactylanthus taylorii* (Mystropetalaceae). New Zealand Journal of Botany. doi:10.1080/0028825X.2022.2035411.

Morgan-Richards M, Trewick SA, Stringer I. 2010. Geographic parthenogenesis and the common tea-tree stick insect of New Zealand. Molecular Ecology. 19(6):1227–1238. doi:10.1111/j.1365-294X.2010.04542.x.

Morgan-Richards M, Trewick SA, Wallis GP. 2001. Chromosome races with Pliocene origins: evidence from mtDNA. Heredity. 86(3):303–312.

Nelson GJ. 1975. Reviews: biogeography, the vicariance paradigm, and continental drift. Systematic Zoology. 24:490–504.

Newnham R, Mcglone M, Moar N, Wilmshurst J, Vandergoes M. 2013. The vegetation cover of New Zealand at the Last Glacial Maximum. Quaternary Science Reviews. 74:202–214. doi:10.1016/j.quascirev.2012.08.022.

Nielsen SV, Bauer AM, Jackman TR, Hitchmough RA, Daugherty CH. 2011. New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol. 59(1):1–22. doi:10.1016/j.ympev.2010.12.007.

O'Neill SB, Buckley TR, Jewell TR, Ritchie PA. 2009. Phylogeographic history of the New Zealand stick insect *Niveaphasma annulata* (Phasmatodea) estimated from mitochondrial and nuclear loci. Mol Phylogenet Evol. 53(2):523–536. doi:10.1016/j.ympev.2009.07.007.

Painting CJ, Myers S, Holwell GI, Buckley TR. 2017. Phylogeography of the New Zealand giraffe weevil *Lasiorhynchus barbicornis* (Coleoptera: Brentidae): A comparison of biogeographic boundaries. Biological Journal of the Linnean Society. 122(1):13–28. doi:10.1093/biolinnean/blx051.

Pons J, Fujisawa T, Claridge EM, Anthony Savill R, Barraclough TG, Vogler AP. 2011. Deep mtDNA subdivision within Linnean species in an endemic radiation of tiger beetles from New Zealand (genus *Neocicindela*). Mol Phylogenet Evol. 59(2):251–262. doi:10.1016/j.ympev.2011.02.013.

Provan J, Bennett KD. 2008. Phylogeographic insights into cryptic glacial refugia. Trends Ecol Evol. 23(10):564–571. doi:10.1016/j.tree.2008.06.010.

Rawlence NJ, Metcalf JL, Wood JR, Worthy TH, Austin JJ, Cooper A. 2012. The effect of climate and environmental change on the megafaunal moa of New Zealand in the absence of humans. Quaternary Science Reviews 50:141–153. doi:10.1016/j.quascirev.2012.07.004

Rawlence NJ, Potter BCM, Dussex N, Scarsbrook L, Orlovich DA, Waters JM, McGlone M, Knapp M. 2021. Plio-Pleistocene environmental changes shape present day phylogeography of New Zealand's southern beeches (Nothofagaceae). New Zealand Journal of Botany. 59(1):55–71. doi:10.1080/0028825X.2020.1791915.

Rissler LJ. 2016. Union of phylogeography and landscape genetics. Proc Natl Acad Sci U S A. 113 (29):8079–8086. doi:10.1073/pnas.1601073113.

Robertson BC, Steeves TE, McBride KP, Goldstein SJ, Williams M, Gemmell NJ. 2007. Phylogeography of the New Zealand blue duck (*Hymenolaimus malacorhynchos*): implications for translocation and species recovery. Conserv Genet. 8(6):1431–1440. doi:10.1007/s10592-007-9294-2.

Rogers GM. 1989. Beech and conifer community interactions in Moawhango Ecological Region, North Island, New Zealand. New Zealand Journal of Ecology. 12:47–61.

Seidel M, Sýkora V, Leschen RAB, Clarkson B, Fikáček M. 2021. Ancient relicts or recent immigrants? Different dating strategies alter diversification scenarios of New Zealand aquatic beetles (Coleoptera: Hydrophilidae: *Berosus*). Molecular Phylogenetics and Evolution. 163:107241. doi:10.1016/j.ympev.2021.107241.

Shepherd LD, de Lange PJ, Perrie LR, Heenan PB. 2017. Chloroplast phylogeography of New Zealand Sophora trees (Fabaceae): extensive hybridization and widespread Last Glacial Maximum survival. Journal of Biogeography. 44(7):1640–1651. doi:10.1111/jbi.12963

Shepherd LD, Frericks J, Biggs PJ, de Lange PJ. 2019. Phylogeography of the endemic New Zealand tree *Entelea arborescens* (whau; Malvaceae). New Zealand Journal of Botany. 57(3):154–168. doi:10.1080/0028825X.2019.1577277.

Shepherd LD, Perrie LR, Brownsey PJ. 2007. Fire and ice: volcanic and glacial impacts on the phylogeography of the New Zealand forest fern *Asplenium hookerianum*. Mol Ecol. 16(21):4536–4549. doi:10.1111/j.1365-294X.2007.03451.x.

Shepherd LD, Perrie LR. 2011. Microsatellite DNA analyses of a highly disjunct New Zealand tree reveal strong differentiation and imply a formerly more continuous distribution. Molecular Ecology. 20(7):1389–1400. doi:10.1111/j.1365-294X.2011.05017.x.

Shepherd LD, Simon S, Langton-Myers S, Morgan-Richards M. 2022. Insights into Aotearoa New Zealand's biogeographic history provided by the study of natural hybrid zones. Journal of the Royal Society of New Zealand. DOI: 10.1080/03036758.2022.2061020.

Suggate RP, Almond PC. 2005. The Last Glacial Maximum (LGM) in western South Island, New Zealand: implications for the global LGM and MIS 2. Quaternary Science Reviews. 24(16–17):1923–1940. doi:10.1016/j.quascirev.2004.11.007.

Tardelli Canedo P, Baker CM, Morisawa R, Pessereau EJ, Boyer SL. 2021. Phylogeography of *Neopurcellia salmoni*, a widespread mite harvestman from the South Island of New Zealand, with the first report of male polymorphism in the suborder Cyphophthalmi (Arachnida: Opiliones). The Journal of Arachnology. 49(2):205–216. doi:10.1636/JoA-S-20-003.

Te Punga MT. 1954. The Late Tertiary and Quaternary geological history of western Wellington [PhD]. Wellington: Victoria University of Wellington.

Trewick S, Bland K. 2012. Fire and slice: palaeogeography for biogeography at New Zealand's North Island/South Island juncture. Journal of the Royal Society of New Zealand. 42(3):153–183. doi:10.1080/03036758.2010.549493.

Trewick SA, Morgan-Richards M. 2005. After the deluge: mitochondrial DNA indicates Miocene radiation and Pliocene adaptation of tree and giant weta (Orthoptera: Anostostomatidae). J Biogeogr. 32(2):295–309. doi:10.1111/j.1365-2699.2004.01179.x.

Trewick SA, Olley L. 2016. Spatial size dimorphism in New Zealand's last endemic raptor, the Karearea *Falco novaeseelandiae*, coincides with a narrow sea strait. Ibis. 158(4):747–761. doi:10.1111/ibi.12398.

Trewick SA, Pilkington S, Shepherd LD, Gibb GC, Morgan-Richards M. 2017. Closing the gap: avian lineage splits at a young, narrow seaway imply a protracted history of mixed population response. Mol Ecol. 26(20):5752–5772. doi:10.1111/mec.14323.

Trewick SA. 2001. Scree weta phylogeography: surviving glaciation and implications for Pleistocene biogeography in New Zealand. N Z J Zool. 28(3):291–298. doi:10.1080/03014223.2001.9518271.

Trewick SA, Wallis GP. 2001. Bridging the "beech-gap": New Zealand invertebrate phylogeography implicates Pleistocene glaciation and Pliocene isolation. Evolution. 55(11):2170–2180.

Trewick SA, Wallis GP, Morgan-Richards M. 2011. The invertebrate life of New Zealand: A phylogeographic approach. Insects. 2(3):297–325. doi:10.3390/insects2030297.

Vandergoes MJ, Fitzsimons SJ. 2003. The Last Glacial-Interglacial Transition (LGIT) in south westland, New Zealand: paleoecological insight into mid-latitude southern hemisphere climate change. Quat Sci Rev. 22(14):1461–1476. doi:10.1016/S0277-3791(03)00074-X.

Wagstaff SJ, Clarkson BR. 2012. Systematics and ecology of the Australasian genus *Empodisma* (Restionaceae) and description of a new species from peatlands in northern New Zealand. PhytoKeys. 13:39–79. doi:10.3897/phytokeys.13.3259.

Wallis GP, Jorge F. 2018. Going under down under? Lineage ages argue for extensive survival of the Oligocene marine transgression on Zealandia. Molecular Ecology. 27(22):4368–4396. doi:10.1111/mec.14875.

Wallis GP, Trewick SA. 2009. New Zealand phylogeography: evolution on a small continent. Molecular Ecology. 18(17):3548–3580. doi:10.1111/j.1365-294X.2009.04294.x.

Wallis GP, Waters JM, Upton P, Craw D. 2016. Transverse Alpine speciation driven by glaciation. Trends in Ecology & Evolution. 31(12):916–926. doi:10.1016/j.tree.2016.08.009.

Wardle P. 1963. Evolution and distribution of the New Zealand flora, as affected by quaternary climates. New Zealand Journal of Botany. 1(1):3–17. doi:10.1080/0028825X.1963.10429318.

Waters JM, Burridge CP, Craw D. 2020. River capture and freshwater biological evolution: A review of Galaxiid Fish Vicariance. Diversity. 12(6):216. doi:10.3390/d12060216.

Waters JM, Fraser CI, Hewitt GM. 2013. Founder takes all: density-dependent processes structure biodiversity. Trends in Ecology & Evolution. 28(2):78–85. doi:10.1016/j.tree.2012.08.024.

Waters JM, Rowe DL, Apte S, King TM, Wallis GP, Anderson L, Norris RJ, Craw D, Burridge CP. 2007. Geological dates and molecular rates: Rapid divergence of rivers and their biotas. Syst Biol. 56(2):271–282. doi:10.1080/10635150701313855.

Weir JT, Haddrath O, Robertson HA, Colbourne RM, Baker AJ. 2016. Explosive ice age diversification of kiwi. Proc Natl Acad Sci USA. 113(38):E5580–E5587. doi:10.1073/pnas.1603795113.

Weston KA, Robertson BC. 2015. Population structure within an alpine archipelago: strong signature of past climate change in the New Zealand rock wren (*Xenicus gilviventris*). Molecular Ecology. 24(18):4778–4794. doi:10.1111/mec.13349.

Winterbourn MJ, Pohe SR, Goldstien SJ. 2017. Genetic and phenotypic variability in Stenoperla prasina (Newman, 1845) (Plecoptera: Eustheniidae) in relation to latitude and altitude in New Zealand. Aquatic Insects. 38(1–2):49–65. doi:10.1080/01650424.2017.1302091.

Withers SJ, Parsons S, Hauber ME, Kendrick A, Lavery SD. 2021. Genetic divergence between isolated populations of the North Island New Zealand Rifleman (*Acanthisitta chloris granti*) implicates ancient biogeographic impacts rather than recent habitat fragmentation. Ecology and Evolution. 11(11):5998–6014. doi:10.1002/ece3.7358.

Zamudio KR, Bell RC, Mason NA. 2016. Phenotypes in phylogeography: species' traits, environmental variation, and vertebrate diversification. Proc Natl Acad Sci U S A. 113(29):8041–8048. doi:10.1073/pnas.1602237113.