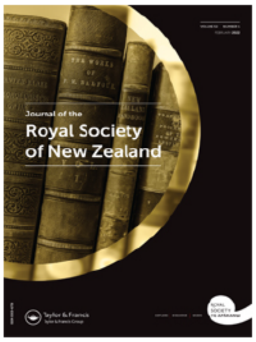

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REVIEW ARTICLE

Insights into Aotearoa New Zealand's biogeographic history provided by the study of natural hybrid zones

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ABSTRACT

Hybridisation is commonly observed in geographical zones of contact between distinct lineages. These contact zones have long been of interest for biogeographers because they provide insight into the evolutionary and ecological processes that influence the distribution of species as well as the process of speciation. Here we review research on hybrid zones and zones of past introgression, both terrestrial and marine, in Aotearoa New Zealand. Many of New Zealand's hybrid zones occur between lineages or species that diverged prior to the Last Glacial Maximum (LGM), with numerous divergences dating to the early Pleistocene or Pliocene. Few secondary contact zones have been detected in terrestrial plants and in marine taxa. This may reflect a lack of the intensive sampling required to detect hybrid zones in these groups but for plants may also indicate widespread Pleistocene survival across the country. Lastly, we suggest avenues for research into New Zealand hybrid zones that are likely to be fruitful.

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Introduction

Hybridisation is reproduction between individuals from different lineages or species that have come into contact resulting in offspring of mixed ancestry (Harrison 1993). The geographic regions where divergent, largely allopatric, lineages meet and interbreed are called hybrid zones (Barton and Hewitt 1985; Gompert et al. 2017). Contact zones and hybrid zones are important because they are natural laboratories for testing the consequences of secondary contact between formerly isolated lineages originating from a common ancestral population. Contact zones have the potential to be stable and form a barrier to further range expansion (Hewitt 1988; Morgan-Richards and Townsend 1995).

Not all contact zones are hybrid zones (Harrison and Larson 2016). When lineages that have begun to diverge in isolation make contact with one another a number of outcomes are possible, as illustrated in Figure 1. If barriers to reproduction between the

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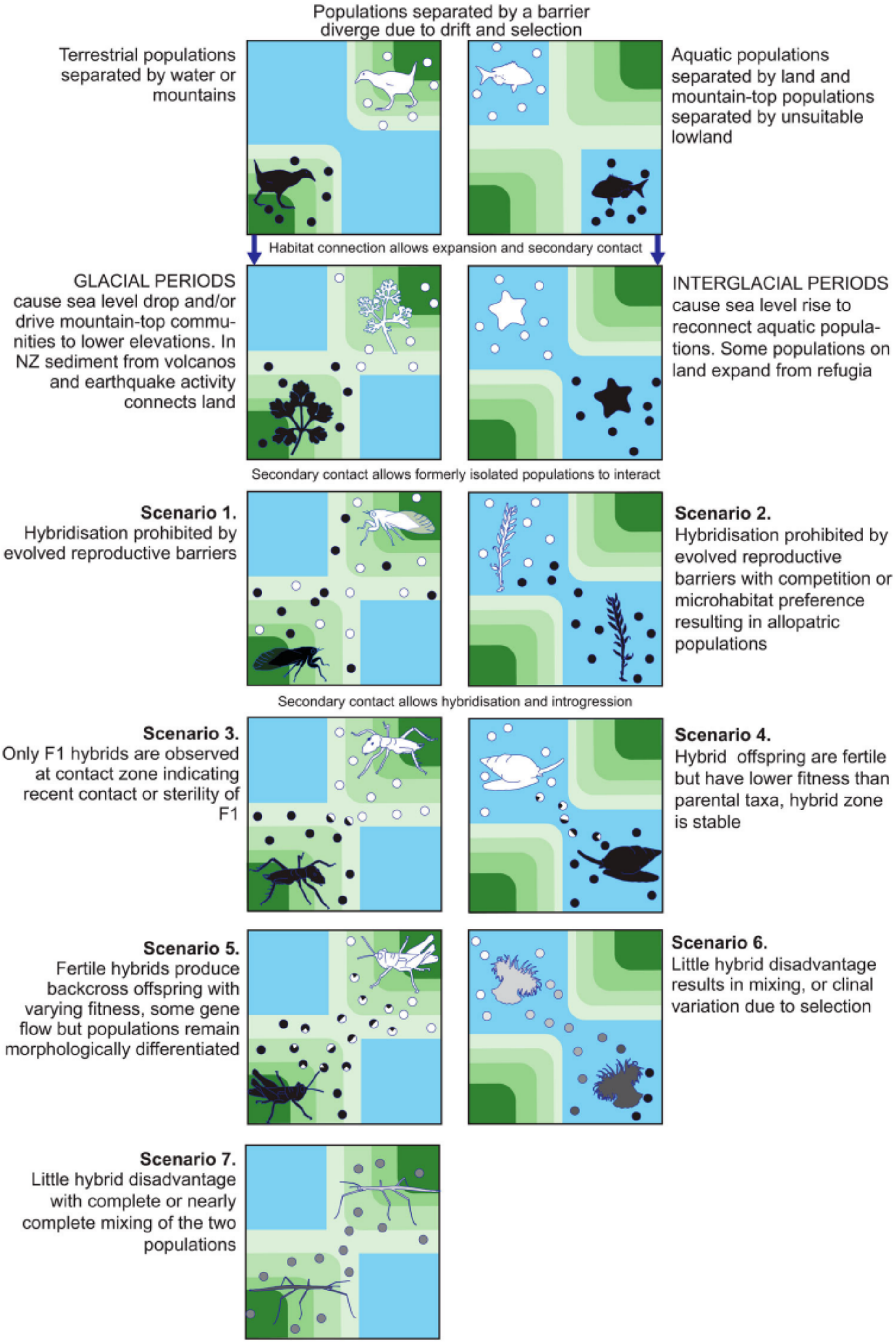

Populations separated by a barrier diverge due to drift and selection

Terrestrial populations separated by water or mountains

Aquatic populations separated by land and mountain-top populations separated by unsuitable lowland

Habitat connection allows expansion and secondary contact

GLACIAL PERIODS cause sea level drop and/or drive mountain-top communities to lower elevations. In NZ sediment from volcanos and earthquake activity connects land

INTERGLACIAL PERIODS cause sea level rise to reconnect aquatic populations. Some populations on land expand from refugia

Secondary contact allows formerly isolated populations to interact

Scenario 1. Hybridisation prohibited by evolved reproductive barriers

Scenario 2. Hybridisation prohibited by evolved reproductive barriers with competition or microhabitat preference resulting in allopatric populations

Secondary contact allows hybridisation and introgression

Scenario 3. Only F1 hybrids are observed at contact zone indicating recent contact or sterility of F1

Scenario 4. Hybrid offspring are fertile but have lower fitness than parental taxa, hybrid zone is stable

Scenario 5. Fertile hybrids produce backcross offspring with varying fitness, some gene flow but populations remain morphologically differentiated

Scenario 6. Little hybrid disadvantage results in mixing, or clinal variation due to selection

Scenario 7. Little hybrid disadvantage with complete or nearly complete mixing of the two populations

Figure 1. Secondary contact of populations that have diverged in isolation can result in a multitude of possible outcomes. We illustrate the main patterns expected. Terrestrial and aquatic contact zones are equally likely to show any of the seven illustrated scenarios.

formerly allopatric lineages have evolved (scenarios 1 & 2), or offspring are infertile (scenario 3) then contact zones form but not hybrid zones. Where reproduction results in offspring with some ability to backcross the degree of nuclear and/or organelle introgression will usually depend on hybrid fitness (Figure 1). Generally, the longer that lineages have been separated the less gene flow is expected, although this correlation is weakened by the fact that closely related lineages can be reproductively isolated due to instantaneously-acting factors such as ploidy changes or symbiont identity (Coyne and Orr 2004; Bridgeman et al. 2018). Thus, these zones can offer insight into the evolution of reproductive barriers to gene flow, increasing our understanding of the speciation process.

The location of hybrid zones can result from steep environmental gradients where related species are adapted to contrasting habitats, e.g. New Zealand stoneflies (*Zelandoperla* spp.; McCulloch et al. 2019), tree ferns (*Dicksonia* spp.; Shepherd et al. 2019) and brown algae (*Carpophyllum* spp.; Hodge 2009) or be a consequence of human-induced habitat modification and/or population declines, e.g. between kiwi (*Apteryx* spp.) species (Shepherd et al. 2021) and between previously isolated freshwater fish species (*Galaxias* spp.) that have been connected by artificial water races (Esa et al. 2000). Alternatively, hybrid zones may reflect the biogeographic history of taxa when previously isolated populations expand their distributions and make contact (Soltis et al. 2006; Hewitt 2011). In particular, suture zones (Remington 1968; Swenson and Howard 2005; Moritz et al. 2009), where the hybrid zones of multiple taxa co-occur, can provide insights into biogeographic history if their occurrence reflects shared underlying causal factors, although their location may result from other processes such as distinct selection pressures resulting from environmental steps or gradients (Endler 1977; Rissler 2016).

The majority of hybrid zones in Northern Hemisphere temperate regions are thought to result from secondary contact following expansion from separate LGM refugia (Hewitt 1988; Swenson and Howard 2005; Schmitt 2007; Abbott 2017). This may also be the case for some New Zealand contact zones, such as within rock wren (Weston and Robertson 2015), New Zealand cicadas (Marshall et al. 2008, 2011; Hill et al. 2009; Wade 2014) and fungus beetles *Hisparonia hystrix* (Leschen et al. 2008). Despite many New Zealand taxa apparently surviving in numerous 'microrefugia' during the glacial periods of the Pleistocene (Wallis and Trewick 2009; Wood et al. 2017), so far, few concordant hybrid zones that date to LGM divergence have been detected. Some forest species may have survived the LGM only in northern and coastal New Zealand and expanded south and inland during interglacials (Buckley et al. 2009, 2010; Marshall et al. 2009; Morgan-Richards et al. 2019). Either there was no opportunity for populations from alternative refugia to meet or hybrid zones have not yet to be been identified where these lineages made contact. In contrast, the ranges of many cold-tolerant species, such as New Zealand alpine grasshoppers and alpine cicadas, probably expanded during glacial phases so do not show a signature of interglacial range expansion or secondary contact (Carmelet-Rescan et al. 2021).

Current species distributions and levels of endemism in New Zealand are more likely to result from changes in landforms that occurred prior to the onset of the Pleistocene (>2.6 million years ago (Ma); Wood et al. 2017; Taylor-Smith et al. 2020). Throughout the Pliocene (2.6–5.3 Ma) reproductive incompatibilities would have had more time to evolve and lineages would therefore have accumulated higher levels of differentiation.

Secondary contact between such lineages would be less likely to result in hybridisation. For example, in cicada populations Marshall et al. (2008) found that 2 Ma of divergence is long enough to result in pre-zygotic reproductive isolation, although for chromosome races of the Auckland tree wētā this length of time is insufficient for reproductive barriers to evolve (Morgan-Richards et al. 2001; Morgan-Richards and Wallis 2003). In addition, secondary contact that first occurred before the onset of the Pleistocene could have been disrupted by repeated glacial cycles altering species distributions. Contact zones are dynamic and change over time as the climate/habitat changes (Wielstra 2019); at some points in time hybridisation might occur and at other points in time it might not (Butlin et al. 2008).

The focus of this review is secondary contact hybrid zones and regions where past hybridisation has led to organelle introgression (zones of past introgression). In New Zealand, many contact zones – some of them hybrid zones – have been identified. Some have been studied in detail but many have not. All are fertile grounds for future research as new techniques are developed. We discuss them below to encourage further research.

New Zealand secondary contact hybrid zones

Examples of secondary contact hybrid zones in New Zealand that have been examined with molecular analyses are shown in Figure 2. The most well-studied zones are discussed below.

Northland

Four hybrid zones (Zones 2–5; Figure 2) have been recorded between Auckland tree wētā (*Hemideina thoracica*) lineages in Northland that differ in chromosome number (Morgan-Richards and Wallis 2003). Molecular clock analyses indicate that these chromosome races diverged during the Pliocene (Morgan-Richards et al. 2001). Examination of the hybrid zones with chromosomal and mitochondrial (mtDNA) markers found differences in hybrid zone width of up to two orders of magnitude but that width did not correlate with the extent of chromosomal differentiation (Morgan-Richards and Wallis 2003). The degree of hybridisation at a contact zone is determined not only by genetic divergence, but also by hybrid fitness and mate recognition in animals (Wade 2014; Morgan-Richards et al. 2021).

The divergence of *Clitarchus* stick insect species in the Far North of Northland also date to the Pliocene (Myers et al. 2017). The examination of two *Clitarchus* hybrid zones (Zones 1 and 2; Figure 2) demonstrated that, despite likely forming at similar times, they differ in the extent of mtDNA and nuclear introgression (Myers et al. 2017). At Zone 1 a stable hybrid swarm was evident, but genetic swamping was occurring at Zone 2 (Scenarios 5–7; Figure 1).

During the Pliocene, when lineages of Auckland tree wētā and *Clitarchus* stick insects were diverging, Northland was an archipelago of islands created by an old volcanic arc (25–15 Ma; Ballance and Williams 1992; Graham 2008). Hybrid zones are located where these Pliocene islands are now connected by land, when previously isolated terrestrial populations expanded their ranges and met (Figure 1). Zone 2, at

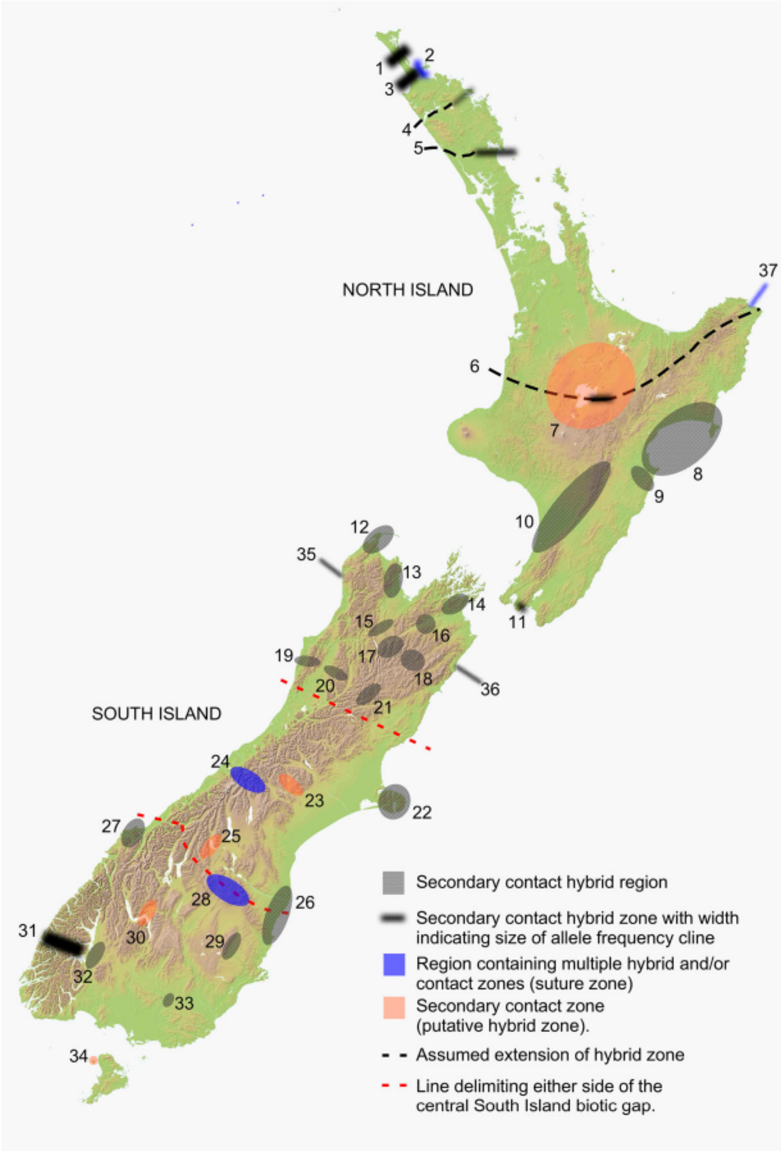

Figure 2. Examples of secondary contact hybrid zones detected in New Zealand. Zones 1, 2. Stick insect (*Clitarchus* spp.) Myers et al. (2017); Zones 2–6. Auckland tree wētā (*Hemideina thoracica*), Morgan-Richards et al. (2001), Morgan-Richards and Wallis (2003); Zone 7. short-tailed bats (*Mystacina tuberculata*), Lloyd (2003); Zone 8. *Kikihia* cicadas, Marshall et al. (2008, 2011); Zone 9–10. wētā (*Heimideina* spp.), McKean et al. 2016; Zone 11. Gecko (*Woodworthia maculata*), Fitness et al. 2012; Zones 12 –21, 23, 26–28, 33. *Kikihia* cicadas, Marshall et al. (2008), Wade (2014); Zone 22. wētā (*Heimideina* spp.), Van Heugten et al. 2017; Zone 24. Rock wren (*Xenicus gilviventris*), Weston and Robertson (2015); fungus beetle (*Hisparonia hystrix*), Leschen et al. (2008); Zones 23, 25, 30, 32. Campbell's cicada (*Maoricicada campbelli*), Hill et al. (2009); Zone 28. *Galaxias* freshwater fish, Allibone et al. (1996), Alpine wētā (*Heimideina maori*), King et al. (2020); Campbell's cicada (*Maoricicada campbelli*), Hill et al. (2009); Zone 29. Alpine wētā (*Heimideina maori*), King et al. 2003; Zone 31. Fiordland tokoeka (*Apteryx australis*), Weir et al. (2016); Bemmels et al. (2021); Zone 36. short-tailed bats (*Mystacina tuberculata*), Lloyd (2003); Zones 35, 36. Greenshell mussel (*Perna canaliculus*), Gardner and Wei (2015); Zone 37. *Buccinulum* whelks (Gemmell et al. 2018).

the base of Karikari Peninsular (Figure 2), occurs in Auckland tree wētā and *Clitarchus* stick insects and is likely to be a suture zone. It is possible that additional suture zones are present between other former Pliocene islands but contrasting phylogeographic patterns have been observed in the few studies that have undertaken extensive sampling in Northland (e.g. *Oligosoma* skinks, Hare et al. 2008 and Kauri snails, Spencer et al. 2006), suggesting differing responses to historical processes. In other genera, unique haplotypes have restricted distributions within Northland (e.g. in five *Kikihia* species, Ellis et al. 2015 and in New Zealand giraffe weevil, Painting et al. 2017), but no evidence of secondary contact or hybridisation has yet been found.

Taupō volcanic zone

Genetic data have demonstrated that many taxa have contact zones in the Taupō volcanic zone, so this general area may be a suture zone although, surprisingly, few examples have identified hybridisation. A southern and a central chromosome race of the Auckland tree wētā (*Hemideina thoracica*) meet and hybridise at Zone 6 (Figure 2; Morgan-Richards et al. 2000). Three phylogroups of short-tailed bats intersect at Zone 7, where they are assumed to hybridise (Figure 2; Lloyd 2003).

At Taupō, secondary contact is thought to be a consequence of the recolonisation of lineages that had been previously isolated by volcanic eruptions in the region. The Taupō volcanic zone in the central North Island has been active for the last 2 Ma, with the most recent large-scale eruption at Lake Taupō around 232 AD (Barker et al. 2021). Repeated eruptions over the last 2 Ma must have temporarily eliminated much of the local biota. Differences in the position of each contact zone likely relates to the locations and sizes of the colonising source populations, as well as their habitat requirements. A number of other species have distinct eastern and western lineages either side of the Taupō volcanic zone (e.g. the fern *Asplenium hookerianum* Shepherd et al. 2007; North Island brown kiwi *Apteryx mantelli*, Shepherd and Lambert 2008; Bemmels et al. 2021; the parasitic flowering plant *Dactylanthus taylorii*, McLay et al. 2022; and the frog *Leiopelma hochstetteri*; Fouquet et al. 2010). In the case of the stick insect *Argosarchus horridus* the diversity of mtDNA lineages in central North Island might reflect LGM refugia inferred from ecological niche modelling on the east and west coasts (Buckley et al. 2009). However, limited sampling and/or recent population extinctions mean that hybridisation between these lineages has not been assessed.

Southern North Island

Further south, F_1 tree wētā (but not later generation hybrids, scenario 3 in Figure 1) are found where there is overlap in the distributions of *Hemideina thoracica* with *H. trewicki* and *H. crassidens* (Zones 9 and 10; Figure 2; McKean et al. 2016). Climate-dependent competitive exclusion probably explains the complex distribution of *H. thoracica* and *H. crassidens* in North Island New Zealand and as the contact of this species pair is probably older than the Pleistocene the contact location must have moved during each glacial cycle (Bulgarella et al. 2014).

Zone 8 (Figure 2) is where *Kikihia* "muta east" and *Kikihia* "aotea" met and likely hybridised (Marshall et al. 2011). *Kikihia* "muta east" individuals from that area have well-differentiated mtDNA but possess a song that is more similar to the "aotea" songs than the usual *K. muta* song. The split between the "muta" and "aotea" mtDNA clades is estimated to be between 1 and 2 Ma (Ellis et al. 2015), and is therefore within the 2 Ma 'sympatry threshold', where sympatric *Kikihia* species whose divergence exceeds this timeframe appear not to hybridise (Marshall et al. 2008).

On the south coast near Wellington a size cline (Zone 11; Figure 2) in the common gecko *Woodworthia maculata* is concordant with at least one genetic cline (Fitness et al. 2012) and mitochondrial diversity is high suggesting either large stable populations or secondary contact followed by hybridisation. However, because their phenotypic cline tracks an environmental gradient, it is also possible that these clines have formed *in situ* from selection pressure combined with isolation-by-distance, rather than secondary contact (Murphy 2010).

Northern South Island

A number of hybrid zones between *Kikihia* cicada species (Zones 12–21; Figure 2) have been identified in northern South Island (Marshall et al. 2008; 2011; Wade 2014). Hybrids have been identified morphologically, genetically and through intermediate song characteristics (Marshall et al. 2011). Nuclear microsatellite genotyping and mtDNA sequencing have revealed varying levels of introgression sometimes involving nuclear genomes only, more rarely mitochondrial genomes only (Wade 2014). Zone 21 (Figure 2) is particularly notable because here at the confluence of the Boyle and Waiau Rivers, five genomes intermix: coming from the east, a *Kikihia* population carrying the nuclear genome of one species (*K. muta*) and the mitochondrial genome of a second species (*K.* "tuta"), and coming from the west, a *Kikihia* population characterised by a mixed nuclear genome of a northwest coast and a southwest coast species and solely the mitochondrial genome of the southwestern species. Additional hybrid zones are likely to exist because these studies were restricted to sites with road access.

Ecological niche modelling of the LGM potential distributions of the two west coast *Kikihia* species that meet at Zones 19 and 20 (Figure 2) indicated that they may have formed a contact zone prior to the LGM, possibly even dating to their divergence ~1.5 Ma (Wade 2014). The northern South Island (Nelson, Marlborough and Kaikoura) was not as heavily glaciated as farther south and *Kikihia* likely survived *in situ* in this region with common ancestors of many of the species thought to date to c. 2 Ma (Marshall et al. 2008) and a *Kikihia* hybrid swarm composed of mixed genotypes of three or more putative species (Wade 2014). The well-differentiated alpine grasshoppers (*Brachaspis* spp.) that diverged c. 10 Ma (Koot et al. 2020) also hybridise in this region (Zone D, Figure 3; Trewick 2001).

Central South Island

The central South Island biotic gap (delimited by red dotted lines in Figure 2) is a region of low endemicity and a number of species that occur both to the north and south are absent in this region (Burrows 1965). As well as being a biotic gap this region may also be a suture zone for lineages that were previously excluded but that are now in contact (Leschen et al. 2008). Poorly dispersing taxa that had been excluded from the

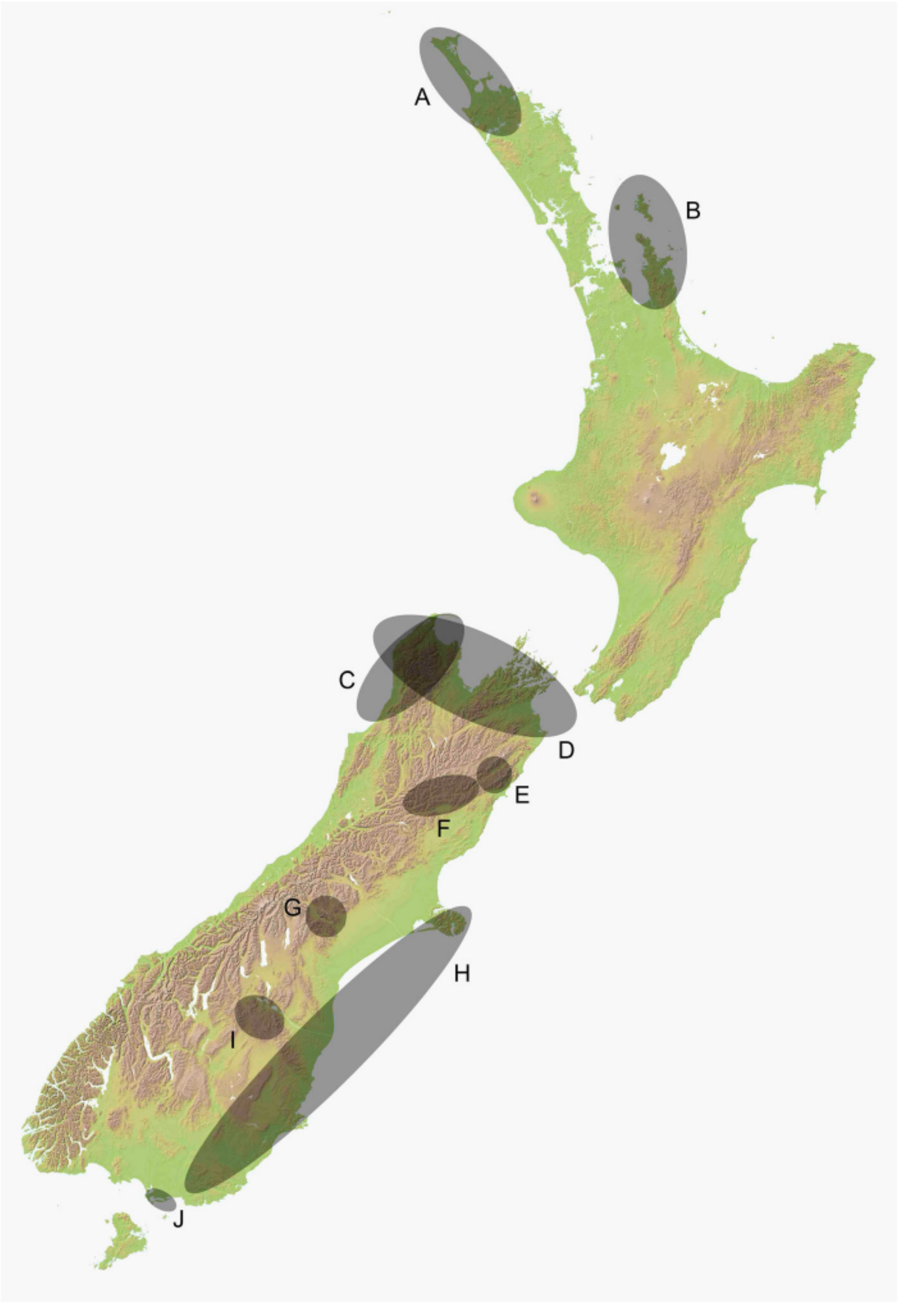

Figure 3. Examples of zones of past hybridisation between species has resulted in organelle introgression. Zone A, B, C, *Metrosideros* trees, Gardner et al. (2004); Zones D and F, *Kikihia* cicadas, Marshall et al. (2008, 2011), Wade (2014); Zones E and G, *Pachycladon* rockcresses, Becker et al. (2013); Zone H, *Pseudopanax* lancewoods, Gemmell et al. (2022); Zone J. *Oligosoma* skinks, Chapple et al. (2012); Zone I. *Oligosoma* skinks, Greaves et al. (2007).

region may have had insufficient time to subsequently recolonise, whereas better dispersers may form hybrid zones where recolonising lineages make contact. During Pleistocene glacial periods the extreme climate and extensive glacial ice in this region are thought to have extirpated populations that could not survive cold harsh conditions, while other more cold-hardy species survived. One example is found in the cicada *Maoricicada campbelli,* which is adapted to tundra-like conditions. In central Canterbury (Zone 23; Figure 2), small relict *M. campbelli* populations are part of a northern South Island and North Island radiation involving four out of five extant clades that dates to 0.69–1.03 Ma. The fifth clade is restricted to the Otago region and diverged about a million years earlier (see below).

In the rock wren (*Xenicus gilviventris*), an alpine passerine (Weston and Robertson 2015), microsatellite analyses detected introgression across a 60 km contact zone (Zone 24; Figure 2) between northern and southern lineages. Molecular dating estimated that the two lineages split around 2 Ma. Weston and Robertson (2015) suggested that, despite being a cold-adapted alpine species, rock wren likely still experienced population contractions to northern and southern refugia during glacial periods, with their specific habitat requirements possibly posing additional limits on their distribution.

The fungus beetle *Hisparonia hystrix* also shows a zone of secondary contact at Zone 24 (Figure 2), where hybridisation is assumed to be occurring (Leschen et al. 2008). MtDNA haplotypes of *H. hystrix* from the central South Island are shared or closely related to haplotypes found to the north and south, and range expansions of these lineages between 60,000 and 20,000 years ago were inferred.

Banks Peninsula was formed from volcanic eruptions during the Miocene and was probably an island until the plains of Canterbury, formed by outwash from Quaternary glacial erosion following the tectonic uplift of Southern Alps, created a land connection. Banks Peninsula has a number of endemic taxa and some hybridise with close relatives where their ranges make contact (Zone 22; Figure 2). For example, the tree wētā endemic to Banks Peninsula (*Hemideina ricta*) meets and mates with the Canterbury tree wētā (*H. femorata*) on the north-east of the Peninsula (Van Heugten et al. 2017). Although these two species form F_1 hybrids there is no evidence of gene flow (scenario 3; Figure 1; Morgan-Richards and Townsend 1995; Van Heugten et al. 2017).

Southern South Island

The common grasshopper *Phalacridium marginale* hybridises with the endemic *P. otagoense*, which is restricted to the dry central/southern South Island (Sivyer et al. 2018). A lack of assortative mating with respect to species has resulted in hybridisation between these two lowland flightless grasshoppers where their ranges overlap (Zone 28 and 25; Figure 2). Gene flow has resulted in mitochondrial introgression and created populations of individuals that are phenotypically intermediate between the two species (scenario 7; Figure 1; Morgan-Richards et al. 2021). Contact between the two lineages might have been promoted by the expansion of *P. marginale* as it responded to human modification of the vegetation.

The rare grasshopper *Sigaus childi* is also restricted to Central Otago (Koot et al. 2022) and morphologically distinct from the widespread sympatric *S. australis.* A set of 79 neutral genetic markers revealed only a single locus with correspondence between genotype and species identification suggesting extensive gene flow between these two lineages (scenario 5; Figure 1; Dowle et al. 2014). In Otago introgression has also been implicated for *Kikihia muta* grass cicadas on the South Island east coast at Zone 26, where this species meets and hybridises with the more cold adapted *K. angusta* (Marshall et al. 2008; Wade 2014).

In Fiordland two lineages of the kiwi species Tokoeka (*Apteryx australis*) are differentiated with both mtDNA and nuclear SNP data. Introgression is evident where they meet at Zone 31 (scenario 4; Figure 1; Figure 2; Weir et al. 2016; Bemmels et al. 2021). Molecular dating indicates that these lineages may have evolved in refugia during the last one or two glacial cycles when Tokoeka populations may have been separated by fingers of ice (Weir et al. 2016). Hybrid zones between more deeply diverged lineages are also present in Fiordland. At Jackson Bay (Zone 27; Figure 2) there is a hybrid zone between two *Kikihia* species (Wade 2014) that are estimated to have split from one another at approximately 2 Ma (Marshall et al. 2008).

Campbell's cicada inhabits a variety of open habitats such as subalpine screes, glacial moraines and river edges on North and South Islands and was likely able to rapidly expand its range into new habitats following ice retreat after glacial maxima. An Otago clade of *Maoricicada campbelli* appears to have diverged in the early Pleistocene (1.45–2.09 Ma) and is sister to all other *M. campbelli* clades. It has a slightly different song and is currently surrounded by, and may hybridise with, up to five sister clades (Zones 25, 28, 30 and 32; Figure 2; Hill et al. 2009). These contact zones were described based on mitochondrial data and song, but unpublished data from one nuclear gene suggests introgression and further genomic studies would likely be illuminating.

Two mtDNA phylogroups of short-tailed bats (*Mystacina tuberculata*) are sympatric on Whenua Hou/Codfish Island (Zone 34) with this sympatry suggested to result from secondary contact following separate post-LGM expansion down the east and west coasts of the South Island from northern South Island refugia (Lloyd 2003). Survival of short-tailed bats in the southern South Island during the LGM was dismissed by Lloyd (2003) owing to 'the severity of the glacial maximum in southern South Island', but with recent studies indicating widespread forest survival, albeit in small isolated stands (Wood et al. 2017; Rawlence et al. 2021), it is conceivable that these bats also survived. Ancient DNA analyses of short-tailed bat bones from extinct eastern South Island populations may distinguish between these hypotheses.

Most of the hybrid zones in the southern South Island (Figure 2) are between deeply diverged lineages that date to the early Pleistocene or older, with Tokoeka and short-tailed bats exceptions. There appear to be few hybrid zones shared between the taxa examined to date, suggesting that each has responded differently to climatic and geological impacts in the region. However, skinks, grasshoppers and cicadas all have multiple lineages that meet at St Marys Range, forming a region of hybridisation (Zone 28; Figure 2) but we have not identified distinct and concordant contact zones within this region.

Marine

Gardner and Wei (2015) detected greenshell mussel (*Perna canaliculus*) hybrid zones (Zones 35 and 36; Figure 2) on the west and east coasts of the South Island just to the south of Cook Strait using microsatellite genotyping. These are secondary contact hybrid zones between two lineages estimated to have diverged 0.3–1.3 Ma, possibly as a result of global sea-level changes (Gardner and Wei 2015). The width of the hybrid zones varied greatly between loci (from 0.35 to 121 km) but showed similar patterns on both the east and west coasts. Localised currents and/or coastal upwellings are thought to be hindering contemporary gene flow by preventing larval dispersal and maintaining the hybrid zones (Gardner and Wei 2015) and this region is also a known biogeographic break in other taxa, such as the cushion star *Patiriella regularis* (Waters and Roy 2004).

On the east coast of North Island, near the tip of East Cape, marine currents are also thought to be responsible for changes in species composition (Gardner et al. 2010). The rocky shore whelk *Buccinulum vittatum* hybridises with *B. colensoi* at Hicks Bay where, despite shells looking like *B. vittatum*, nuclear introgression from *B. colensoi* is detected (scenario 3, Figure 1; Zone 37, Figure 2; Gemmell et al. 2018). At East Cape the southerly moving east-Auckland ocean current becomes the east coast current and moves offshore and a branch of a north-moving current comes close to the coast, potentially restricting gene flow. This is the same place where two lineages within *Haliotis iris* (pāua) meet (Will et al. 2011, 2015), where brown algae hybrids are found (*Carpophyllum* spp. Hodge et al. 2010), and where mtDNA haplotype frequency clines have been detected within the whelks *Cominella maculosa* and *C. virgata* (Fleming et al. 2018). Interestingly, the diversity within *Haliotis iris* and the two *Cominella* species over the same geographical range was an order of magnitude smaller than that seen within the *Buccinulum vittatum* complex, suggesting that divergence of populations in the latter might have begun much earlier (Gemmell et al. 2018).

Hybridisation and organelle introgression

The location of zones of past introgression can inform the biogeographic history of the species involved. In the Northern Hemisphere such zones are particularly common in plants and have been suggested to reflect the position of glacial refugia, where prolonged contact between species resulted in interspecific gene flow and chloroplast sharing (Hewitt 1999). A similar scenario has been suggested in New Zealand for *Metrosideros* trees (Gardner et al. 2004), where chloroplast haplotypes are shared between multiple species and higher diversity occurs in proposed LGM refugia (Zones A, B, C; Figure 3). Wood et al. (2017) had an alternative interpretation of Gardner et al.'s (2004) data, suggesting that the higher diversity in these putative refugial regions may result from the donation of distinct haplotypes from now extinct "ghost" species to the shared gene pool in these areas. However, there is no evidence for this hypothesis and it would be very difficult to discriminate from alternative scenarios, even with genomic markers. In *Kikihia* cicadas, zone D (Figure 3) hosts a hybrid swarm of mitochondrial and nuclear genotypes of several different species, *K.* "northwestlandica", *K.* "tuta", *K.* "nelsonensis" and *K. astragali* (Marshall et al. 2011; Wade 2014).

At Zone F (Figure 3), *Kikihia muta* (indicated by microsatellites and song) all possess *K.* "tuta" mtDNA, indicating past hybridisation perhaps driven by a selective sweep allowing a normally lowland coastal species to spread inland (Marshall et al. 2008; Wade 2014). This *K.* "tuta" mtDNA is also found in a third species *K. paxillulae.* The fact that the ranges of *K. paxillulae* and *K. "tuta"* do not overlap, suggests that this mtDNA was inherited from a *K. muta* individual that had previously hybridised with

K. "*tuta*". The mtDNA of *K. muta* is found in no other species which might be because some mtDNA lineages survive better in hybrid backgrounds than others, as suggested by Arntzen et al. (2009).

Molecular analyses of the alpine herbs rockcresses (*Pachycladon* spp.) indicated past introgression of chloroplasts between species at Zones E and G (Figure 3; Becker et al. 2013). The authors suggest this chloroplast sharing is a consequence of species surviving Pleistocene glaciations in shared refugia, where hybridisation and introgression not only resulted in the transfer of chloroplasts but also glucosinolate hydrolysis alleles, whose products are used for chemical defense against herbivory and pathogens.

The lowland lancewood trees *Pseuodopanax ferox* and *P. crassifolius* both have widespread distributions across New Zealand. *Pseuodopanax ferox* exhibits a single chloroplast haplotype in South Island (Shepherd and Perrie 2011) whereas *P. crassifolius* has a single different haplotype across both islands, except in Zone H (Figure 3), where some individuals exhibit the South Island *P. ferox* haplotype (Gemmell et al. 2022). This asymmetric introgression was suggested to be a consequence of either small LGM populations of *P. crassifolius* compared to *P. ferox*, and/or postglacial expansion of *P. crassifolius* into this region occupied by *P. ferox* (Gemmell et al. 2022).

At Zone I (Figure 3) Chapple et al. (2012) found four scree skinks (*Oligosoma waimatense*) with divergent mtDNA haplotypes that were more similar to those found in the Otago skink (*O. otagense*). Otago and scree skinks diverged during the Miocene and no longer occur in sympatry but are thought to have come into secondary contact during Pleistocene interglacials (Chapple et al. 2012). Also in Zone I, Buckley et al. (2006) found a population of cicadas that was a southward extension of *Maoricicada mangu*; individuals in this population looked and sounded like northern populations but had a mitochondrial haplotype that matched no extant species, suggesting ancient ghost-lineage hybridisation. A number of species exhibit hybrid zones (Zone 28; Figure 2) and phylogeographic breaks in the vicinity of Zone I suggesting a significant barrier to gene flow in the past, somewhere in this area.

At Tiwai Point, Foveaux Strait (Zone J; Figure 3) introgression of a divergent mtDNA lineage of *Oligosoma chloronoton* skinks from Whenua Hou/Codfish Island into mainland populations has occurred (Greaves et al. 2007). The two lineages are thought to predate the Pleistocene with secondary contact occurring following migration across Foveaux Strait, which was bridged during glacial periods (Newnham et al. 1999).

Concordance of contacts and zones

New Zealand has a complex geological history, which has resulted in the formation of many contact zones between distinct lineages (Figure 2), only some of which can be broadly considered suture zones (e.g. Zones 24 and 28; Figure 2). This contrasts with patterns in the Northern Hemisphere, where suture zones are apparently more common (Remington 1968; Swenson and Howard 2005). A number of the hybrid zones in New Zealand likely formed before the LGM and therefore have survived substantial shifts in species ranges as the climate has cycled.

The numerous hybrid zones detected within the South Island (Figure 2) suggest complex patterns of refugial survival in different taxa, combined with different habitat requirements and dispersal rates. However, a few hybrid zones are shared by multiple unrelated taxa eg. Zone 24 in the biotic gap and Zone 28, indicating shared past barriers to gene flow in these locations. Phylogeographic breaks in the distributions of other taxa also occur in these regions (e.g. Apte et al. 2007), supporting this hypothesis (Marske and Boyer, in prep).

North Island has a more climatically stable history, particularly in the far north (Wood et al. 2017). This stability has resulted in the retention of older hybrid zones between Pliocene lineages of invertebrates. Volcanism and glacial cycles have had a major impact on the biota of the central North Island, leading to a cluster of contact zones between lineages within species of bats, ferns and wētā.

Similar to the Northern Hemisphere, chloroplast sharing between tree species is common (Gardner et al. 2004; Shepherd et al. 2017; Gemmell et al. 2022), supporting suggestions for the important role for hybridisation in the history of New Zealand plants (Cockayne 1923; Rattenbury 1962; Morgan-Richards et al. 2009). Chloroplast introgression has occurred at various scales. In *Metrosideros* trees high haplotype diversity and chloroplast sharing have been recorded within proposed major LGM refugia (Figure 3; Gardner et al. 2004). In contrast, *Sophora* trees exhibit endemic regional chloroplast haplotypes shared between species (Shepherd et al. 2017). These occur outside proposed major refugia, supporting the concept of widespread microrefugia for this genus.

Organelle introgression has also been observed between New Zealand animal taxa. In addition to the cicada examples mentioned in the main body of the text, seven cicadas of the genus *Kikihia* form a mitochondrially defined group, the Westlandica Group (Marshall et al. 2008), that all share a shared mitochondrial ancestor; some members of the group are hypothesised to have been recruited by more recent hybridisation. This group does not appear in the nuclear genome tree (Banker et al. 2017).

Future research avenues

Many studies to date have discovered contact zones as a consequence of widespread phylogeographic sampling, e.g. Hooker's spleenwort (Shepherd et al. 2007), short-tailed bats (Lloyd 2003) and chromosome races of the Wellington tree wētā (Morgan-Richards 2000; Bulgarella et al. 2014), but have not followed up with detailed sampling within the contact zone to determine whether hybridisation is occurring.

Evidence of past hybridisation could be sought where connections between populations existed recently. During the LGM, when sea levels were lower, land connected the North and South Islands (Trewick and Bland 2012) and populations that are known to be distinct on either side of the Cook Strait would have been in contact. For example, weka and their ectoparasites are genetically distinct on North and South Islands (Trewick et al. 2017), so did habitat connection during the LGM result in hybridisation? Tomtits (Ngirungiru/Miromiro; *Petroica macrocephala;* Miller and Lambert 2006) whio (blue ducks; *Hymenolaimus malacorhynchos*; Robertson et al. 2007) and tokoriro (*Miotopus richardsae*; Fitness et al. 2018) also have distinct mitochondrial lineages on either side of the strait that would have been in recent contact, so seeking evidence of introgression from nuclear markers would be revealing for these taxa. In contrast, marine organisms would have been separated by the glacial land connection of North and South Island, allowing divergence of populations due to genetic drift but these populations are now connected. Sampling in Cook Strait of taxa such as the siphon whelk *Penion ormesi* that has distinct populations east and west, could estimate gene flow and determine the consequence of secondary contact (Vaux et al. 2020). Genomic data from bull kelp suggests recent colonisation of the south coast of North Island from southern populations (Vaux et al. 2021), highlighting the potential for nuclear DNA data to reveal recent range expansion and contact zones within Cook Strait.

For those hybrid zones that have been detected to date, genomics has the potential to greatly improve our understanding of the processes that are involved (Gompert et al. 2017). Genomics also enables the identification of genetic exchange of neutral and adaptive characters, as well as identifying allele interactions contributing to reduced hybrid fitness. Specifically, mutations contributing to reproductive isolation and local adaptation may be identified. However, genomics have not yet been widely used to examine natural New Zealand hybrid zones (but see Dowle et al. 2014; Gemmell et al. 2018; Shepherd et al. 2019; Bemmels et al. 2021). The ability to cheaply generate a large number of independent molecular markers, combined with hybridisation detection software offer the potential to provide new insights into New Zealand hybrid zone dynamics. If genomics is used in conjunction with ecological information, phenotypic and/or behavioural data such as mate signals, pollinators, or physiology we can expect to illuminate the fitness consequences of hybridisation and improve our understanding of the evolution of reproductive barriers.

Most research into New Zealand hybrid zones to date has focused on animals (Figure 2). This may in part be because many plant species hybridise across wide areas wherever they occur in sympatry, rather than in secondary contact zones. However, there is the opportunity to examine contact zones not centred on an ecological transition between species pairs, such as *Weinmannia racemosa* and *W. silvicola*, and *Podocarpus totara* and *P. acutifolius* (Wardle 1972; de Lange 2022).

There is the potential to incorporate ancient DNA from museum and herbarium specimens (Lado et al. 2018) in order to add a temporal perspective to the study of New Zealand hybrid zones, particularly with the advances in genomics methods suitable for dealing with fragmented DNA. Although New Zealand has an excellent recent fossil record, fossils are not found uniformly across the country but concentrated in sites with good preservation, which may not correspond to the position of hybrid zones.

Lastly, continuing research into hybrid zones will be important for monitoring the biological effects of climate change. Not only are existing hybrid zones likely to shift their position in response to changing climate, but new hybrid zones may form as a consequence of species range expansions. Because the expansion of one species may come at the expense of another, there may be conservation implications resulting from these changes.

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