

INVITED REVIEW

New Zealand phylogeography: evolution on a small continent

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Abstract

New Zealand has long been a conundrum to biogeographers, possessing as it does geophysical and biotic features characteristic of both an island and a continent. This schism is reflected in provocative debate among dispersalist, vicariance biogeographic and panbiogeographic schools. A strong history in biogeography has spawned many hypotheses, which have begun to be addressed by a flood of molecular analyses. The time is now ripe to synthesize these findings on a background of geological and ecological knowledge. It has become increasingly apparent that most of the biota of New Zealand has links with other southern lands (particularly Australia) that are much more recent than the breakup of Gondwana. A compilation of molecular phylogenetic analyses of ca 100 plant and animal groups reveals that only 10% of these are even plausibly of archaic origin dating to the vicariant splitting of Zealandia from Gondwana. Effects of lineage extinction and lack of good calibrations in many cases strongly suggest that the actual proportion is even lower, in keeping with extensive Oligocene inundation of Zealandia. A wide compilation of papers covering phylogeographic structuring of terrestrial, freshwater and marine species shows some patterns emerging. These include: east–west splits across the Southern Alps, east–west splits across North Island, north–south splits across South Island, star phylogenies of southern mountain isolates, spread from northern, central and southern areas of high endemism, and recent recolonization (postvolcanic and anthropogenic). Excepting the last of these, most of these patterns seem to date to late Pliocene, coinciding with the rapid uplift of the Southern Alps. The diversity of New Zealand geological processes (sinking, uplift, tilting, sea level change, erosion, volcanism, glaciation) has produced numerous patterns, making generalizations difficult. Many species maintain pre-Pleistocene lineages, with phylogeographic structuring more similar to the Mediterranean region than northern Europe. This structure reflects the fact that glaciation was far from ubiquitous, despite the topography. Intriguingly, then, origins of the flora and fauna are island-like, whereas phylogeographic structure often reflects continental geological processes.

Keywords: biogeography, dispersal, genetic structure, geology, mtDNA, New Zealand, phylogeography, review, vicariance

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It still remains necessary to emphasize that tentative conclusions are hypotheses for testing and that the gulf between raw data and paleogeographic conclusions has often been crossed by a rather flimsy bridge of projection and extrapolation... In the very inexact science of

biogeography, hypotheses can seldom be directly proved, though they are tested by new data at every step, and in Charles Darwin's words 'the doctrine must sink or swim according as it groups and explains phenomena' (Fleming 1975).

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Introduction

Nineteenth century biogeographers sought to explain distributions of plants and animals with only a hazy

idea of their phylogeny: that of the current taxonomy. The near simultaneous emergence of phylogenetics, vicariance biogeography and molecular genetics paved the way for the emergence of phylogeography (Avice *et al.* 1979, 1987; Avice 2000). A full understanding of the phylogeography of a region requires a multi-taxon approach that integrates phylogeny, palaeontology, geology, ecology and climate. Our current knowledge of phylogeographic pattern is highly heterogeneous across the globe. We know quite a bit about disjunctions in the southeastern US (Soltis *et al.* 2006), postglacial routes of colonization in boreal species (Taberlet *et al.* 1998; Arbogast & Kenagy 2001; Demboski & Cook 2001), and radiations on the Hawaiian (Wagner & Funk 1995; Fleischer *et al.* 1998; Roderick & Gillespie 1998), Caribbean (Malone *et al.* 2000) and Canary (Juan *et al.* 2000; Emerson 2002) islands, but little about many other parts of the globe, particularly southern lands (Platnick 1992; Moritz *et al.* 2000; Beheregaray 2008). This review synthesizes findings and patterns emerging from phylogeographic studies of the fauna and flora of New Zealand.

The synthetic nature of phylogeography enables both the testing of existing hypotheses derived from many disciplines, and complementary development of new hypotheses for testing in those disciplines. Some comparative studies have revealed genetic-geographic breaks where no *a priori* expectation of such breaks existed (Avice 1992; Gascon *et al.* 2000), necessitating novel ecological and geological explanations. In other cases, a clear geological history allowed biological inferences of dispersal and evolutionary rates (DeSalle & Giddings 1986; Knowlton *et al.* 1993; Thorpe *et al.* 1994). Several features of New Zealand make it a fascinating place to study phylogeography: it is a continental landmass well separated from others (Trewick *et al.* 2007; McDowall 2008); its distinct biota make it a biodiversity hotspot (Myers *et al.* 2000); the geology is dynamic and well-studied (Suggate *et al.* 1978; Kamp 1992; Soons & Selby 1992; Cooper & Millener 1993; Campbell & Hutching 2007); there is a good fossil record (Mildenhall 1980; Pole 1994; Lee *et al.* 2001, 2007a,b 2009); there is a strong history in ecological research (Atkinson & Cameron 1993; Daugherty *et al.* 1993; Towns & Ballantine 1993) and a wealth of biogeographic hypotheses (Fleming 1962, 1979; Kuschel 1975; Gibbs 2006; Campbell & Hutching 2007).

Phylogeographic studies on continental landmasses tend to focus on vicariant processes, overlain by extinction and recolonization in glaciated areas. In contrast, island biogeography is often concerned with origins and routes of dispersal. New Zealand is a continental temperate island, with extensive southern glaciated alpine regions and northern volcanoes. These features

predicate complex and interesting phylogeographic pattern. We summarize salient features of New Zealand geology and ecology, and on this background, scrutinize molecular phylogenetic evidence pertaining to the origins of the flora and fauna of New Zealand. Finally, we address phylogeographic structure within New Zealand plants and animals.

Geological history of New Zealand

New Zealand (NZ) consists of three main islands (North Island, South Island, Stewart Island), a few hundred nearby islands (e.g. Great Barrier (northern group), Resolution (southwestern; Fiordland), D'Urville [central; Cook Strait/Marlborough Sounds]) and several offshore groups (Three Kings, Kermadecs, Chathams, Bounty, Antipodes, Campbell, Auckland, Snares), with 700 islands >5 ha (Fig. 1). The main islands comprise a narrow, mountainous land, some 1500 km in length, 150–300 km wide (east–west) and 26 million ha, slightly smaller in size and topography than the state of California. It extends from latitude 34°25'S–47°20'S (29°S–52°S including all islands) and is separated from the nearest large landmass (Australia) by the Tasman Sea (Neill & Trewick 2008). About 75% of the land is above 200 m with 19 peaks exceeding 3000 m (all South Island).

New Zealand is derived from Zealandia, part of the gondwanan supercontinent. At about 82 Ma, Zealandia became separated from what was to become Australia, Antarctica and South America (Kamp 1986; Cooper & Millener 1993; Campbell & Hutching 2007; Trewick



Fig. 1 The New Zealand region, showing nearby islands. Shading represents the largely submerged continent of Zealandia.

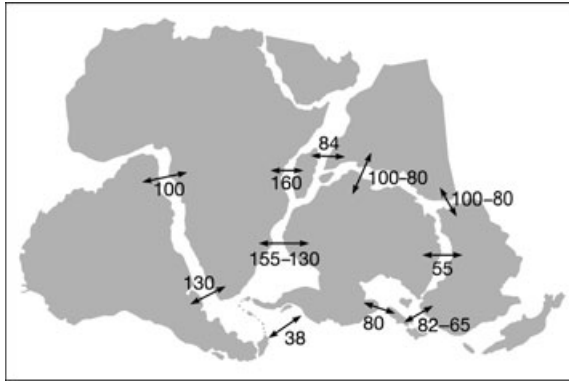


Fig. 2 Reconstruction of Gondwana with approximate splitting times in millions of years (after Stevens 1980).

et al. 2007; Graham 2008; Fig. 2). The subsequent opening of the Tasman Sea established the current ocean barrier of about 1500 km between Zealandia and Australia as early as 65 Ma. The New Caledonian part of Zealandia separated from the northern part of the Lord Howe Rise 74–65 Ma as the New Caledonia Basin opened (Yan & Kroenke 1993), although islands have probably formed along the Norfolk and Reinga rises since then (Herzer *et al.* 1997). The Southern Ocean did not open properly until about 30 Ma (Veevers 1991), which led to the cooling of Antarctica as it drifted to its current position over the pole.

From about 60–24 Ma, Zealandia gradually stretched, thinned and submerged, resulting in a major marine inundation, the Oligocene transgression. Zealandia was reduced to (at most) a few low-lying islands (Suggate *et al.* 1978; Cooper 1989; Cooper & Millener 1993; Cooper & Cooper 1995; Campbell & Hutching 2007). There remains some uncertainty concerning the extent of marine inundation at its peak in the late Oligocene, and today about 93% of Zealandia is submerged. Typical shoreline reconstructions are based on putative shallow marine limestone deposits, and have been interpreted as indicating a major island comprising present day Otago-Southland, and other islands equivalent to the Nelson and Northland regions (Cooper 1989). However, many geologists have noted that there is little geological evidence for any one continuous landmass through the Oligocene (LeMasurier & Landis 1996; Macphail 1997), and a recent review (Landis *et al.* 2008) shifted the burden of proof to demonstrating its existence. Nevertheless, total inundation is hard for biologists to reconcile with some apparently archaic elements of the fauna (Cooper & Millener 1993; Daugherty *et al.* 1993; Winkworth *et al.* 1999; Ericson *et al.* 2002; McDowall 2002; Stöckler *et al.* 2002), which otherwise would have had to disperse to NZ post-Oligocene. Some rich Oligocene and early Miocene fossil records have been taken as

evidence for a continuous landmass (Lee *et al.* 2007a,b, 2009; Worthy *et al.* 2009). NZ may have existed in this submerged state for a few million years, and the impact on the biota must have been dramatic (Fleming 1979) if not catastrophic (Landis *et al.* 2008). The last major marine transgression began in the late Miocene and reached its maximum in the Pliocene, producing numerous sea straits in North Island (Fleming 1975).

The Alpine Fault is the NZ continental boundary of the Pacific and Indo-Australian plates and runs approximately SW-NE for >600 km along most of the length of South Island. Inception of tectonic activity along the fault at about 25–23 Ma marked the start of the formation of NZ (Trewick *et al.* 2007; Graham 2008). The fault has undergone 440–470 km dextral strike/slip displacement (Sutherland 1999), up to 420 km having occurred in the last 11–16 Ma (Cutten 1979; King 2000; Fig. 3a). This movement averages 20 mm/year since 25 Ma, and about 40 mm/year since the late Miocene (Sutherland 1994; Cooper & Norris 1995; Cutten 1995; Sutherland & Norris 1995). Tectonic activity led to periods of volcanism up to 13 Ma on the east coast of South Island and to the present day on North Island. The Otago and Banks peninsulas are prominent South Island east coast remnants of shield volcanoes. Lake Taupo in central North Island is a flooded crater of a large explosive volcano, which has erupted several times, most recently about 1850 years ago, burying much of North Island in metres of ash (Suggate *et al.* 1978; McDowall 1996; Newnham *et al.* 1999; Morgan-Richards *et al.* 2000; Alloway *et al.* 2007). All North Island volcanic mountains are recent (<1 Ma). Starting about 5 Ma, compression along the Alpine Fault elevated a major axial range, the Southern Alps (Kaikoura orogeny), producing the first extensive alpine habitat and extreme gradient of rainfall (Batt *et al.* 2000; Chamberlain & Poage 2000; Fig. 3b). Uplift rates along the range measure 2–11 mm/year (Wellman 1979), with a total of up to 16 km in the central section near Aoraki (Mt Cook), NZ's highest point (3764 m), and thus about 12 km of erosion (Craw 1995), exacerbated by rainfalls of up to 16 m/year on the divide (Griffiths & McSaveney 1983; Alloway *et al.* 2007). A combination of high rainfall and landslips has led to formation of large, braided rivers running east-southeast from the Southern Alps, building a vast plain of fused alluvial fans that extend some 500 km along the eastern flank of central South Island (Canterbury Plain). Parallel with the main axial range, many other ranges are rising, particularly across semi-arid Otago, giving this region its characteristic basin-range formation. This region was covered with a system of Miocene freshwater lakes (Lake Manuherikia) some 15–8 Ma, as evidenced by sediments containing crocodile and galaxiid fish fossils, along with many tree species indicative

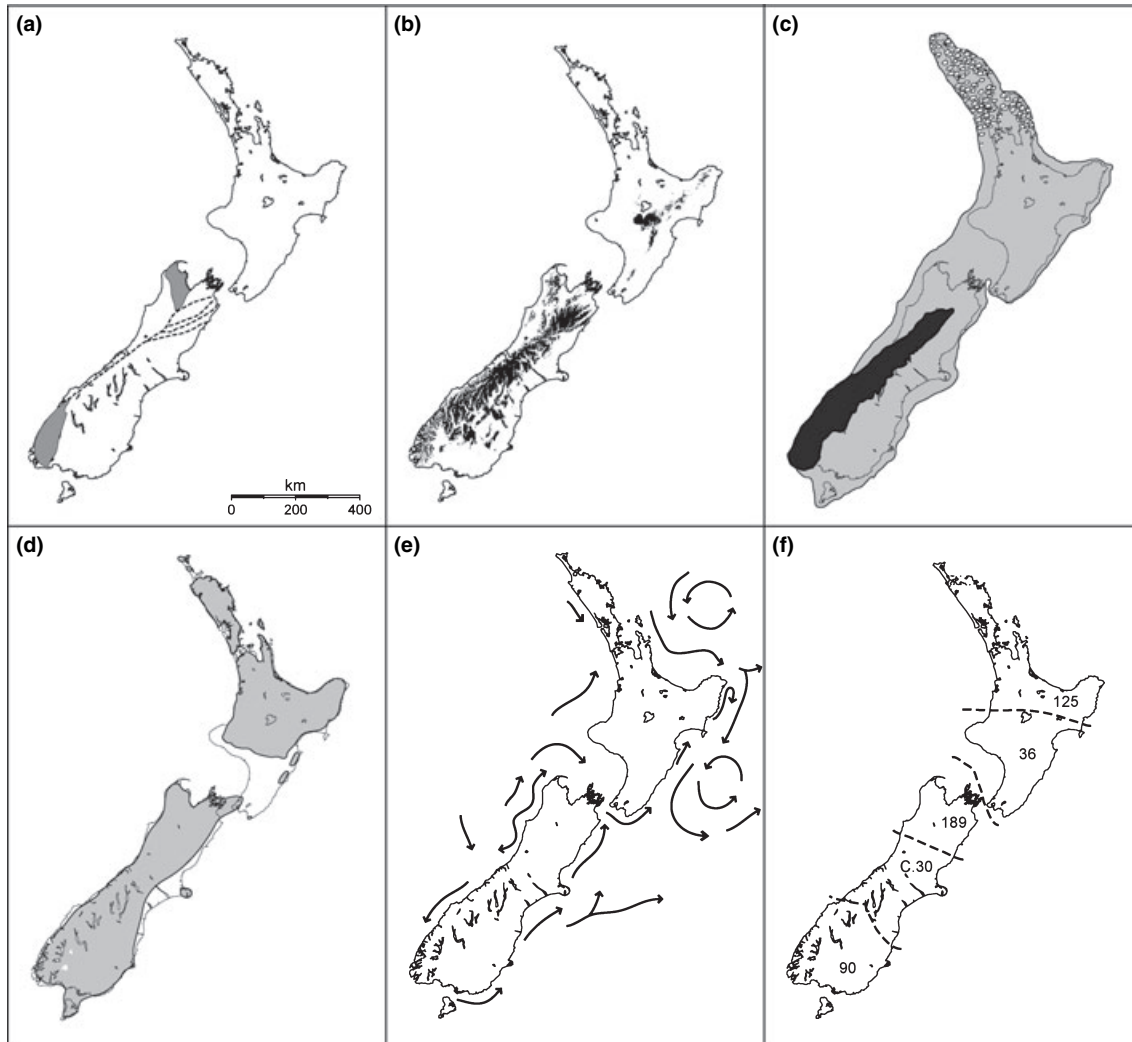


Fig. 3 (a) Formation of current South Island as a result of shear along the Alpine Fault over 25 Ma. The Takaka terrane is shaded. (b) Land over 1000 m (black), comprising the Southern Alps and northern volcanic plateau. (c) The extent of ice at the Last (Otiran) Glacial Maximum (black) and reconstructed coastline (after Fleming 1962). (d) Reconstruction of New Zealand during the Pliocene, showing the wide Manawatu sea strait and smaller northern straits and islands. (e) Marine currents and gyres dominating coastal waters (after Graham 2008; p212). (f) Three regions of high endemism and two relative gaps, as demonstrated by vascular plants (after Wardle 1991).

of a warmer climate (Youngson *et al.* 1998; Lee *et al.* 2009; Worthy *et al.* 2009).

New Zealand underwent repeated cycles of glaciation in the Pleistocene (Carter 2005). Although glaciers covered up to 30% of South Island (Fig. 3c), large areas (in addition to North Island) went unscathed (Marlborough, eastern and central Otago/Southland). Unlike widespread ice sheet formation in North America and north/central Eurasia, NZ's entirely montane (not polar) glaciers were fragmented on the peripheries, leaving some unglaciated valleys and nunataks. During these times, notably at the last glacial maximum, lowered sea level connected the three major islands and most of the current offshore islands.

Ecological history of New Zealand

In conjunction with geological events, the climate has seen major changes. After a warm late Eocene, fossil fauna and flora suggest a relatively stable warm to cool temperate climate through most of the Oligocene, Miocene and Pliocene (Fleming 1975; Cooper & Millener 1993; Lee *et al.* 2001). During the Pliocene marine transgression, seas were subtropical but the climate only slightly warmer (Fleming 1975). The late Pliocene saw a rapid cooling leading into Pleistocene glacial and interglacial cycles (Cooper & Millener 1993). The last glaciation depressed the temperature by an average of 4.5–6 °C and lowered the snowline by 850–1000 m

(Willett 1950; Wardle 1988). Forest dominated the northern third of North Island and western Nelson, but was reduced to small isolated pockets on South Island and lost entirely from the Chathams and subantarctic islands (Alloway *et al.* 2007). Grass and shrubland took their place (McGlone *et al.* 1995; Alloway *et al.* 2007).

Gigantism is often alluded to in NZ birds (*Dinornis*, *Strigops*, *Harpagornis*), gecko (*Hoplodactylus delcourti*), orthopterans (*Deinacrida*), phasmids (*Acanthoxylla*, *Argosarchus*, *Clitarchus*), beetles (*Dorcus*, *Prionoplus*), giraffe weevil (*Lasiornychus*), ghost moths (*Aenetus*), centipedes (*Cormocephalus*), pill millipedes (*Procyliosoma*), land snails (*Paryphanta*, *Placostylus*, *Powelliphanta*), slugs (*Amphicornophorus*, *Pseudaneitea*), flatworms (*Artioposthia*, *Geoplana*), earthworms (*Spenceriella*) and subantarctic megaherbs (*Anistome*, *Bulbinella*, *Gentianella*, *Pleurophyllum*, *Stilbocarpa*) (Meads 1990; Daugherty *et al.* 1993). Moa radiated in the absence of other large herbivores and insects in the absence of rodents. Parrots evolved the alpine hawk-like kea and flightless nocturnal kakapo. Some groups exhibit extensive endemic radiations (e.g. moa, rails, skinks, moths, springtails, true flies, ensiferan crickets (weta), beetles, earthworms, land snails, Compositae, *Hebe*, *Coprosma*; Watt 1975; Emberson 1998), whereas others exhibit little diversity (e.g. other terrestrial birds, amphibians, freshwater fishes, butterflies, odonates, hymenopterans). Although few fossils of small, putatively terrestrial mammals have been recovered from mid-Miocene deposits (19–16 Ma, Worthy *et al.* 2006), no other terrestrial nonvolant mammals are known.

Isolation has led to high rates of endemism. At the species level, terrestrial arthropods, dicotyledons and grasses are all about 90% endemic (Godley 1975; Watt 1975; Dugdale 1989; Klimaszewski 1997). At the genus level, some groups display high levels of endemism (e.g. beetle genera 43% endemic), whereas others show little (e.g. dicots 14%, grasses 10%, ferns 2%) (Godley 1975). Partial or complete lack of flight is common in terrestrial birds (moa, kiwi, takahe, kakapo, goose, coot), lepidopterans, coleopterans, orthopterans, dipterans and plecopterans. Prior to the arrival of humans, the country was almost entirely covered in bush: diverse lowland podocarp/evergreen forest, montane southern beech (*Nothofagus*), and kauri (*Agathis*) in the far north (Molloy *et al.* 1963; Atkinson & Cameron 1993; Hall & McGlone 2006). Settlement by Polynesian peoples within the last 800 y (Anderson 1991) resulted in major forest burn-off associated with moa hunting (Molloy *et al.* 1963; Holdaway & Jacomb 2000). The first major mammalian predator, the Polynesian rat (kiore), was introduced at this time, possibly earlier (Holdaway 1996), and major problem predators followed European settlement some 150 years ago (Craig *et al.* 2000).

Thirty-three introduced bird species and 34 mammals have established (Atkinson & Cameron 1993), from a combination of fur trade, farming, misguided predator control programmes and 'acclimatisation' of 19th century immigrants. At least 21 species of freshwater fish (McDowall 2000) are naturalized. Native vascular plants (2500, 86% endemic) are outnumbered by introduced ones, of which at least 1600 are well established (Atkinson & Cameron 1993; Craig *et al.* 2000). Further removal of forest and drainage of lowland has destroyed many communities, with some 90% of wetland lost. Less than 30% of native forest remains, and many species have either gone extinct or are threatened with extinction, among which birds are the most widely known with 40% already extinct (Atkinson & Cameron 1993). Over 30% of NZ's total land area is now under reserve status; conservation issues facing NZ have been summarized elsewhere (Craig *et al.* 2000).

Origins of the New Zealand biota

The origins of the NZ biota have vexed biogeographic debate for decades. Argument often became unnecessarily polarized (Craw *et al.* 1999) into dispersalist (McDowall 1978; Pole 1994) and vicariance (Rosen 1978; Craw 1979) schools. Fleming (1962) proposed seven biogeographic elements in the flora and fauna: endemic (archaic), palaeoaustral, neoaustral, Australian, Malayo-Pacific, Holarctic and cosmopolitan. These encompassed broad groups of organisms (e.g. marine/terrestrial, flying/flightless, dispersive/sedentary). The analytical tools of phylogeography make the issue of origins an empirical question, provided that appropriate outgroups can be identified. The null hypothesis may be vicariance (Croizat *et al.* 1974; Sanmartín & Ronquist 2004): ancestors of the modern biota have existed in the region since the isolation of Zealandia from Australia. If phylogenetic data make this assertion untenable, then alternative origins and mechanisms for dispersal should be sought. These might be hard to find for taxa that we expect to be poor dispersers across oceans (ratites, frogs, freshwater limited fish), but we should not be surprised to find recent overseas linkages for volant birds, mammals and insects, tough-seeded coastal plants (Sykes & Godley 1968), and plants with wind dispersal mechanisms (Raven 1973).

There is a rapidly growing list of NZ plants (Linder & Crisp 1995) and animals that have close genetic affiliations with forms found in Australia, South America, New Caledonia and other Pacific rim or island landmasses (Table 1). Consequently, a consensus is emerging that dispersal has been a major process leading to the formation of the flora and fauna (McGlone *et al.* 2001; Winkworth *et al.* 2002b, 2005; Sanmartín &

Table 1 Molecular genetic data pertaining to origins of NZ biota: timing and source

Taxon	Markers	Molecular dating: origins	Reference	Notes
<i>Sphenodon</i> tuatara	Complete mtDNA; <i>Rag-1</i>	268–275 Ma; archaic?	Rest <i>et al.</i> 2003; Hugall <i>et al.</i> 2007	NZ fossils 19–16 Ma
<i>Leiopelma</i> frog	<i>Rag-1</i> , <i>Cxcr-4</i> , <i>Ncx-1</i> , 16S-ND1	184–180 Ma; archaic?	Roelants & Bossuyt 2005	Calibration date only; consistent with constrained tree
<i>Lepidothamnium</i> podocarp	<i>rbcL</i>	109 Ma; archaic?	Wardle <i>et al.</i> 2001	NZ late Cretaceous fossils
<i>Luzuriaga</i> ; Liliales	<i>rbcL</i>	92 Ma; archaic?	Wardle <i>et al.</i> 2001	NZ Quaternary fossils
<i>Agathis</i> conifer	<i>rbcL</i> ; <i>rbcL</i> , <i>matK</i> , <i>trnD-trnT</i>	92–78 Ma; archaic?	Stöckler <i>et al.</i> 2002; Knapp <i>et al.</i> 2007	Late Oligocene fossils
<i>Hoplodactylus</i> , <i>Naultinus</i> ; geckos	16S	83–74 Ma; archaic?	Chambers <i>et al.</i> 2001	Calibration date only; consistent with outgroup
<i>Emeus</i> , <i>Dinornis</i> ; moa	Complete mtDNA	82 Ma; archaic?	Cooper <i>et al.</i> 2001	Calibration date only; consistent with outgroup
<i>Acanthisitta</i> wrens	<i>c-myc</i> , <i>Rag-1</i>	85–82 Ma; archaic?	Ericson <i>et al.</i> 2002	Weak calibration
Hyriidae freshwater mussels	28S, COI	Archaic?	Graf & Ó Foighil 2000	No calibration
<i>Panoplirops</i> crayfish	COI, 12S, 16S, 28S	Archaic?	Shull <i>et al.</i> 2005	Consistent with tree structure only
Petalidae harvestmen	COI, 16S, 18S, 28S, H3	Archaic?	Boyer & Giribet 2007, 2009	
<i>Gumera</i>	ITS, <i>rbcL</i> , <i>rps16</i>	Archaic?	Wanntorp & Wanntorp 2003	NZ pollen 80 Ma
<i>Pseudopanax</i> lancewoods	<i>rbcL</i>	27.3 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ late Cretaceous fossils
<i>Apteryx</i> kiwi	<i>rbcL</i>	<75.2 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ Eocene fossils
	Complete mtDNA; nuclear	72–55.6 Ma; Aus-NC	Cooper <i>et al.</i> 2001; Haddrath & Baker 2001; van Tuinen & Hedges 2001	
<i>Mysticina</i> short-tailed bat	DNA-DNA hybrid; <i>ADRA2B</i> , <i>BRCA</i> , <i>RAG1</i> , <i>VWF</i>	54, 47 Ma; SAM	Kirsch <i>et al.</i> 1998; Teeling <i>et al.</i> 2003	
	<i>cytb</i> ; 12S, 16S, tRNA ^{Val}	45 & 41–32 Ma	Kennedy <i>et al.</i> 1999; Van Den Bussche & Hooper 2000, 2001	
<i>Podocarpus</i> podocarp	<i>rbcL</i>	54.6 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ late Cretaceous fossils
<i>Griselinia</i> ; Apiales	<i>rbcL</i>	51.2 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ Miocene fossils
<i>Laurelia</i> ; Laurales	<i>rbcL</i> , <i>rpl16</i> , <i>atpB-rbcL</i> , <i>trnL-F</i> , <i>psbA-trnH</i> , <i>trnT-L</i>	50–30 Ma; Ant/Aus	Renner <i>et al.</i> 2000	NZ pollen 37 Ma
<i>Astelia</i> ; Liliaceae	<i>rbcL</i>	37.5 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ Paleocene fossils
Callaeatidae; wattlebirds	<i>cytb</i> , ND2, 12S	<47.8 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ mid-Eocene fossils
<i>Callania</i> limpet	12S, 16S	39–34 Ma; Aus	Shepherd & Lambert 2007	Related NZ fossils 38 Ma
<i>Corynocarpus</i> ; Cucurbitales	ITS, <i>rbcL</i>	>38 Ma?; Aus/Asia?	Goldstien <i>et al.</i> 2006a	
<i>Fuchsia</i> ; Onagraceae	ITS, <i>trnL-trnF</i> , <i>rpl16</i>	30 Ma; NC	Wagstaff & Dawson 2000	NZ pollen 30 Ma
<i>Nothofagus</i> southern beech	ITS, <i>trnL-trnF</i> , <i>rpl16</i> , <i>rbcL</i> ; <i>atpB-psal</i> , <i>trnL-trnF</i>	<66 & <48 Ma; 27–20 & 33–13 Ma; Aus	Berry <i>et al.</i> 2004	NZ pollen 65 Ma
	<i>rbcL</i>	30.7 Ma; SAM?	Martin & Dowd 1993; Knapp <i>et al.</i> 2005	
<i>Nothofagus</i> , <i>Lophozonia</i> , <i>Fuscospora</i>	ITS, <i>rbcL</i> , <i>atpB-rbcL</i>	49–5 & 37–3 Ma; Aus	Wardle <i>et al.</i> 2001	NZ late Cretaceous fossils
			Cook & Crisp 2005b	NZ late Cretaceous fossils

Table 1 Continued

Taxon	Markers	Molecular dating; origins	Reference	Notes
<i>Lyallia</i> , <i>Hectorella</i> ; Portulacaceae	<i>rbcL</i> , <i>trnK-matK</i>	25.6–18.6 Ma; Kerguelen	Wagstaff & Hennion 2007	
<i>Hemiphysa</i> pigeon	12S, COII, ND2, <i>cytb</i> , COI, <i>Rag-1</i> , IRBP, FIB7	24 Ma; Aus	Pereira <i>et al.</i> 2007	
<i>Aphis-Paradoxaphis</i> ; Aphidini	COII, <i>tRNA^{Leu}</i> , <i>EF1α</i>	25–16 Ma, 29–24 Ma; Aus	von Dohlen & Teulon 2003	
<i>Oligosoma</i> skink	<i>cytb</i> , ND2, ND4, 12S, 16S, <i>Rag-1</i>	22.6–16 Ma; NC	Chapple <i>et al.</i> 2009	
<i>Calmsia</i> , <i>Olearia</i> , <i>Brachyglottis</i> +31 other genera; Asteraceae	ITS	<23 Ma; many events	Wagstaff & Breitwieser 2002	NZ pollen 23 Ma
Elaeocarpaceae; Elaeocarpaceae	ITS, <i>trnL/trnF</i>	21 Ma; Aus	Crayn <i>et al.</i> 2006	NZ early Miocene pollen
<i>Carpfia</i> , <i>Oreobolus</i> ; sedges	<i>rbcL</i>	20.5 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ Oligocene fossils
Trochid topshells	COI, 16S, actin	30.1–8.8 Ma; Aus	Donald <i>et al.</i> 2005	Consistent fossils
<i>Ascarina</i> ; Chloranthaceae	<i>rbcL</i> , <i>rpl20-rps12</i> , <i>trnL</i> , <i>trnL-F</i>	Miocene; NC/Asia?	Zhang & Renner 2003	
<i>Montigena</i> , <i>Carmichaelia</i> , <i>Clanthus</i> ; Fabaceae	ITS	Miocene(?); Aus	Wagstaff <i>et al.</i> 1999	Late Pliocene <i>Carmichaelia</i>
<i>Aristotelia</i> ; Elaeocarpaceae	ITS, <i>trnL/trnF</i>	17 Ma; Aus	Crayn <i>et al.</i> 2006	NZ early Miocene pollen
deep bodied Galaxiidae	<i>cytb</i> , 16S	Miocene; Aus	Waters <i>et al.</i> 2000b	
<i>Neochanna</i> mudfish	<i>cytb</i> , 16S	22–6.3 Ma; Aus	Waters <i>et al.</i> 2000b;	
			Waters & McDowall 2005	
<i>Retropinna</i> , <i>Stokellia</i> ; smelt	16S	Miocene; Aus	Waters <i>et al.</i> 2002	
<i>Austrolittorina</i> winkle	COI	Miocene? Aus	Waters <i>et al.</i> 2007a	
<i>Diadema palmieri</i> sea urchin	COI, ATPase	14–6.5 Ma; Indo-Pacific	Lessios <i>et al.</i> 2001	
<i>Perna</i> mussel	COI, ITS	19.9–5.8 Ma; Indo-west Pacific/Atl	Wood <i>et al.</i> 2007	
<i>Polystichum</i> fern	<i>rbcL</i>	13 Ma; Aus	Perrie <i>et al.</i> 2003	NZ pollen <5 Ma
<i>Amphipsalta</i> , <i>Notopsalta</i> ; cicada	COI, COII, 12S, 16S, <i>EF1α</i>	<11.6 Ma; Aus	Buckley <i>et al.</i> 2002;	
			Arensburger <i>et al.</i> 2004	
<i>Kikihia</i> , <i>Maoricicada</i> , <i>Rhodopsalta</i> ; cicada	COI, COII, 12S, 16S, <i>EF1α</i>	<11.6 Ma; NC/Aus	Buckley <i>et al.</i> 2002; Arensburger <i>et al.</i> 2004a	
<i>Kikihia</i> cicada	COII, ATPase6, ATPase8	11 Ma; Aus	Arensburger <i>et al.</i> 2004b	
<i>Discaria</i> buckthorns	<i>rbcL</i>	10.2 Ma; SAM?	Wardle <i>et al.</i> 2001	
<i>Galaxias maculatus</i> , inanga	<i>cytb</i> , 16S; CR, 16S	9.4–5.3 Ma; 6–2 Ma, <30 Ma; Aus	Waters & Burridge 1999; Waters <i>et al.</i> 2000a,b	NZ quaternary fossils
<i>Oligosoma</i> , <i>Cyclodina</i> ; skink	ND2, <i>c-mos</i> , <i>Rag-1</i>	7.9 Ma; NC/Lord Howe	Smith <i>et al.</i> 2007	
<i>Lasaea</i> clam	COIII	Late Miocene/Pliocene; SAF, Kerguelen	Taylor & Ó Foighil 2000	
<i>Galaxias brevipinnis</i> , koaro	ATPase, ND5–6, <i>cytb</i>	Late Miocene/Pliocene; Aus	Waters <i>et al.</i> 2001; Waters & Wallis 2001a	Related fossils 23 Ma
<i>Scutus</i> sea slug	COI	Late Miocene/Pliocene? Aus	Waters <i>et al.</i> 2007a	Related fossils 40 Ma
Peridophytes; 31 generic pairs of fern	<i>rbcL</i>	Mostly <30 Ma; worldwide dispersal	Perrie & Brownsey 2007	
<i>Ranunculus</i> , buttercup	ITS, <i>J_{sA}</i>	Tertiary; Aus/NC/SAM?	Lockhart <i>et al.</i> 2001	Radiation is 5 Ma

Table 1 Continued

Taxon	Markers	Molecular dating; origins	Reference	Notes
<i>Pittosporum</i>	ITS, <i>trnL-F</i>	Pliocene(?); Aus	Gemmill <i>et al.</i> 2002; Chandler <i>et al.</i> 2007	
<i>Petroica</i> ; robins and tomtit	<i>cytb</i> , CR	Pliocene(?); Aus	Miller & Lambert 2006	
<i>Iphiginiia</i> ; Colchicaceae	<i>psbB</i> , <i>trnH</i> , <i>trnL</i> , <i>atpB-rbcL</i> , <i>ndhF</i>	Pliocene? Aus	Case <i>et al.</i> 2008	
<i>Myosotis</i> ; Boraginaceae	ITS, <i>matK</i> , <i>ndhF</i> , <i>trnK-psbA</i>	14.7–2 Ma; Eur/N Am	Winkworth <i>et al.</i> 1999, 2002a	NZ pollen 2 Ma
<i>Coriaria</i> ; Cucurbitales	<i>rbcL</i>	6.8 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ Pliocene fossils
<i>Donatia</i> cushion plant	<i>rbcL</i>	6.8 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ quaternary fossils
<i>Psychrophilia</i> buttercup	<i>rbcL</i>	6.8 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ quaternary fossils
<i>Leptocarpus</i> rushes	<i>rbcL</i>	6.8 Ma; SAM?	Wardle <i>et al.</i> 2001	NZ late Miocene fossils
<i>Phyllocladus</i> ; Podocarpaceae	ITS, <i>rbcL</i> , <i>matK</i>	6.3 Ma; Aus/NG?	Wagstaff 2004	NZ paleocene pollen
<i>Forstera</i> , <i>Phyllachne</i> ; Styliidiaceae	ITS, <i>rbcL</i>	6 Ma; Aus or S Am	Wagstaff & Wege 2002	NZ pollen 2 Ma
<i>Anoteropsis</i> lycosid spider	COI, ND1	5 Ma; Aus	Vink & Paterson 2003	
<i>Ooperipatellus</i> , <i>Perripatoides</i> ; peripatus	COI	5.5 Ma?; Aus	Gleeson <i>et al.</i> 1998	
<i>Scieranthus</i> ; Caryophyllaceae	ITS	7.7–1.2; Europe	Smissen <i>et al.</i> 2003b	
<i>Oourisia</i> ; Plantaginaceae	ITS, ETS, <i>matK</i> , <i>rps16</i>	<5 Ma?; S Am (Aus?)	Meudt & Simpson 2006	NZ pollen 25 Ma (Asteraceae)
<i>Abrotanella</i> ; Asteraceae	ITS, <i>trnK/matK</i>	<4 Ma; 2 + events	Wagstaff <i>et al.</i> 2006	NZ Pliocene pollen
<i>Hebe</i> ; Scrophulariaceae	ITS, <i>rbcL</i>	3.9 Ma; Aus	Wagstaff <i>et al.</i> 2002	
Hepialid moths	COI, COII	4–3 Ma; Aus	Brown <i>et al.</i> 1999	
<i>Sopitoria</i> ; Fabaceae	<i>atpB-rbcL</i>	5–2 Ma; NW Pacific	Hurr <i>et al.</i> 1999	
<i>Tetrachondria</i> ; Lamiales	<i>rbcL</i>	2.5 Ma; S Am	Wagstaff <i>et al.</i> 2000	
<i>Pachycladon</i> complex; Brassicaceae	ITS	3.5–1 Ma; Aus	Heenan <i>et al.</i> 2002	
<i>Gentianella</i> ; Gentianaceae	ITS	2.7–1.4 Ma; S Am	von Hagen & Kadereit 2001; Glenny 2004	NZ pollen 2.6–1.6 Ma
<i>Weinmannia</i> ; Cunoniaceae	ITS, <i>trnL-F</i>	NC or Pacific?	Bradford 2002	<1% to sister
<i>Cardamine</i> , <i>Lepidium</i> , <i>Notothlaspi</i> , <i>Rorippa</i> ; Brassicaceae	ITS	≥5 events; multiple sources	Mitchell & Heenan 2000	
Gnaphalieae; Asteraceae	ITS	>6 events (Pliocene?); Aus	Breitwieser <i>et al.</i> 1999	NZ pollen 25 Ma (Asteraceae)
<i>Craspedia</i> ; Asteraceae	ITS, ETS, <i>psbA-trnH</i>	Plio/Pleistocene?; Aus	Ford <i>et al.</i> 2007	NZ pollen 25 Ma (Asteraceae)
<i>Oreostylidium</i> ; Styliidiaceae	ITS, <i>rbcL</i>	2 Ma; Aus	Wagstaff & Wege 2002	NZ pollen 2 Ma
<i>Porphyrio</i> , <i>Rallus</i> ; rails	12S, <i>cytb</i>	2 Ma; global	Trewick 1997	
<i>Cephalorhynchus</i> dolphin	CR	2 Ma; S Af	Pichler <i>et al.</i> 2001	
<i>Latrodectus</i> spider	COI; ND1	<2 Ma?; Aus/Af/Europe?	Garb <i>et al.</i> 2004; Griffiths <i>et al.</i> 2005	
<i>Harpagornis</i> eagle	<i>cytb</i> , ND2	1.8–0.7 Ma; Aus	Bunce <i>et al.</i> 2005	
<i>Cocciasterius muricata</i> seastar	COI, CR, ITS2	1.3–0.6 Ma; Aus	Waters & Roy 2003a,b	
<i>Lepidium</i> ; Brassicaceae	ITS, <i>trnT-L</i> , <i>trnL</i> intron, <i>trnL-F</i>	1.3–0.3 Ma; Aus/S Af/Am	Mummenhoff <i>et al.</i> 2004	Hybrid origins

Table 1 Continued

Taxon	Markers	Molecular dating; origins	Reference	Notes
<i>Himantopus</i> black stilt	CR, <i>cytb</i>	<1 Ma; Aus	Chambers & MacAvoy 1999	
<i>Cyanoramphus</i> parakeet	<i>cytb</i> , CR	0.5 Ma, Norfolk I or NC	Chambers <i>et al.</i> 2001	
<i>Pyrrhobryum</i> <i>minioides</i> moss	<i>atpB-rbcL</i> , <i>trnL</i> , <i>rps4</i>	Recent; Aus	McDaniel & Shaw 2003	
<i>Eudiptula</i> blue penguin	12S, <i>cytb</i> , CR	Recent; Aus	Banks <i>et al.</i> 2002	
<i>Himantopus</i> pied stilt	CR, <i>cytb</i>	Recent; Aus	Chambers & MacAvoy 1999	
<i>Zosterops lateralis</i> white eye	ND2-3, TGFB2	Recent; Aus	Moyle <i>et al.</i> 2009	1830
<i>Nemadactylus</i> , <i>Goniistius</i> ; perciform fishes	COI, <i>cytb</i>	Recent; Aus	Burridge 2000	
<i>Sitobion</i> aphids	microsatellites	Recent; Aus	Wilson <i>et al.</i> 1999	Possibly anthropogenic
<i>Tursiops</i> dolphin	CR	Recent gene flow; global	Tezanos-Pinto <i>et al.</i> 2009	
<i>Nemadactylus</i> tarakihi	Microsatellites	Ongoing gene flow; Aus	Burridge & Smolenski 2003	
<i>Nerita</i> sea snail	COI	Ongoing gene flow; Aus	Waters <i>et al.</i> 2005	
<i>Jasus</i> lobster	Allozyme; mtDNA RFLP	Ongoing gene flow; Aus	Smith & McKoy 1980; Ovenden <i>et al.</i> 1992	

Af, Africa; Am, America; Ant, Antarctic; Atl, Atlantic; Aus, Australia; Ma, millions of years ago; NC, New Caledonia; NG, New Guinea.

Ronquist 2004; McGlone 2005). Indeed, some have gone further and questioned whether there are necessarily any truly vicariant gondwanan elements in NZ (Pole 1994, 2001; Waters & Craw 2006; Trewick *et al.* 2007; Goldberg *et al.* 2008; Landis *et al.* 2008).

The most likely vicariant lineages include moa, wrens, tuatara, frogs, kauri and freshwater mussels and crayfish (koura). Isozyme and karyological comparisons of leiopelmatid frogs, well known for primitive skeletal and muscular features, show great divergence from all other groups, to the extent that they may be sister to all other frogs (Green *et al.* 1989). Sequence analysis (Roe-lants & Bossuyt 2005), however, supports a sister relationship with extant *Ascaphus* in North America, which probably had its origins in South America where related fossils exist (Cox 1998). Chloroplast sequence divergence between kauri (*Agathis* conifer) and other austral relatives provides no evidence of post-Oligocene linkages and is consistent with vicariance (Stöckler *et al.* 2002; Knapp *et al.* 2007).

One of NZ's two extant bat species (short-tailed, *My-stacina*) has no close relatives: estimates of divergence from a New World sister range from 54 Ma (Kirsch *et al.* 1998) to 35 Ma (Pierson *et al.* 1986). These suggestions of post-Gondwanan origins are supported by mtDNA (Kennedy *et al.* 1999; Van Den Bussche & Hooper 2000, 2001) and nuclear gene analysis (Teeling *et al.* 2003), suggesting dispersal through a warmer Antarctica, or perhaps via Australia across the Tasman. For some other species, authors invoke partial vicariant explanations involving Antarctica that are debatable in the absence of calibrations (Schuettelpelz & Hoot 2004).

Two other icons of Gondwana, kiwi and southern beech (*Nothofagus*), appear to have colonized NZ more recently (Martin & Dowd 1993). Phylogenetic analysis of chloroplast DNA, constrained by fossil evidence, strongly suggests contemporaneous invasions by two subgenera of *Nothofagus* in the Oligocene (Cook & Crisp 2005b; Knapp *et al.* 2005), consistent with the absence of fossil pollen in NZ before this time. Pioneering ancient DNA work on mitochondrial 12S from subfossil moa suggested that moa are not sister to kiwi (Cooper *et al.* 1992). The depth of moa in the tree is consistent with gondwanan roots (Cooper *et al.* 1993), but the sister relationship of kiwi and emu-cassowary suggests that kiwi ancestors arrived here later, possibly through a New Caledonian arc by successive colonization of the Norfolk and Reinga ridges (Cooper *et al.* 1992, 2001; Herzer *et al.* 1997; Haddrath & Baker 2001; van Tuinen & Hedges 2001). A recent extensive nuclear gene analysis raises the possibility that kiwi ancestors could even have been flighted (Harshman *et al.* 2008).

The idea of colonization from New Caledonia (NC) in the Tertiary along now-submerged ridges is a repeated

theme, despite minimal evidence of biotic links between present day NC and NZ (Sanmartín & Ronquist 2004). This link has been made for skinks (*Oligosoma*; 28 species), whose radiation may date to the late Oligocene (Hickson *et al.* 2000), although more extensive datasets suggest early (Chapple *et al.* 2009) or late (Smith *et al.* 2007) Miocene. Although NZ geckos (*Hoplodactylus*, *Naultinus*; 16 + species) could be a vicariant element (Chambers *et al.* 2001), more recent dispersal via NC is possible. NC is also an implicated route for parrots, wattlebirds (Shepherd & Lambert 2007), cicada (Arensburger *et al.* 2004b), *Placostylus* (Ponder *et al.* 2003) and *Corynocarpus* (Wagstaff & Dawson 2000).

Like other island archipelagos (Chubb *et al.* 1998; McDowall 2003), the NZ freshwater fish fauna is relatively depauperate and of comparatively recent diadromous origins (McDowall & Whitaker 1975), dominated by galaxiids and gobiids (McDowall 2000). The inanga (*Galaxias maculatus*), one of the world's most widespread freshwater species, led Darwin to comment on the unlikelihood of Chilean, Australian and NZ populations maintaining connectedness through oceanic dispersal (Darwin 1872). Phylogenetic analysis of mtDNA control region has shown that he was indeed right: the three landmasses are (almost) reciprocally monophyletic for deeply divergent clades (Waters *et al.* 2000a), despite little obvious nuclear gene differentiation (Berra *et al.* 1996). It is likely that inanga evolved on one landmass and spread to others several million years ago. Darwin interpreted the gondwanan distribution of this species as possibly indicating spread from warmer Antarctica (≥ 30 Ma) (Darwin 1872), but molecular data suggest more recent intercontinental connections (Waters *et al.* 2000a). *Cytb* data suggest that NZ mudfish (*Neohanna*), containing four localized endemics confined to freshwater (Gleeson *et al.* 1999), are likely to be derivatives of a diadromous Australian lineage (Waters *et al.* 2000b), now represented by *N. cleaveri* (McDowall 1997a; Waters & White 1997; Waters & McDowall 2005). The galaxioids as a group suggest several Miocene-Pliocene exchanges between NZ and both Australia and NC (Waters *et al.* 2000b).

African links are rare in animals, and marine in both cases (dolphin, Pichler *et al.* 2001), with evidence for the Kerguelen Island as a staging post (*Lasaea*, Taylor & Ó Foighil 2000). Plants show a broad array of links, involving in particular Australia and South America, but including Africa, Europe and North America (Winkworth *et al.* 1999, 2002b; Linder *et al.* 2003; Mummehoff *et al.* 2004; Perrie & Brownsey 2007; Bergh & Linder 2009). Pollen records for about 100 species found in NZ and South Australia show that only eight appear in NZ before they do in Australia, consistent with colonization by dispersal in many cases (Macphail 1997).

Evidence from mitochondrial and nuclear genes indicates that the NZ anostomatid weta comprise three distinct groups: tusked weta related to NC taxa, ground weta related to Australian species and an endemic radiation of giant and tree weta. This suggests that either NZ maintained multiple gondwanan lineages since isolation, or that one or more lineages arrived after isolation from different sources. mtDNA analysis indicates that the giant/tree weta radiation occurred in the Miocene and Pliocene, perhaps in response to island formation and orogenics, and that the three major lineages predate the Oligocene, possibly even the opening of the Tasman Sea (Trewick & Morgan-Richards 2005; Pratt *et al.* 2008). Cicada show similar origins (Buckley *et al.* 2002; Arensburger *et al.* 2004a).

When genetic distance information alone is used, we need to be certain that differentiation is sufficiently low to implicate dispersal rather than gondwanan origins (Heads 2005), which it clearly is in many cases (Table 1). Some authors have claimed support for vicariance with genetic distances that are strongly indicative of more recent trans-Tasman dispersal (Entwhistle *et al.* 2000) – a single nucleotide substitution in one case (Edgecombe & Giribet 2008).

Where the fossil record is extensive and implies continuous existence, as can be the case for pollen, some authors have assumed gondwanan origins and used this time to infer rate of nucleotide substitution (Suh *et al.* 1993). Although this approach is potentially useful, it does rest on the assumption that the fossils are indeed the direct ancestors of the extant species, i.e. that a more recent colonization event has not occurred, and this possibility might be difficult to rule out given the poor taxonomic resolution provided by pollen, for example.

Showing that a radiation is post-Oligocene is insufficient to demonstrate post-Oligocene arrival, as ancestors may have been on NZ long before. Lineage turnover (i.e. extinction of deeper lineages in NZ) means that time to coalescence indicates minimal time-depth for arrival in NZ (Hickson *et al.* 2000; Baker *et al.* 2005). In contrast, in the case of apparently archaic species, any extinction of sister groups elsewhere (e.g. extinction of lineages in Australia) could preclude detection of more recent dispersal (e.g. tuatara, sole surviving lineage of Rhynchocephalia). The recent discovery of plesiomorphic Oligo-Miocene mystacinid fossils in Australia (Hand *et al.* 2005), for example, suggests a more recent arrival of bats to NZ (ca 20 Ma) than molecular comparisons of extant species alone can detect, reinforcing that the times in Table 1 are maximal estimates of arrival. Consequently, there is an imbalance in the ability to disprove vicariance vs. dispersal: one can disprove vicariance (i.e. linkages that are much more recent than

vicariant break up), but deep lineages are only ever 'consistent with' vicariance. Although vicariance biogeographers have often stressed this as a reason to prefer vicariance as a null hypothesis that null hypothesis may well be wrong in many cases (de Queiroz 2005).

Examples of radiations and phylogeographic structure by habitat

Any area of habitat isolated from other such areas represents an island to the plants and animals limited to that habitat (Gillespie & Roderick 2002). NZ is well known for its high degree of species endemism characteristic of offshore islands, but there is abundant evidence for speciation and lineage diversification having taken place on smaller scales of isolation. Here we give some examples of radiations that appear to have been driven by islands in the broad sense, including offshore islands, mountains, lakes, rivers, forest, and marine (coastal/continental shelf).

Offshore island

In some of the interglacials, a sea strait separated Banks Peninsula from the mainland at its contact with the low-lying Canterbury Plain (Captain Cook erroneously called it Banks Island). This separation is reflected in some insularity, including gecko, weta, cicada and coastal fish, genetically close to mainland forms (Fleming 1975; Trewick & Wallis 2001; King *et al.* 2003a; Marshall *et al.* 2008; Hickey *et al.* 2009).

Although Stewart Island has some endemics, Foveaux Strait was probably bridged during glaciation, reflected by shared haplotypes on either side in *Galaxias* (Waters *et al.* 2001) and *Kikihia* (Marshall *et al.* 2009), evidence of introgression of divergent lineages from Codfish Island in mainland *Oligosoma* skinks (Greaves *et al.* 2007) and other close similarities (McGaughan *et al.* 2006; Apte *et al.* 2007; Liggins *et al.* 2008a).

Although several of the many islands making up NZ were joined to main islands during glacial epochs, others have been isolated for longer periods and have high rates of endemism (e.g. Auckland, Campbell, Chathams, Three Kings, Solander, Snares, Poor Knights; Fleming 1975). The origin of the many Chathams endemics has been the subject of debate between dispersalist and panbiogeographic schools (Craw *et al.* 1999; Goldberg *et al.* 2008). It has been argued that the Chathams biota reflects ancient hybrid origins from north and south NZ elements through the parallel arcs model (Craw 1988, 1989; Heads 1989), implying a major disjunction reflecting about 140 Ma of independent evolution. This suggestion is at odds with the taxonomic status of Chatham endemics, usually regarded as close sister

species or subspecies of mainland forms, and geological evidence for marine inundation of Zealandia in the Oligocene (Cooper & Cooper 1995; Herzer *et al.* 1997; Landis *et al.* 2008). Contemporary geological evidence puts a date of 3–1 Ma on the emergence of the Chathams through volcanic activity (Trewick *et al.* 2007). A study of Chathams insects suggested recent (<6 Ma) linkages for two beetles, a cave weta and a cockroach with mainland (South Island) counterparts (Trewick 2000b). Tomtits and robins (Miller & Lambert 2006), rails (Trewick 1997), a skink (Liggins *et al.* 2008b), a galaxiid fish (Waters & McDowall 2005), two lycosid spiders (Vink & Paterson 2003), a damselfly (Nolan *et al.* 2007), a cicada (Arensburger *et al.* 2004b), a cockroach (Chinn & Gemmell 2004), a freshwater isopod (McGaughan *et al.* 2006), an amphipod (Stevens & Hogg 2004), two *Hebe* (Wagstaff & Garnock-Jones 1998) and a *Craspedia* (Ford *et al.* 2007) have similarly recent (Pliocene or later) origins, probably aided by reduced Pleistocene sea-levels in some cases. The Chatham Island and Pitt Island shags are almost genetically indistinguishable from respectively Stewart Island and mainland Spotted shags (Kennedy *et al.* 2000). Gene flow between the Chathams and the mainland has, however, been low enough to permit substantial differentiation, even in marine species with larval dispersal (Smith *et al.* 1989; Hickey *et al.* 2009), and islands within the group show phylogeographic structure (Liggins *et al.* 2008b).

The subantarctic islands are particularly known for their endemic shags (*Phalacrocorax*) and megaherbs. The cushion-forming composites *Abrotanella rosulata* and *A. spathulata*, diverged from their mainland relatives less than 1.8 Ma (Wagstaff *et al.* 2006). The shag radiation dates to less than 0.5 Ma (Kennedy *et al.* 2000) and tomtit subspecies are even more recent (Miller & Lambert 2006). Auckland and Campbell Islands each have their own endemic flightless teal species (*Anas*), morphologically similar to the (historically) widespread NZ mainland brown teal. A comparison of these species with other Australasian teal resolves the NZ taxa as a recent monophyletic group, suggesting a single origin for NZ teal followed by subsequent island radiation, but fails to resolve the trichotomy or indicate direction of dispersal (Kennedy & Spencer 2000). Preliminary 12S analysis of diving petrels from Codfish Island (off Stewart Island) supports the existence of a marginally distinct form, apparently equating to the Kerguelen diving petrel, living alongside the NZ diving petrel (Paterson *et al.* 2000). Wandering albatross from Antipodes and Campbell Islands show no genetic differentiation, and indeed are little different from the Adams Island form (since synonymised, Burg & Croxall 2004). Campbell Island has a distinctive endemic isopod (*Austridotea*) lineage with a Pliocene split from mainland taxa

(McGaughan *et al.* 2006). Enderby, Campbell and Auckland Islands have an endemic limpet (*Notoacmea*), recently resurrected from its mainland sister taxon (Nakano *et al.* 2009). Kelp (*Durvillaea*) is highly structured among offshore southern islands, despite its high dispersal potential (Fraser *et al.* 2009).

Hamilton's frog (*Leiopelma hamiltoni*) is found on only two islands (Hamilton and Maud), and has long been classed as an endemic on the basis of morphology alone, supported by allozyme and immunological data (Daugherty *et al.* 1982). Although the Maud Island form has been described as a separate species (*L. pakeka*) based on isozymes (Bell *et al.* 1998), mtDNA suggests that it should be subsumed with *L. hamiltoni* (Holyoake *et al.* 2001).

Perhaps the most well-known island inhabitant is the tuatara, *Sphenodon punctatus*. This species has widespread Holocene remains on the eastern flanks of both main islands, but is now extinct there (Hay *et al.* 2003). Isozyme data and subtle morphological differences support recognition of *Sphenodon guntheri* from North Brothers Island (Cook Strait) (Daugherty *et al.* 1990; Hay *et al.* 2003), but sequence data show little (mtDNA, albumin) or no (aldolase intron) differentiation among Cook Strait populations (Hay *et al.* 2003). The one consistent pattern is that populations from islands off the northeast coast of North Island form one group and those from Cook Strait islands form another (Hay *et al.* 2004; MacAvoy *et al.* 2007). The North Brothers population appears to be distinct from other Cook Strait populations only as a result of its small population size and subsequent inbreeding (MacAvoy *et al.* 2007). The northern group of islands also shows some differentiation for chloroplast markers in *Metrosideros* (Gardner *et al.* 2004).

Parakeets in the genus *Cyanoramphus* comprise a radiation of about ten species within the last 0.5 Ma (Boon *et al.* 2001; Chambers *et al.* 2001). These include endemics on the Chathams, Antipodes, Lord Howe, Kermadecs and Macquarie Islands, all sister to a New Caledonian species.

These examples point to comparatively recent origins for most endemic island forms, possibly involving peripatric speciation. These findings are in keeping with land connections in the Pleistocene (Lockhart *et al.* 2001) and range expansion/contraction, or dispersal, but much remains to be done to determine whether this is a general pattern. In the case of the Chathams, some 750 km offshore, there is no evidence for a complete land connection, making dispersal by air or sea almost certain.

Contrastingly, the geography of several Pliocene islands (Fig. 3d) in existence some 7–4 Ma, several of which are now connected and constitute North Island,

have been implicated as drivers of radiations in tree weta (*Hemideina*, Morgan-Richards 1997), snails (*Rhytida* and *Placostylus*, Powell 1949) and stag beetles (*Lissotes*, Holloway 1961). *Hemideina thoracica* has nine major COI haplotype groups, whose distributions show a degree of spatial and temporal concordance with reconstructed island boundaries and chromosome races, but uncertainties in these reconstructions and possible gene flow across hybrid zones weaken the correlation (Morgan-Richards *et al.* 2001). Isozyme analysis of three species of *Placostylus* showed deep divergence of Three Kings, North Cape and other Northland endemics, again temporally and geographically consistent with Pliocene sea-straits (Triggs & Sherley 1993). Within the North Cape species, there was considerable divergence. This differentiation was adjudged Pleistocene or later by the authors, and in one case a bipartition was attributed to a Pleistocene sea strait. Rhytidid land snails on Three Kings are also quite divergent from mainland (North Island) species (Spencer *et al.* 2005), as are *Placostylus* snails (Ponder *et al.* 2003) and the monotypic *Pseudoclitarchus* stick insect (Trewick *et al.* 2008a). Mainland populations of *Amborhytida* show some structure across Northland that could be related to Pliocene islands, but *Paryphanta* have a strongly contrasting east–west split (Spencer *et al.* 2005), a pattern also seen in the skink *Oligosoma smithi* (Hare *et al.* 2008) and a corophiid amphipod (Schnabel *et al.* 2000). In general, Northland shows distinctive lineages for a number of species, though little consistent pattern emerges (Gleeson *et al.* 1999; Morgan-Richards & Wallis 2003; Stevens & Hogg 2004; Spencer *et al.* 2005; Smissen *et al.* 2006; Smith *et al.* 2006b,c; Chapple *et al.* 2008; Hare *et al.* 2008).

Still farther back in time, low-lying Oligocene islands have been hypothesized as promoting radiation in *Oligosoma* skinks (Hickson *et al.* 2000) and *Cyanoramphus* parakeets (Chambers *et al.* 2001). This period has also been seen as a time of lineage extinction, leading to post-Oligocene lineage coalescence or bottleneck in moa (Baker *et al.* 2005), kiwi (Cooper *et al.* 1992) and wrens (Cooper & Cooper 1995).

Mountain

The relative rapidity of alpine uplift has been matched by radiation of alpine forms in many groups, notably plants (Raven 1973; Godley 1975; Mark & Adams 1995) and insects (Fleming 1975), and even birds such as kea (*Nestor notabilis*) and rock wren (*Xenicus gilviventris*). Close relatedness of the speciose *Hebe* (Wagstaff & Garnock-Jones 1998, 2000; Wagstaff & Wardle 1999; Wagstaff *et al.* 2002) supports the contention that these alpine radiations have happened recently (Raven 1973), and that morphological evolution has been comparatively

rapid (Winkworth *et al.* 1999, 2005; Wagstaff *et al.* 2002). The phylogeny suggests dispersal followed by two NZ radiations: one correlating with Pliocene uplift and the second with recent Pleistocene glaciations (Wagstaff & Garnock-Jones 1998). A similar pattern is described for Carmichaelinae broom (Wagstaff *et al.* 1999) and *Ranunculus* (Lockhart *et al.* 2001). Other plant genera show this pattern of dispersal followed by rapid adaptation (Raven 1973; Mildenhall 1980; Glenny & Wagstaff 1997; Mitchell & Wagstaff 1997, 2000; Wen *et al.* 2001; Heenan *et al.* 2002; Winkworth *et al.* 2002b; Heenan & Mitchell 2003; Glenny 2004; Wagstaff & Breitwieser 2004; Ford *et al.* 2007), in some cases involving many dispersal events (Breitwieser *et al.* 1999; Wagstaff & Breitwieser 2002). Some alpine groups show evidence of reticulation, suggesting that hybridization has been important in their evolution (Lockhart *et al.* 2001; Winkworth *et al.* 2005; Morgan-Richards *et al.* 2009).

mtDNA and isozyme analysis of the flightless carabid beetle genus *Prodontria* revealed numerous previously undescribed species endemic to particular mountain ranges (Emerson & Barratt 1997). COI sequence data suggest that these species were derived repeatedly from flighted ancestors currently in *Odontria*, in particular the widespread *Odontria striata* (Emerson & Wallis 1995). A cosmopolitan form with high gene flow seems to have spawned propagules that have speciated into flightless local endemics. This radiation is apparently restricted to southern NZ, and phylogeographic reconstruction is consistent with spread from southern South Island northwards. Scree weta (*Deinacrida connectens*; 1600–2000 m), peripatus (*Ooperipatellus*, *Peripatoides*), *Lyperobius* weevils, *Celatoblatta* cockroaches, mite harvestman (*Aoraki*) and beetles (*Brachynopus*, *Mecodema*) also show high intraspecific structuring consistent with late Pliocene uplift, apparently without parallel morphological differentiation (Trewick *et al.* 2000; Trewick & Wallis 2001; Boyer *et al.* 2007; Leschen *et al.* 2008). Genetic analysis of the alpine weta *Hemideina maori* (1000–1500 m), which displays colour polymorphism, has revealed a hybrid zone with a genetic disjunction coinciding with a change to a melanic form (King *et al.* 1996). This situation may represent an adaptive example of primary contact, repeated on other ranges, or secondary contact of recently differentiated forms (King *et al.* 2003b).

Studies on 14 species of *Maoricicada* suggested an alpine radiation during the early Pliocene, possibly in connection with the earlier uplift of the Kaikoura orogeny (Buckley *et al.* 2001a,c; Chambers *et al.* 2001; Buckley & Simon 2007). Finer phylogeographic analysis of montane *Maoricicada campbelli* revealed five major clades (probably reflecting cryptic species), the most basal of which is confined to Central Otago with a split

of 2.3 Ma (Buckley *et al.* 2001b) or later (Hill *et al.* 2009). The sister group to this clade comprises a comb-like clade, with progressively interior branches occurring in North Island, Marlborough, Southern Alps and Waitaki, respectively, reflecting late Pleistocene spread south from North Island. This pattern is intriguing as it suggests lineage formation and colonization of South Island during the period of glaciation. Alpine uplift may also explain the origin of two chromosome races of the Wellington tree weta (*Hemideina crassidens*) at about 3 Ma (Trewick & Wallis 2001; Morgan-Richards 2002). Further phylogenetic analysis of giant and tree weta suggests multiple origins of alpine adaptation (Trewick & Morgan-Richards 2005). Radiations of moa (Baker *et al.* 2005), skink (Greaves *et al.* 2007, 2008; Liggins *et al.* 2008a; O'Neill *et al.* 2008), *Galaxias* fishes (Waters & Wallis 2001b; Waters & Craw 2008), hepialid (*Oxycaenus* group) moths (Brown *et al.* 1999), lycosid (*Anoteropsis*) spiders (Vink & Paterson 2003), *Kikihia* cicada (Arensburger *et al.* 2004b; Marshall *et al.* 2008), *Sigara* water boatmen (Buckley & Young 2008), *Sigaus* grasshoppers (Trewick 2008), *Celatoblatta* cockroaches (Chinn & Gemmell 2004), *Mecodema* carabids, *Lyperobius* weevils and peripatus (Trewick 2000a; Trewick & Wallis 2001) have also been attributed to Pliocene uplift. Contrastingly, speciation of *Wiseana* hepialids (Brown *et al.* 1999), acridid (*Brachaspis*) grasshoppers (Trewick 2001) and most *Kikihia* (Marshall *et al.* 2008, 2009), and subdivision of a freshwater snail (*Potamopyrgus*) (Neiman & Lively 2004) and *Maoricicada* (Hill *et al.* 2009) have been inferred to be within the Pleistocene.

Lake

Globally, lakes are home to some of the best-known adaptive radiations in fishes (Fryer & Iles 1972). Geological and genetic information have been used to show that these radiations can happen rapidly (Avisé 1990; Meyer *et al.* 1990; Schlieven *et al.* 1994). Post-glacial lakes of the nearctic and palearctic show repeated ecological speciation of trophic morphs in many groups (Bernatchez & Dodson 1990; Schluter & McPhail 1993; Taylor & Bentzen 1993; Taylor *et al.* 1996). As NZ has many glacial lakes, and the freshwater fish fauna is depauperate and secondarily derived from diadromous forms (McDowall 1990), comparable radiations might be expected. The fauna is dominated by the Galaxiidae [19 species; (McDowall 2000)], a group of small osmeriform fish. Five of these retain the ancestral diadromous [more specifically amphidromous; (McDowall 1997b)] behaviour, whereby juveniles spend about six months at sea before returning to breed in rivers, where they remain. Populations of inanga have become naturally landlocked in Northland dune lakes, giving rise to a

dwarf form, *Gracilaria gracilis* (McDowall 1990). Control region sequence analysis suggests multiple origins for these populations (Ling *et al.* 2001) and therefore convergent evolution of lake characteristics, paralleling northern hemisphere examples (Johannesson 2001). Further work is required to elucidate their origins and test for lake and regional monophyly. Data need to include detailed sampling of diadromous *G. maculatus*, as this species shows deep differentiation across the Tasman Sea (Waters *et al.* 2000a). It is possible that some NZ populations may have been founded by Australian lineages, giving the impression that events are older than they really are.

Another galaxiid, the koaro (*Galaxias brevipinnis*) penetrates deep into river systems, and has given rise to a species flock some millions of years in age (Waters & Wallis 2001b) through repeated loss of diadromy (Waters & Wallis 2001a). Intriguingly, these stream-resident forms are particularly speciose south of the Waitaki river, in the area covered by palaeolake Manuherikia (15–8 Ma). Estimates of divergence, however, probably postdate the lake (Waters & Wallis 2001a). Koaro populations have also been landlocked in lakes more recently (both naturally and through hydroelectric impoundment), where juvenile migrations continue, but between the lake and its tributaries (McDowall 1990). Isozyme analysis finds little evidence for differentiation among lake populations of koaro, or indeed among NZ populations of any diadromous species (Barker & Lambert 1988; Allibone & Wallis 1993). There is evidence for morphological divergence in some North Island lakes, which possess resident adult lake populations. Preliminary microsatellite DNA analyses failed to find evidence of genetic differentiation between these life history types, but differences among lakes are substantial (King *et al.* 2003a).

River

There are currently some 40 native freshwater fishes, 25 of which have secondarily lost a marine stage to become completely stream/lake resident. Recent work shows that there has been much more speciation in the freshwater environment than was previously recognized (Allibone *et al.* 1996; Gleeson *et al.* 1999; Waters & Wallis 2000, 2001a,b; Ling & Gleeson 2001; McDowall & Waters 2002, 2003). The combination of rapid tectonic uplift, fault movement, glaciation and rapid erosion, can cause major hydrological change through river capture (Bishop 1995). For aquatic species with limited dispersal capabilities, this event can isolate headwater populations and connect them to those of another catchment. One particularly clear example is the Nevis River, Otago, which contains a distinct lineage of nonmigratory

galaxiid (*G. gollumoides*) not found anywhere else in the (Clutha) system, the sister group of which is found in catchments to the south (Waters *et al.* 2001). Other examples include the Opuha-Waitaki (Waters & Craw 2008), Oreti-Clutha (Burrige *et al.* 2007), Clarence-Wairau (Burrige *et al.* 2006) and Kaituna-Wairau (Waters *et al.* 2006, 2007b). When such events can be timed through geological methods, they provide useful calibrations for molecular clocks (Waters *et al.* 2007b; Waters & Craw 2008). This type of hydrological evolution has probably been of general importance for allopatric speciation and range expansion in fish and other groups. Phylogenetic mtDNA analysis of the *G. brevipinnis* group indicated at least three independent losses of diadromy, but also radiation within the freshwater environment subsequent to this loss (Waters & Wallis 2001a). Analysis of three nuclear genes, however, puts the migratory *G. brevipinnis* as sister to the freshwater radiation, consistent with a single loss of diadromy and giving greater significance to river capture. Continued isolation of populations will be contingent to some extent on their habitat as well. At lower elevations and slopes, adjacent catchments may be linked by extreme flooding events, allowing gene flow and preventing divergence locally (Davey *et al.* 2003; Burrige *et al.* 2008). High structure has also been demonstrated in gobiid fish (Smith *et al.* 2005) and North Island caddis (Smith *et al.* 2006c) and mayfly (Smith *et al.* 2006b), but not directed at testing for headwater capture. In contrast, two catadromous eel species (*Anguilla*) show virtually no genetic structure, consistent with a single offshore spawning ground (Smith *et al.* 2001).

Forest

The history of Pleistocene forest refugia in eastern Australia has been examined using a phylogeographic approach (Schneider *et al.* 1998). Fragmentation of habitat on a recent time scale is usually seen as destructive, but it can be a creative evolutionary force if fragments are sufficiently large and stable (Smith *et al.* 1997). In NZ, forest-dwelling brown kiwi show major genetic subdivision, which led to taxonomic revision (Baker *et al.* 1995; Burbidge *et al.* 2003). There is a major disjunction in central South Island, with the northern lineage straddling Cook Strait (Shepherd & Lambert 2008). This disjunction coincides with the South Island gap (see below), a major biogeographic feature (Cockayne 1926). The gap is supposed to derive from Pleistocene extinction of beech in the central narrow 'waist' region of South Island and the inability of beech to close the gap before the next glaciation (Wardle 1963; Burrows 1965; Leathwick 1998). Hence vicariant lineages thus restricted to these opposite ends of South Island may be

expected to coalesce just prior to the Pleistocene glaciations. The northern lineage of brown kiwi includes North Island (*Apteryx mantelli*) and central west coast (*Apteryx rowii*), both sister to southern tokoeka (*Apteryx australis*) (Baker *et al.* 1995; Burbidge *et al.* 2003). The basal split is estimated to be Pliocene, and more likely to reflect uplift than glaciation. In contrast, the fungus beetle *Brachynopus*, also absent from the beech gap, coalesces at about 0.2 Ma, consistent with extirpation during a recent glaciation (Leschen *et al.* 2008). *Kikihia subalpina* shows a pattern of post-glacial dispersal from a Nelson forest refugium (Marshall *et al.* 2009), completely transcending the gap.

Marine

It is been widely established that marine species can show significant phylogeographic structure despite the apparent continuity of the marine medium (Waples 1987; Burton 1998). Phylogeographic splits can arise from ecological and/or historical separation, aided by currents (Palumbi 1994; Barber *et al.* 2000). Currents hit the west coast of NZ and produce a complex pattern of gyres and divergences (Fig. 3e). These have been hypothesized to be the cause of differentiation in some species, particularly those with low dispersal abilities. Breaks evidenced by mtDNA on the west coast below Cook Strait have been demonstrated in mussels (Apte & Gardner 2002; Star *et al.* 2003), brittlestars (Spomer & Roy 2002), seastars (Waters & Roy 2004a; Ayers & Waters 2005) and limpets (Goldstien *et al.* 2006b). Earlier allozyme work reporting small but significant structuring in snapper (Smith *et al.* 1978) and ling (Smith 1979) was corroborated in the case of snapper with microsatellite data, though mtDNA fails to resolve these stocks (Bernal-Ramirez *et al.* 2003).

Control region analysis of Hector's dolphin gave a high F_{ST} of 0.47, and a network with almost completely geographically limited clades corresponding to: North Island west coast, South Island east coast and South Island south and west coasts (Pichler *et al.* 1998; Pichler & Baker 2000), leading to recognition of two species. Bottlenose dolphin are restricted to Northland, Marlborough Sounds and Fiordland, and are less structured ($F_{ST} = 0.17$, Tezanos-Pinto *et al.* 2009).

The hydrology of the deep fiords of southwestern NZ, with their entrance sills and freshwater run-off, offer potential for marine population structuring. Genetic differentiation has been demonstrated in asteroids from these fiords (Perrin *et al.* 2003, 2004; Sköld *et al.* 2003), despite the short time elapsed since glaciation, suggesting a combination of rapid expansion, genetic drift and low gene flow.

In contrast, RFLP analysis of rock lobster (*Jasus edwardsii*) found no evidence for population subdivision over 4600 km of the south Australian and NZ coastline (Ovenden *et al.* 1992). A variety of other markers reveal little or no evidence for differentiation among NZ populations of kina (*Evechinus*) (Mladenov *et al.* 1997), orange roughy (*Hoplostethus*) (Smith *et al.* 2002b) and black and smooth oreos (*Pseudocyttus*) (Smith *et al.* 2002a).

Distributional gaps and their explanations

Functional, spatial and temporal gaps are a general feature of NZ biogeography, and have been widely discussed at an ecological level (Rogers 1989; Haase 1990; Lee 1998; McGlone *et al.* 2001). These gaps include disjunctions in the distribution of certain species (McDowall 1996; Heads 1998) and areas of low endemism (Craw 1989; Wardle 1991; Heads 1997, 1999). NZ is conveniently partitioned into five regions of alternating degrees of endemism: three regions of high endemism (Otago-Southland, north-west Nelson, Northland), interspersed with two regions of low endemism in central South Island and lower North Island (Burrows 1965; McGlone 1985; Rogers 1995; Fig. 3f). This pattern is evident in plants (Wardle 1988, 1991) and insects (Craw 1989; Gibbs 2006).

Explanations for these gaps principally fall into two categories: tectonic (McGlone 1985; Rogers 1989) or climatic (Willett 1950; Wardle 1963, 1988; Burrows 1965). Panbiogeographers made the bold suggestion that the central South Island gap is explained by movement of the Alpine Fault, splitting distributions in the early Miocene (Heads 1997, 1998). Alpine uplift represents a geologically more recent possible tectonic cause of gaps. The more favoured explanation is that glaciation and erosion were heavier in central South Island and the Pleistocene climate harsher in southern North Island, and these caused more extinction events (Cockayne 1926; Willett 1950; Wardle 1963). Species with lower dispersal rates or colonization ability have been unable to recolonize the gaps (Cockayne 1926). Other workers have concluded that current climatic differences maintain this gap (Haase 1990). Despite its appeal, there are numerous problems with the panbiogeographic explanation (Wallis & Trewick 2001). In particular, it is unlikely that these gaps are really this old. Using a suite of 45 invertebrate species, 12S and COI analysis showed little evidence in support of the panbiogeographic hypothesis, either from phylogeographic pattern in the data, or the time frame for vicariance, which in all cases was less than 5.5 Ma (Trewick & Wallis 2001). However, the timing of the splits observed is consistent in many cases with alpine

uplift, so the orogenic element of the tectonic hypothesis derives support from these data, and Pleistocene extinction is de-emphasized. Others have deduced the same from plant radiations (Wagstaff & Wardle 1999; Smissen *et al.* 2003a). Alpine Fault movement could, in theory, explain much older splits (Haase *et al.* 2007), but the idea is difficult to test, as splits of this age could have many causes.

Genetic differentiation in the *Galaxias vulgaris* species complex in central South Island is less than that of Otago and Southland, both for isozymes (Wallis *et al.* 2001) and mtDNA lineages (Waters & Wallis 2001b). These authors attribute the lower central diversity to either Pleistocene extinction or Pliocene radiation. Lineages of *G. vulgaris sensu stricto* (up to 2.4% divergent for control region) in the central region predate at least the later glaciations (Waters & Wallis 2001a), and thus the latter explanation is more likely, in keeping with the recent origin of the Canterbury Plain as a result of alluvial deposition from the alps (Wallis *et al.* 2001). *Galaxias prognathus* and *Galaxias cobitinis* show the same pattern of deep splits between southern rivers but more homogeneity among Canterbury braided rivers. Genetic data similarly show the common gecko, *Haplodactylus maculatus*, to be a complex of at least 30 species (Chapple & Hitchmough 2009), mostly in southern South Island, reiterating the diversity of the region.

An extensive survey of Hard Beech (*Nothofagus truncata*) found high isozyme differentiation among populations for northern North Island populations, but low values elsewhere, indicative of older continuous existence in northern regions (Haase 1992). Two geographically disjunct Fiordland populations were genetically very similar to each other, and distinct from all other regions, consistent with *in situ* survival in a glacial refugium. Frost-sensitive *Metrosideros* shows higher diversity for chloroplast markers in Northland and northwest Nelson, correlating with regions of high endemism and warmer climate, strongly implicating these regions as Pleistocene refugia (Gardner *et al.* 2004).

Wellington tree weta (*H. crassidens*) revealed deep lineages in one chromosome race found in central NZ, but much more recent coalescence in populations to the south of the range in the heavily glaciated central South Island (Morgan-Richards 2002), a pattern mirrored by short-tailed bat (Lloyd 2003b). Similarly, *Kikihia* cicada show high lineage diversity in the Nelson-Marlborough region, and low to the south and east (Marshall *et al.* 2009). Glaciation has also been invoked as the cause of reduced variability in rimu (Hawkins & Sweet 1989) and triplefin fishes (Hickey *et al.* 2009), and species number in gentians (Glenny 2004).

Emerging multi-taxon patterns

Splits across the Southern Alps corresponding to Pliocene isolation through uplift are common (Waters & Wallis 2000; Trewick & Wallis 2001; McDowall 2005; Smith *et al.* 2005; Apte *et al.* 2007; Greaves *et al.* 2007; Buckley & Young 2008; Leschen *et al.* 2008; Liggins *et al.* 2008a; Marshall *et al.* 2009; Fig. 4a), though some dispersal corridors exist (Craw *et al.* 2008). There is also some evidence for east-west phylogeographic disjunction in North Island (Holzapfel *et al.* 2002; Lloyd 2003a,b; Baker *et al.* 2005; Shepherd *et al.* 2007; Shepherd & Lambert 2008; Fig. 4a).

Late Pliocene emergence of the Southern Alps and associated ranges has clearly been accompanied by lineage radiation and speciation (Buckley & Simon 2007). One common pattern is that of local endemism: high phylogeographic structure with little phylogenetic structure (Hickson *et al.* 2000; Trewick *et al.* 2000; Trewick & Wallis 2001; Chinn & Gemmell 2004; Boyer *et al.* 2007; Fig. 4b). These types of patterns suggest star radiations associated with Pliocene uplift and survival of lineages through the Pleistocene, in some cases made more complex by periodic local extinction, recolonization and hybridization (Chinn & Gemmell 2004).

Partly as a result of this mountain building, several species show evidence of higher phylogeographic structure and deep lineages in southern South Island (Emerson & Wallis 1995; Waters & Wallis 2001b; Berry & Gleeson 2005; Trewick 2008; Hill *et al.* 2009), sometimes with progressively more interior nodes occurring through northeastern South Island onto North Island (Lockhart *et al.* 2001; Burbidge *et al.* 2003; Smith *et al.* 2005; Hogg *et al.* 2006; Waters *et al.* 2006; Liggins *et al.* 2008a; Trewick *et al.* 2008b; Fig. 4c) indicating relatively recent origins of these species in North Island.

Phylogeographic structure of a mite harvestman suggests southward expansion from Nelson down the west coast, but it would seem to be Pliocene, unless the COI clock is much faster in this group (Boyer *et al.* 2007). Koura show evidence of a similarly old expansion down the west coast and around Fiordland up the east coast to Banks peninsula (Apte *et al.* 2007; Fig. 4d). The *G. brevipinnis* group shows some similarities with this pattern, with divergent lineages to the south and more homogeneity up the east coast (Wallis *et al.* 2001; Waters & Wallis 2001b), but with the west coast populations expunged by glaciation. This pattern is particularly interesting for two freshwater limited groups, with very low current gene flow evidenced by virtually no haplotype sharing among sites. The ability to extend range by leap-frogging from river to river can be explained by river capture, which will be happening

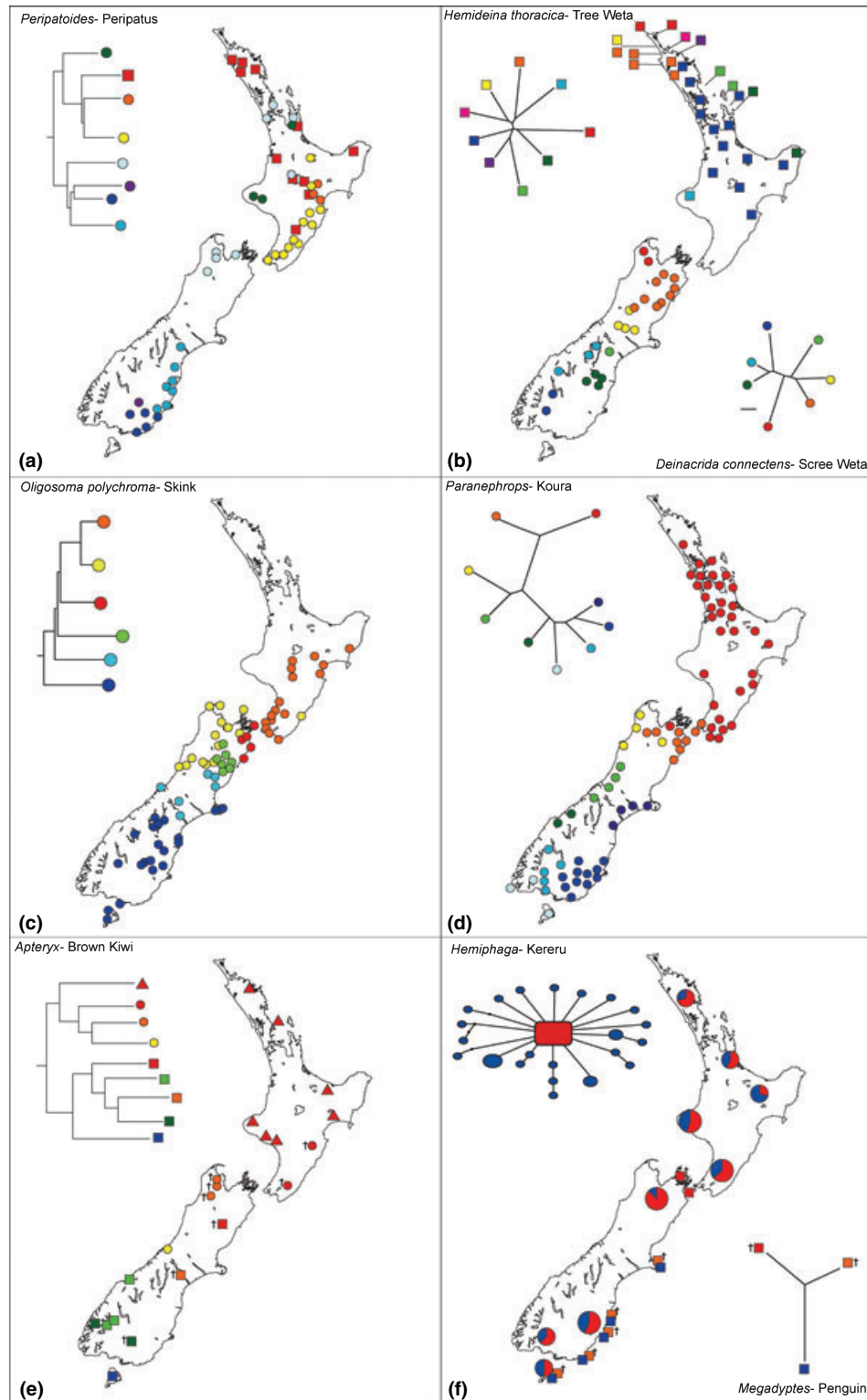


Fig. 4 Examples of some typical phylogeographic patterns shown by the New Zealand fauna (not drawn to scale). (a) North Island and South Island phylogeographic disjunctions (*Peripatoides*, Trewick 2000a). (b) Taupo extinction (*Hemideina thoracica*, Morgan-Richards *et al.* 2001) and local southern endemism (*Deinacrida connectens*, Trewick *et al.* 2000). (c) Expansion out of Southland (*Oligosoma*, Liggins *et al.* 2008a). (d) Expansion out of Nelson around the Southern Alps (*Paranephrops*, Apte *et al.* 2007). (e) Cook Strait linkages (*Apteryx*, Shepherd & Lambert 2008). (f) Recent expansion of pigeon (*Hemiphaga*, Trewick & Goldberg unpubl.) and yellow-eyed penguin (*Megadyptes*, Boessenkool *et al.* 2009; ancient DNA samples in red and orange).

frequently on a small scale at headwaters. Some species (crayfish, eels, some galaxiids, lampreys) are also recognized for their ability to leave the water to traverse dams, weirs and waterfalls, providing further opportunity for range expansion. Extreme flooding at low elevations may also facilitate expansion to adjacent drainages (Burridge *et al.* 2008), possibly even via inshore waters. Other groups show post-Pleistocene southward spread (Lloyd 2003b), possibly out of North Island (Buckley *et al.* 2001b; Burbidge *et al.* 2003; Marshall *et al.* 2009), consistent with postglacial recolonization (Fraser *et al.* 2009).

Conspecific linkages and similar or identical haplotypes are often found straddling Cook Strait (Baker *et al.* 1995; Trewick 1998; Trewick & Wallis 2001; Allibone 2002; Apte & Gardner 2002; Morgan-Richards 2002; Stevens & Hogg 2004; Ayers & Waters 2005; Apte *et al.* 2007; Shepherd *et al.* 2007; O'Neill *et al.* 2008; Shepherd & Lambert 2008; Hickey *et al.* 2009; Fig. 4d–e), consistent with repeated bridging to the west (Lewis *et al.* 1994; King 2000; McDowall 2005). Other authors emphasize phylogeographic gaps at Cook Strait (Haase 1992; Efford *et al.* 2002; Greaves *et al.* 2007, 2008; Liggins *et al.* 2008a; Marshall *et al.* 2009), but limited availability of samples immediately north or south of Cook Strait (Trewick 2000a; Buckley *et al.* 2001b; Burbidge *et al.* 2003; Lloyd 2003a; Perrin *et al.* 2004; Robertson *et al.* 2007; Greaves *et al.* 2008; Jones *et al.* 2008) or lineage extinctions (Holyoake *et al.* 2001) sometimes reduce the power of this inference. Many birds and plants have North Island and South Island subspecies, some of which may show concordant genetic disjunctions (Miller & Lambert 2006; Murphy *et al.* 2006; Smissen *et al.* 2006; Robertson *et al.* 2007). In marine species, it appears that a general phylogeographic break might exist just south of Cook Strait (Smith *et al.* 1981, 1987), perhaps as a result of upwelling to the south inhibiting larval dispersal (Apte & Gardner 2002; Sponer & Roy 2002; Star *et al.* 2003; Perrin *et al.* 2004; Waters & Roy 2004a; Ayers & Waters 2005; Goldstien *et al.* 2006b).

Cases of low diversity in central North Island in contrast to higher diversity to the north and south are most likely attributable to the effects of recent Taupo volcanic eruptions, (Morgan-Richards *et al.* 2001; Holzapfel *et al.* 2002; Lloyd 2003a,b; Gemmell *et al.* 2004; Smith *et al.* 2006b,c; Chapple *et al.* 2008; Shepherd & Lambert 2008; Fig. 4b), possibly explaining a repeated east–west break across North Island (Trewick 2000a; Holzapfel *et al.* 2002; Lloyd 2003a,b; Baker *et al.* 2005; Shepherd *et al.* 2007; Shepherd & Lambert 2008). This effect may overlie or eradicate an older similar pattern dating from the later tectonic emergence of southern North Island, exposing land previously submerged under the Pliocene (Manawatu) sea strait.

Some species of conservation significance show genetic evidence of founder effect and low structure following recent range expansions, either due to human-induced near extinction events (Taylor *et al.* 2007), recent introductions or post-glacial range expansion (J. Goldberg & S.A. Trewick unpubl.; Fig. 4f). Two marine examples show clear recent links between the eastern seaboard and subantarctic islands: *Grahamina* triplefins (Hickey *et al.* 2009) and *Megadyptes* penguin after human-induced extinction (Boessenkool *et al.* 2009), both in addition to a more divergent clade elsewhere in NZ. These examples are, however, rare in NZ, in contrast to northern Europe for example, where genetic homogeneity is commonplace (Wallis & Arntzen 1989).

It is clear that most NZ taxa harbour phylogeographic structure that must have survived most or all of the Pleistocene glaciations. The NZ pattern suggests many refugia, in contrast to the heavily glaciated northern Europe regions where wholesale recolonization from the south prevails (Taberlet *et al.* 1998).

Conclusions

Clearly, more and better data are needed to resolve the evolutionary origins and phylogeographic pattern in the NZ flora and fauna. We can at least say that most of the NZ flora derives from long-distance dispersal (Raven 1973; Pole 1994; Winkworth *et al.* 2002b, 2005; Sanmartín & Ronquist 2004; McGlone 2005), and the same may be generally true for animals (McDowall 2002; Waters & Craw 2006; Trewick *et al.* 2007). More work on arthropods is needed; they are likely to include recent and ancient dispersers as well as gondwanan relicts (Gressitt 1961, 1970; Boyer & Giribet 2007). If further paleontological data reveal evidence of uninterrupted fossil records through the Oligocene, complete inundation is made less likely (Winkworth *et al.* 1999; Lee *et al.* 2009). Notwithstanding these gaps in our knowledge, many commentators have already debunked the concept of NZ as a gondwanan relictual ark (McGlone 2005; Waters & Craw 2006; Trewick *et al.* 2007; Landis *et al.* 2008). Nonetheless, the NZ flora and fauna shows high endemism and is an important component of global biodiversity.

A general limitation to establishing colonization routes using phylogenetic analysis is that while the phylogenetic relationships may be robust, the direction of dispersal often is not. In his review of the evolution of alpine plant groups, Raven (1973) says: 'It is, however, almost impossible to imagine how any plant or animal could migrate from NZ to Australia against the prevailing westerlies ...'. However, just as westerlies provide passage from Tasmania to NZ within a day, they can reach South America 3 days later, South Africa

in another 4 days, and back to western Australia in as little as 3 days. The same, albeit much slower, may apply to sea currents (Coombs & Landis 1969). In the cases of blue penguin, parakeet, teal, geckos, marine snails and weta, although the phylogenetic affiliations of NZ, New Caledonian and Australian taxa are clear, it is moot whether we consider dispersal *to* NZ as significantly more likely than colonization *from* NZ (Ó Foighil *et al.* 1999; Cook & Crisp 2005a; Pratt *et al.* 2008), when a chain of dispersal events could be inferred, involving capes and islands of the Southern Ocean (Buroker *et al.* 1983; Wagstaff *et al.* 2000; Wagstaff & Wege 2002; Waters & Roy 2004b; Donald *et al.* 2005; Meudt & Simpson 2006; Wagstaff & Hennion 2007; Fraser *et al.* 2009). Indeed, some analyses suggest NZ as a greater source than recipient in trans-Tasman animal exchanges (McDaniel & Shaw 2003; Sanmartín & Ronquist 2004). Molecular diversity and range of little blue penguins, for example, have been taken to suggest that they colonized Australia from NZ as cooling started in the late Pleistocene, before recolonizing Otago much more recently (Banks *et al.* 2002). *Metrosideros* (Myrtaceae) has probably colonized much of Oceania (including Hawaii and New Caledonia) from NZ, consistent with the older NZ fossil record, aided by westerly winds (Wright *et al.* 2000, 2001). This dispersal occurred in at least two separate episodes, including an extensive one during the Pleistocene (Wright *et al.* 2000). Similarly, seven dispersal events from mainland NZ are inferred for *Hebe*, including Australia, New Guinea, Chile and Falkland Islands (Wagstaff *et al.* 2002). More recent dispersal events may often over-write earlier exchanges, and inferences of the frequency of dispersal may be more indicative of colonization opportunity, so the potential for dispersal is much greater than we actually observe.

Phylogenetic reconstruction alone is not strictly sufficient to distinguish vicariant and dispersal hypotheses, as mismatching cladograms can always be reconciled by invoking extinction events (Page 1994). Combined analysis of morphological, *rbcL* and ITS data for *Nothofagus* gives a well-supported phylogeny suggesting two separate linkages between NZ and Tasmania, generating an area cladogram [South America (Australia, NZ)] at odds with continental breakup [NZ (SA, AUS)] (Manos 1997). Reconciliation with the fossil record led Manos (1997) to prefer the vicariance-extinction explanation, while the same area cladogram was accepted as evidence for dispersal in the inanga when reconciled with molecular clock considerations (Waters *et al.* 2000a). Even if we assume that our phylogeny faithfully reflects organismal phylogeny (Ballard & Rand 2005), and ignore lineage extinction, another issue is the reconstruction of geographic state on the phylogeny. The geographic states of ancestral lineages can be quite uncertain (Sch-

luter *et al.* 1997). We have used examples where a comb-like structure (i.e. several progressively internally branching lineages) correlates with geographic position as evidence for origin or progression of colonization, but any one example is unlikely to be robust (Cook & Crisp 2005a). Faith in this conclusion is only warranted when repeated pattern is observed across many taxa. Finally, recent radiations alone do not indicate recent arrival: evidence for recent dispersal demands a recent link with lineages elsewhere.

Much more work is needed before we can establish whether there are regions that consistently show disjunctions. Perhaps the major conclusion that we can draw at the moment is the tendency of the extreme south and extreme north to house more and/or deeper endemic lineages, coincident with regions of high endemism. South Island genetic breaks variously occur at the Clutha River (Emerson & Wallis 1994; Waters *et al.* 2001; Burrige *et al.* 2007; O'Neill *et al.* 2008; Trewick 2008), Taieri River (Trewick 1999), Waitaki River (Emerson & Barratt 1997; Trewick 2000a; Buckley *et al.* 2001b; Wallis *et al.* 2001; Waters & Wallis 2001b; Smith *et al.* 2005; Greaves *et al.* 2007; O'Neill *et al.* 2008; Waters & Craw 2008), upper Rangitata River (Liggins *et al.* 2008a) central westcoast (Baker *et al.* 1995; Burbidge *et al.* 2003; Apte *et al.* 2007), Waiau River (Buckley & Young 2008; Liggins *et al.* 2008a), Wairau River (Liggins *et al.* 2008a) and Buller River (Morgan-Richards 2000). More studies of disjunctions should be done using species pairs that could best be expected to be restricted to the terrain that they are on. Some plant species, for example, may be restricted to soils derived from limestone or ultramafic rock (Wardle 1988).

The existence of extensive phylogeographic structure is generally in contrast with northern Europe, Asia or America: most NZ taxa maintain β -lineages (Jansson & Dynesius 2002) extending back to the Pliocene or early Pleistocene at least. The complex geological history of NZ has led to many different patterns at different time depths, depending on the ecology and life histories of the species examined. Some processes (e.g. recent extinctions, glaciation, volcanism) partially over-write phylogeographic structure of the past (e.g. tectonic, Pliocene island, repeated dispersal events), again in a species dependent way. Fuller understanding will come with more and better data, in conjunction with ecological genomics, which promises the ability to determine the nature and origin of adaptations.

Genetic analyses have been informative to conservation programs in aiding identification of taxa (Wallis 1994; Allibone *et al.* 1996; McDowall & Wallis 1996; Emerson & Barratt 1997; McDowall 1997c; Trewick 1998, 1999, 2001; McDowall & Chadderton 1999; Pichler & Baker 2000; Ling & Gleeson 2001; McDowall &

Waters 2002, 2003; Smith *et al.* 2006a; Nakano *et al.* 2009) and can be used to suggest taxon or regional priorities (May 1990; Vane-Wright *et al.* 1991; Faith 1994; Moritz 2002). Phylogeographic analysis, with its context of time and space, promises much more (Moritz *et al.* 2000). Most significantly, it may help us to identify and thus protect processes underlying the origination of adaptations and biodiversity (Crandall *et al.* 2000; Moritz *et al.* 2000). It might also allow us to distinguish 'natural' hybridization from that resulting from human disturbance (Morgan-Richards *et al.* 2009); in combination with information on palaeoclimate, it might be possible to distinguish natural declines (e.g. shrinking distributions during warmer interglacials) from human induced declines, and reveal something about habitat requirements of cryptic taxa.

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