

Chapter 5

Biogeography of New Zealand Lizards

David G. Chapple and Rodney A. Hitchmough

Abstract New Zealand has a diverse lizard fauna, comprising diplodactylid geckos and skinks and over 100 recognised species or taxa. Geckos are thought to have colonised New Zealand during the Eocene or Oligocene (40.2–24.4 mya), prior to the ‘Oligocene drowning’ event. In contrast, skinks reached New Zealand during the Miocene (~18.3 mya) via long-distance overwater dispersal from New Caledonia along the Lord Howe Rise and Norfolk Ridge. Investigations of the biogeography of New Zealand lizards have long been hampered by two key factors: recent range contractions and local extinctions following the successful establishment of 31 exotic mammalian species and taxonomic gaps and a limited grasp on the true diversity of the endemic lizard fauna. However, subfossil records have improved our understanding of the prehuman distributions of several previously widespread species, and intensive taxonomic activity over the last two decades has provided a more accurate estimate of lizard diversity. This enhanced knowledge has enabled the key historical processes responsible for the diversification of lizards within New Zealand to be identified. These include sea-level changes during the Pliocene–Pleistocene in northern New Zealand, the Pliocene marine inundation of the lower North Island, the impact of water barriers such as Cook Strait (separating the North and South Islands) and Foveaux Strait (separating the South Island and Stewart island), tectonic activity along the Alpine Fault and regional north–south differentiation within the South Island. We provide an updated list of 22 biogeographic categories for New Zealand lizards. We highlight that the essential framework is now in place with which to investigate the biogeographic patterns evident in the New Zealand lizard fauna and examine the processes that have created them.

Keywords Gecko • Geology • Skink • Phylogeography • Climate • Diplodactylidae • Scincidae

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5.1 New Zealand's Geological and Climatic History

New Zealand contains one of the most diverse lizard faunas of any cool, temperate region on Earth (Daugherty et al. 1994; Chapple et al. 2009; Nielsen et al. 2011; Hitchmough et al. 2016a). High species richness may be driven by geological and topographic diversity (Anderson and Ferree 2010), as it increases habitat heterogeneity and provides the ecological conditions that promote speciation (Coyne and Orr 2004). Similarly, climate is a key determinant of a species' distribution (Angilletta 2009; Kearney and Porter 2009; Clusella-Trullas et al. 2011). Thus, investigation and interpretation of the biogeographic patterns evident in New Zealand lizards requires a detailed understanding of the geological and climatic history of the region.

New Zealand represents a mix of old and new. It displays attributes of both a continental fragment, a result of its Gondwanan heritage, and a long-isolated oceanic archipelago (Daugherty et al. 1993; Gibbs 2006; reviewed in Wallis and Trewick 2009). New Zealand is the main emergent landmass of the largely submerged subcontinent Zealandia (93% of it remains submerged today; Mortimer 2004; Neall and Trewick 2008; Goldberg et al. 2008; Fig. 5.1), which split off from Gondwana approximately 82 million years ago (mya) (Cooper and Millener 1993; Gibbs 2006; Landis et al. 2008; Wallis and Trewick 2009). The Tasman Sea formed around 65 mya and led to the current 1500 km isolation of New Zealand from Australia (Cooper and Millener 1993; Gibbs 2006; Campbell and Hutching 2007; Wallis and Trewick 2009). Zealandia was subsequently stretched and thinned over the next 40 myr (64–24 mya), causing a gradual subsidence of the New Zealand landmass and increased marine inundation (Gibbs 2006; Trewick et al. 2007; Landis et al. 2008; Neall and Trewick 2008; Wallis and Trewick 2009). The extent to which New Zealand became submerged (referred to as the 'Oligocene drowning'; Suggate et al. 1978; Cooper and Millener 1993; Gibbs 2006; Wallis and Trewick 2009) is an area of active debate and controversy (e.g. Trewick et al. 2007; Landis et al. 2008), but it likely persisted throughout this period as a series of low-lying islands (e.g. Cooper and Cooper 1995; Lee et al. 2009).

Modern New Zealand had its beginnings immediately following the Oligocene drowning and, like Lazarus rising, arose from the Pacific as a result of tectonic and volcanic activity (Gibbs 2006; Trewick et al. 2007; Landis et al. 2008). This rebirth also marked the start of the most tumultuous period in New Zealand's history, as due to its placement on the boundary of the Pacific and Indo-Australian plates, there has been continual tectonic uplift, predominantly along the Alpine Fault which runs SW–NE along the majority of the South Island (Gibbs 2006; Trewick et al. 2007; Landis et al. 2008). This has resulted in New Zealand becoming a land of fire and ice (Trewick and Bland 2012). The tectonic activity that became pervasive in New Zealand resulted in volcanic activity that persisted until ~13 mya in the South Island and through to the present day in the North Island (Wallis and Trewick 2009). The ever-increasing topography of the Southern Alps (>3000 m), combined with the cooling of global temperatures since the Pliocene (Markgraf et al. 1995),

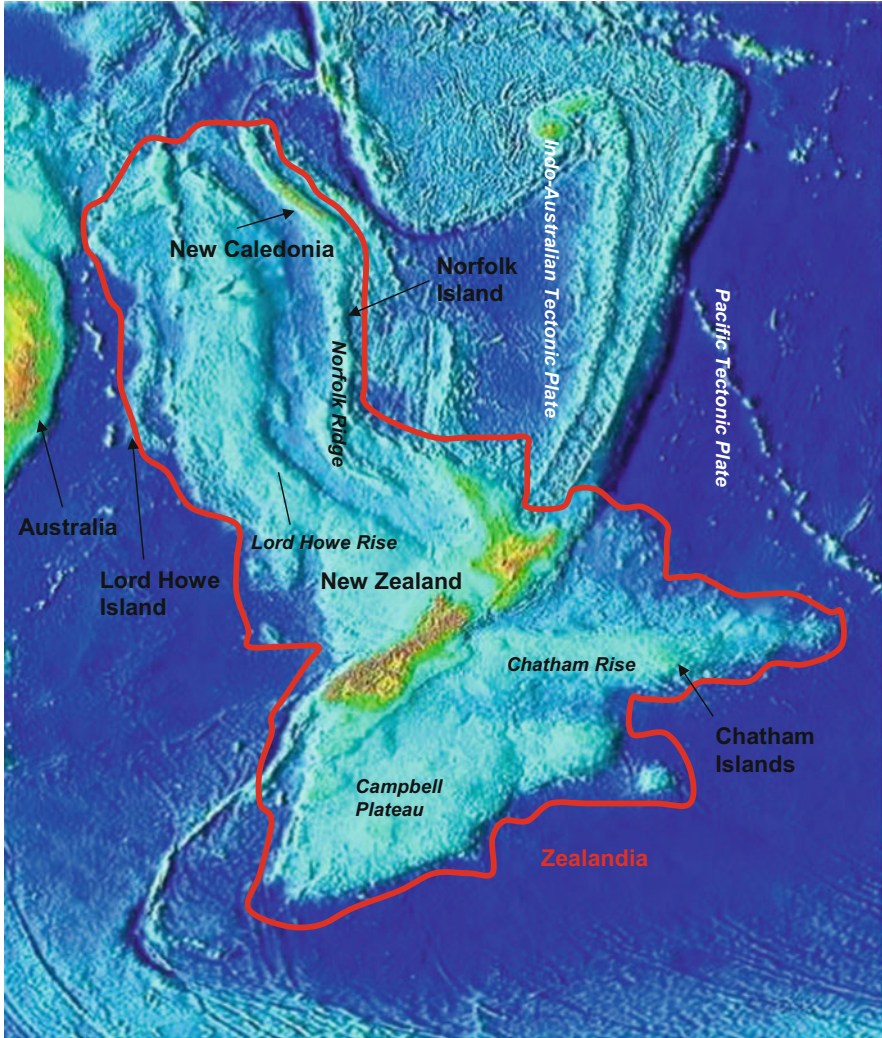


Fig. 5.1 Geographic extent of present day Zealandia (modified with Permission from Chapple et al. 2009). The red line indicates the approximate extent of the largely submerged continental crust of Zealandia. The locations of the Chatham Islands, Chatham Rise, Campbell Plateau, New Zealand, Lord Howe Island, Lord Howe Rise, Norfolk Island, Norfolk Ridge, New Caledonia and Australia are indicated. New Zealand is located on the boundary of the Indo-Australian and Pacific tectonic plates. The Alpine Fault refers to where this plate boundary diagonally bisects the South Island of New Zealand from the southwest to the northeast

leads to the formation of an alpine zone (Gage 1980; Suggate 1982; Stevens et al. 1995; Chamberlain et al. 1999; Lee et al. 2001; Gibbs 2006; Landis et al. 2008; Wallis and Trewick 2009). Throughout the Pliocene cooling, and the subsequent Pleistocene glacial cycles, the North Island was largely spared from

extensive glaciation (Newnham et al. 1999; Carter 2005). In contrast, large swathes of the South Island (up to 30%) were covered by glaciers during the Pleistocene (Newnham et al. 1999; Carter 2005).

Marine inundation once again became a characteristic of the New Zealand landscape during the Pliocene and Pleistocene, but on a more regional scale, and this time due to sea-level changes driven by glacial cycles (Lewis et al. 1994; Worthy and Holdaway 2002). During the Pliocene, the lower North Island was inundated, with the formation of the Manawatu Strait, which separated present-day Taranaki/Hawke's Bay from the Nelson/Marlborough region of the South Island (Bull and Whitaker 1975; Rogers 1989; Worthy and Holdaway 2002). The Pleistocene saw the formation of Cook Strait (separating North Island and South Island) and Foveaux Strait (separating South Island and Stewart Island) and the presence of an island archipelago in the Northland region (Lewis et al. 1994; Stevens et al. 1995; Worthy and Holdaway 2002). Sea-level fluctuations (up to 135 m below present levels) associated with Pleistocene glacial cycles result in the intermittent presence of land bridges across Cook Strait and Foveaux Strait and the reconnection of previously isolated regions of Northland (Lewis et al. 1994; Stevens et al. 1995; Worthy and Holdaway 2002).

Present-day New Zealand has a predominantly north–south orientation and spans 13° latitude (34–47°S; Fig. 5.2). It is situated in the Southwest Pacific and comprises two main islands (North Island, 113,729 km²; South Island, 150,437 km²) and Stewart Island (1680 km²; Fig. 5.2).

5.2 Origin and Colonisation of the New Zealand Lizard Fauna

Two key, but linked, questions have polarised the field of New Zealand biogeography: (i) do particular taxa have Gondwanan or post-Gondwanan origins? and (ii) did the resident biota persist in New Zealand through the Oligocene drowning or colonise afterwards? (Waters and Craw 2006; Gibbs 2006; Trewick et al. 2007; Landis et al. 2008; Sharma and Wheeler 2013). Whilst there is strong evidence that tuatara and Leiopelmatid frogs have Gondwanan origins and were present in New Zealand throughout the Oligocene (Rest et al. 2003; Roelants and Bossuyt 2005; Hugall et al. 2007; Cree 2014), skinks (Scincidae) and geckos (Diplodactylidae) arrived in New Zealand after its separation from Gondwana (Chapple et al. 2009; Nielsen et al. 2011).

Early researchers postulated a post-Oligocene colonisation of geckos into New Zealand, with overwater dispersal in the Miocene of an Asian lineage first to Australia then to New Zealand via New Caledonia (Kluge 1967; Bull and Whitaker 1975). Several authors subsequently proposed a vicariant Gondwanan origin for New Zealand geckos (Bauer 1990; Hitchmough 1997; Chambers et al. 2001). However, recent molecular studies have indicated diplodactylid geckos

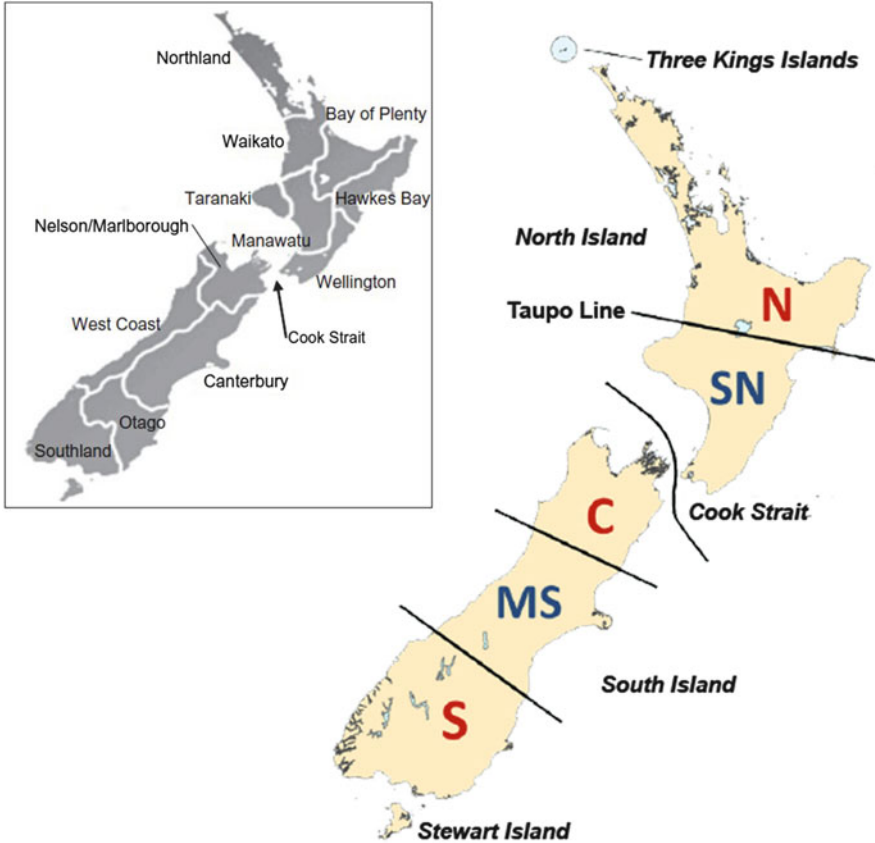


Fig. 5.2 Map of New Zealand indicating the approximate location of the Taupo line and the major biogeographic regions: N, northern North Island; SN, southern North Island; C, central New Zealand; MS, mid-South Island; and S, southern South Island (adapted with permission from Di Virgilio et al. 2014). *Inset*: major geographic regions in New Zealand (adapted with permission from O'Neill et al. 2008)

colonised New Zealand via long-distance overwater dispersal from Australia about 40.2 mya (53.5–28.9 mya) during the Eocene or Oligocene and prior to (or during) the Oligocene drowning (between 40.2 and 24.4 mya; Nielsen et al. 2011).

Similarly, skinks were initially suggested to have multiple colonisations of New Zealand, from Australia and/or Southeast Asia, during the Pliocene–Pleistocene (McCann 1955; Towns 1974; Bull and Whitaker 1975; Hardy 1977; Robb 1973, 1980). Subsequent studies based on allozymes and DNA sequence data indicated a single colonisation (from New Caledonia or the Southwest Pacific) and pushed back the arrival of skinks into New Zealand to the late Oligocene–early Miocene (~20–23 mya; Towns et al. 1985; Hickson et al. 2000; Smith et al. 2007). However, a more comprehensive molecular study (Chapple et al. 2009) indicated

that Eugongylineae skinks colonised New Zealand from New Caledonia, via overwater dispersal and island hopping along the Lord Howe Rise and Norfolk Ridge, during the Miocene (18.3 mya, range 16–22.6 mya). Indeed, the St. Bathans fossil deposit confirms that both skinks and geckos were present in New Zealand during the Miocene (~19–16 mya; Lee et al. 2009; Worthy 2016).

5.3 Diversification of Lizards Within New Zealand

Lizards exhibited high rates of diversification following their colonisation of New Zealand, with skinks radiating into at least 61 species within a single genus (*Oligosoma*) and geckos into at least 43 species across seven genera (*Dactylocnemis*, *Hoplodactylus*, *Mokopirirakau*, *Naultinus*, *Toropuku*, *Tukutuku* and *Woodworthia*; Hitchmough et al. 2016a, b). Two key factors have acted to obscure our understanding of the diversification and spread of New Zealand lizards. First, the introduction of a diverse array of mammals into New Zealand, an archipelago that was previously largely devoid of terrestrial mammals (Worthy and Holdaway 2002; Worthy et al. 2006), resulted in widespread range contractions of numerous lizard species (Townes et al. 1985, 2016; Tingley et al. 2013; Nelson et al. 2015; Hitchmough et al. 2016b). This alteration of geographic ranges has restricted our capacity to grasp biogeographic patterns of New Zealand lizards, although molecular or fossil data can often be used to reconstruct these prehuman distributions of native lizard species (Worthy and Holdaway 2002; Chapple et al. 2008a; Lee et al. 2009; Worthy 2016). Secondly, gaps in taxonomic knowledge, pronounced until recently (Hitchmough et al. 2016a), have masked the true lizard diversity present in New Zealand. For instance, numerous regions of the country have yet to be explored in detail to assess their lizard diversity. Expeditions that have been conducted to remote areas of the South Island (e.g. Jewell and Tocher 2005; Jewell 2007) have uncovered several new lizard species (Chapple and Patterson 2007; Bell and Patterson 2008; Patterson and Bell 2009; Chapple et al. 2011). Furthermore, a large proportion of New Zealand's known lizard diversity (45 %) is yet to be formally described (Hitchmough et al. 2016a, b).

Despite these hurdles, numerous studies over the last decade have investigated the biogeographic and phylogeographic patterns evident in New Zealand lizards. Published studies have focused predominantly on skinks (Berry and Gleeson 2005; Chapple and Patterson 2007; Greaves et al. 2007, 2008; Hare et al. 2008; Liggins et al. 2008a, b; O'Neill et al. 2008; Chapple et al. 2008a, b, c, 2009, 2011, 2012; Miller et al. 2009; Patterson et al. 2013; Di Virgilio et al. 2014; Nelson-Tunley et al. 2016), with less attention paid to geckos (Townes et al. 1985; Nielsen et al. 2011; Di Virgilio et al. 2014). These studies have demonstrated that the New Zealand lizard fauna is characterised by continental-level biogeographic patterns (e.g. deep genetic splits) over relatively short geographic distances, the result of strong regional tectonic or eustatic processes (e.g. uplift along Alpine Fault; marine inundation associated with tectonic activity or glacial cycles),

combined with strong gradients over short distances in altitude, rainfall, vegetation and substrate. Diversification of both skinks and geckos has occurred across several periods, namely, the mid–late Miocene, the late Miocene–Pliocene and the Pliocene–Pleistocene (Chapple et al. 2009; Nielsen et al. 2011). This has resulted in nine key biogeographic patterns within the New Zealand lizard fauna.

5.3.1 *Non-land-bridge Northern Island Groups*

Most New Zealand islands, along with all three main islands, were connected in a single large landmass when sea levels dropped during the Pleistocene glaciations. However, some groups lying in deeper water continued to be isolated as islands throughout that period. These include the Three Kings and Poor Knights and possibly the Mokohinaus/Pokohinaus, at least for most of the time. These three groups (particularly the first two) have high levels of endemism in their lizard faunas. For the Three Kings, two of its six resident lizard species are endemic, for the Mokohinaus one of seven; for the Poor Knights, three of eight species. In addition, other populations on these islands such as the Poor Knights Islands population of *O. oliveri* and the Three Kings Islands population of *O. ornatum* have diverged in body size and/or morphology from other populations of the species. The more distantly isolated New Zealand island groups, the Kermadecs in the subtropics and the various subantarctic island groups, have never had any records of terrestrial reptiles. Apparent endemism of lizards on other land-bridge islands is now understood to be secondary to the effects of invasive mammals causing extinctions of those species on the mainland where they were widespread before human settlement.

5.3.2 *Northland Diversification*

Sea-level changes during the Pliocene–Pleistocene modified the landscape of Northland, with the repeated connection, and subsequent isolation, of offshore islands (Rogers 1989; King 2000; Worthy and Holdaway 2002). At its extreme, island groups such as the Poor Knights and Three Kings have been separated from the North Island mainland for up to 1–2 myr (Hayward 1986, 1991). These sea-level fluctuations appear to have resulted in substantial diversification in both skinks (Chapple et al. 2008a, b, c, 2009; Hare et al. 2008; Patterson et al. 2013) and geckos (*Dactylocnemis* and *Naultinus*; Nielsen et al. 2011). Three undescribed geckos and a skink are endemic to the Aupouri or Aupouri, plus Karikari Peninsulas. However, as of yet, there has been little consistency in terms of the timing and placement of biogeographic breaks across taxonomic groups (Wallis and Trewick 2009).

5.3.3 Taupo Line Biogeographic Barrier

A substantial discontinuity in lizard distributions occurs across a line (referred to as the Taupo line) which roughly follows the axial ranges in the East Cape area, then passes just south of Lake Taupo, north of Tongariro National Park and then south through the King Country and inland Taranaki to meet the coast somewhere west of Whanganui (Fig. 5.2). The Taupo line represents a significant species transition zone, with relatively few species possessing distributions that span this boundary (McCann 1955; Chapple et al. 2009). The distributional boundaries of all the lizard species involved do not coincide exactly, but all roughly follow this line. *N. elegans*, *M. granulatus*, *D. pacificus*, *O. aff. infrapunctatum* ‘crenulate’, *O. striatum* and the eastern coastal endemic skinks *O. suteri*, *O. moco* and *O. smithii* are found only north and west of this line, whereas *N. punctatus*, *M.* ‘southern North Island’, inland populations of *W. maculata*, *O. lineoocellatum*, *O. polychroma* and *O. aff. infrapunctatum* ‘southern North Island’ are found only south and east of this line (McCann 1955, 1956; Hare et al. 2008; Liggins et al. 2008a; Chapple et al. 2009; Nielsen et al. 2011). In fact no gecko species currently with viable mainland populations crosses this line, except for *W. maculata*, which is widespread inland south of the line, but in the north is confined to coastal habitats. *H. duvaucelii* also spans the line (and Cook Strait) but is currently almost entirely confined to mammal-free offshore islands. Populations on islands in Cook Strait form a distinct clade and are also diagnostically different in morphology from northern populations (Morgan-Richards et al. 2016).

The Taupo line is located near the northern edge of where the Manawatu Strait was located during the Pliocene (Bull and Whitaker 1975; Rogers 1989; Worthy and Holdaway 2002). If this contact zone represents secondary contact following isolation across the Pliocene Manawatu Strait, the species meeting there might be expected to be sister taxa and to have similar depths of genetic divergence, reflecting the age of the isolation event. In contrast, none of the congeneric gecko pairs or ecologically similar or closely related skink pairs are sister species, and depths of genetic divergence between them cover a very broad spectrum, from 24.4 ± 8.9 mya for *D. pacificus* and *W. maculata* to <1 mya for *N. elegans* and *N. punctatus* (Nielsen et al. 2011). The depth of divergence in *M.* is intermediate between these extremes. *M.* ‘southern North Island’ is sister to the remainder of the genus, whilst more *M. granulatus* has recently colonised the North Island from the South Island (Nielsen et al. 2011). The skinks show similar patterns, with those north and south of the line mostly separated by the deepest split in the New Zealand skink radiation. However, the two North Island taxa of the *O. infrapunctatum* complex appear to represent independent colonisations of the North Island by different South Island ancestors (Greaves et al. 2008).

5.3.4 Cook Strait

Cook Strait is the shallow waterway that separates the present-day North and South Islands (Fig. 5.2). However, during Pleistocene glacial cycles, land bridges linking the two islands were present intermittently, potentially facilitating the movement of lizards across this region (Lewis et al. 1994; Worthy and Holdaway 2002). The evidence for dispersal across these Cook Strait land bridges varies among species, with genetic studies indicating recent dispersal between the two islands in several skink species (*O. zelandicum*, *O. maccanni*, *O. infrapunctatum*, *O. lineoocellatum*, *O. polychroma*; Greaves et al. 2007, 2008; O'Neill et al. 2008; Liggins et al. 2008a). Similarly, the current distribution of several gecko species (*M. granulatus*, *W. maculata*, *W.* 'Marlborough mini', *H. duvaucelii*) and pattern of genetic variation within them are also suggestive of linkages across Cook Strait (Hitchmough 1997; Nielsen et al. 2011). In contrast, Cook Strait represents a distributional barrier for several skink (e.g. *O. aeneum*, *O. ornatum*, *O. whitakeri*; Chapple et al. 2008a, 2009; Miller et al. 2009) and gecko species (e.g. *Naultinus* spp., *W. chrysoisiretica*, probably *Toropuku stephensi*; Nielsen et al. 2011) (Figs. 5.3 and 5.4). Intriguingly, skink species that are continuously distributed across the Taupo line are less likely to have distributions that span Cook Strait, and vice versa (reviewed in Chapple et al. 2009; Fig. 5.4); this does not apply to geckos.

5.3.5 Alpine Fault

The Southern Alps, located along the Alpine Fault in the South Island, have experienced dramatic topographic uplift since the Miocene. This tectonic activity appears to have driven east–west biogeographic breaks (of Miocene–Pliocene origin) in several skink (*O. polychroma*, Liggins et al. 2008a; *O. lineoocellatum*, Greaves et al. 2007) and gecko species (*Mokopirirakau*, *Naultinus*; Nielsen et al. 2011). This has led to many individual lizard species exhibiting distributions that are restricted entirely to the east, or to the west, of the Southern Alps (Chapple et al. 2009; Nielsen et al. 2011; Figs. 5.3 and 5.4). Indeed, most species with ranges spanning Cook Strait are widely distributed across the North Island, but are restricted to the western side of the Southern Alps in the South Island (Table 5.1; Figs. 5.3 and 5.4). *Woodworthia*, despite having its highest diversity immediately east of the Southern Alps, is almost entirely absent to the west.

5.3.6 North–South Splits in the South Island

One of the earliest biogeographic patterns that was characterised in the New Zealand biota was the alternating extremes of high and low endemism in the

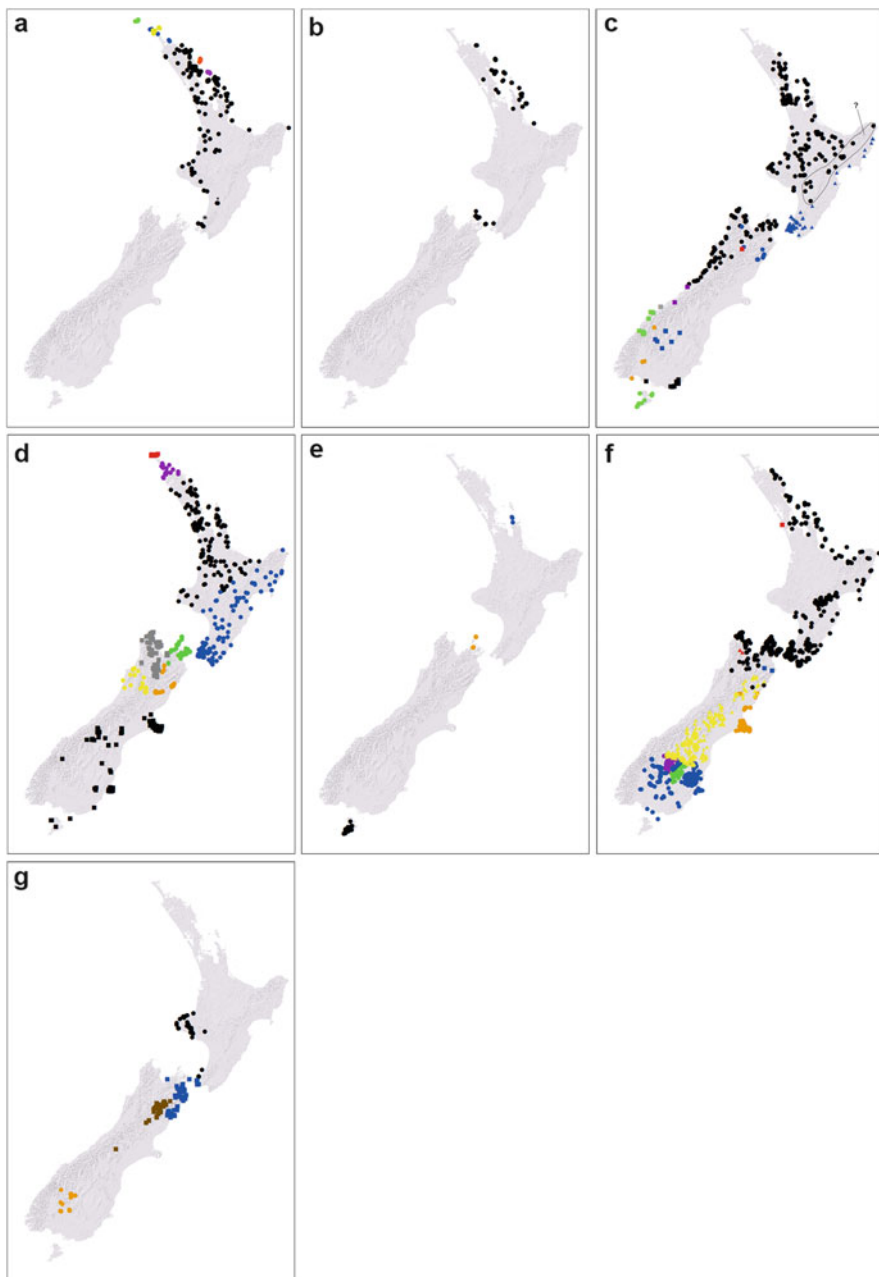


Fig. 5.3 Distribution of New Zealand gecko species. The distributional data follows the Department of Conservation BioWeb Herpetofauna database (used with permission from Benno Kappers, Department of Conservation). (a) *Dactylocnemis*: *D. pacificus* (black; note that the records in the southern North Island marked with an asterisk are probably the result of human-assisted transport), *D. 'Matapia Island'* (blue), *D. 'Mokohinau'* (purple), *D. 'North Cape'* (yellow), *D. 'Poor Knights'*

eastern South Island from Nelson–Marlborough (high), Canterbury (low) and Otago–Southland (high) (Wardle 1991; Wardle et al. 1988; Craw 1989; Gibbs 2006) (a similar pattern is seen on the West Coast). This is thought to be due to a combination of tectonic activity and climatic processes (e.g. Pleistocene glacial cycles). In lizards, this appears to have resulted in biogeographic breaks, at both the intra- and interspecific level, in skinks (e.g. *O. polychroma*, *O. maccanni*, *O. chloronoton–lineoocellatum*, *O. otagense–waimatense*; Greaves et al. 2007; O’Neill et al. 2008; Liggins et al. 2008a; Chapple et al. 2012) and geckos (*Naultinus*, *Woodworthia*; Nielsen et al. 2011). The pattern of reduced endemism in Canterbury noted for other biotic groups is less true for the lizards: Marlborough has eight endemic species or deeply divergent intraspecific clades (*N. manukanus*, *N. rudis*, *W.* ‘Marlborough mini’, *W.* ‘Kaikouras’, *O. longipes* sensu stricto, *O.* aff. *polychroma* clades 2 and 3, *O.* aff. *lineoocellatum* clade 2a and in addition *W. maculata* and *M. kahutarae* are found in Marlborough but not in Canterbury), Canterbury six (*W.* cf. *brunnea*, *O.* aff. *longipes* ‘southern’, *O.* aff. *longipes* ‘Rangitata’, *O.* aff. *polychroma* clade 4, *O.* aff. *lineoocellatum* clades 2b and 2c) and Otago–Southland thirteen (*W.* ‘Otago/Southland large’, *W.* ‘Cromwell’, *W.* ‘Central Otago’, *W.* ‘southern mini’, *O. otagense*, *O. grande*, *O. inconspicuum*, *O. burganae*, *O. repens*, *O. toka*, *O.* aff. *chloronoton* clades 3a, 3b and 3c). A much smaller number of species span these boundaries: *W.* ‘Southern Alps’ extends from Canterbury well into South Marlborough, as does *O. waimatense* (although with deeply divergent southern and northern clades), and *W.* ‘pygmy’ extends from south Marlborough well south into Canterbury. *N. gemmeus* and *O.* aff. *polychroma* clade 5 extend across Otago/Southland and much of Canterbury, as does *O. maccanni*, but in the latter case with much deeper intraspecific genetic structuring. There are also a few unconfirmed sightings and sloughed skins of *Mokopirakau* from the eastern South Island, but their history and taxonomic identity are unknown so they are not considered here.

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Fig. 5.3 (continued) (*orange*), *D.* ‘Three Kings’ (*green*). **(b) *Hoplodactylus***: *H. duvaucelii* (*black*). **(c) *Mokopirakau***: *M. cryptozoicus* (*orange circles*), *M. granulatus* (*black circles*), *M. kahutarae* (*blue circles*), *M. nebulosus* (*green circles*), *M.* ‘Cascades’ (*green squares*), *M.* ‘cupola’ (*red square*), *M.* ‘Okarito’ (*purple squares*), *M.* ‘Open Bay Islands’ (*grey squares*), *M.* ‘Roys Peak’ (*blue squares*) *M.* ‘southern forest’ (*black squares*), *M.* ‘southern NI’ (*blue triangles*). Note that the taxonomic affinities of some populations in the North Island (as highlighted) are unknown. **(d) *Naultinus***: *N. elegans* (*black circles*), *N. gemmeus* (*black squares*), *N. grayii* (*purple circles*), *N. manukanus* (*green circles*), *N. punctatus* (*blue circles*), *N. rudis* (*orange circles*), *N. stellatus* (*grey squares*), *N. tuberculatus* (*yellow circles*), *N.* ‘North Cape’ (*red squares*). **(e) *Toropuku* and *Tukutuku***: *Toropuku stephensi* (*orange*), *Toropuku* ‘Coromandel’ (*blue*), *Tukutuku rakiurae* (*black*). **(f) *Woodworthia* (part 1)**: *W. maculata* (*black circles*), *W.* ‘Central Otago’ (*green circles*), *W.* ‘Cromwell’ (*purple circles*), *W.* ‘Kaikouras’ (*blue squares*), *W.* ‘Mount Arthur’ (*red triangles*), *W.* ‘Otago/Southland large’ (*blue circles*), *W.* ‘Southern Alps’ (*yellow triangles*), *W.* aff. *maculata* ‘Muriwai’ (*red square*), *W.* c.f. *brunnea* (*orange circles*). **(g) *Woodworthia* (part 2)**: *W. chrysoisiretica* (*black circles*), *W.* ‘Marlborough mini’ (*blue squares*), *W.* ‘pygmy’ (*brown square*), *W.* ‘southern mini’ (*orange circle*)

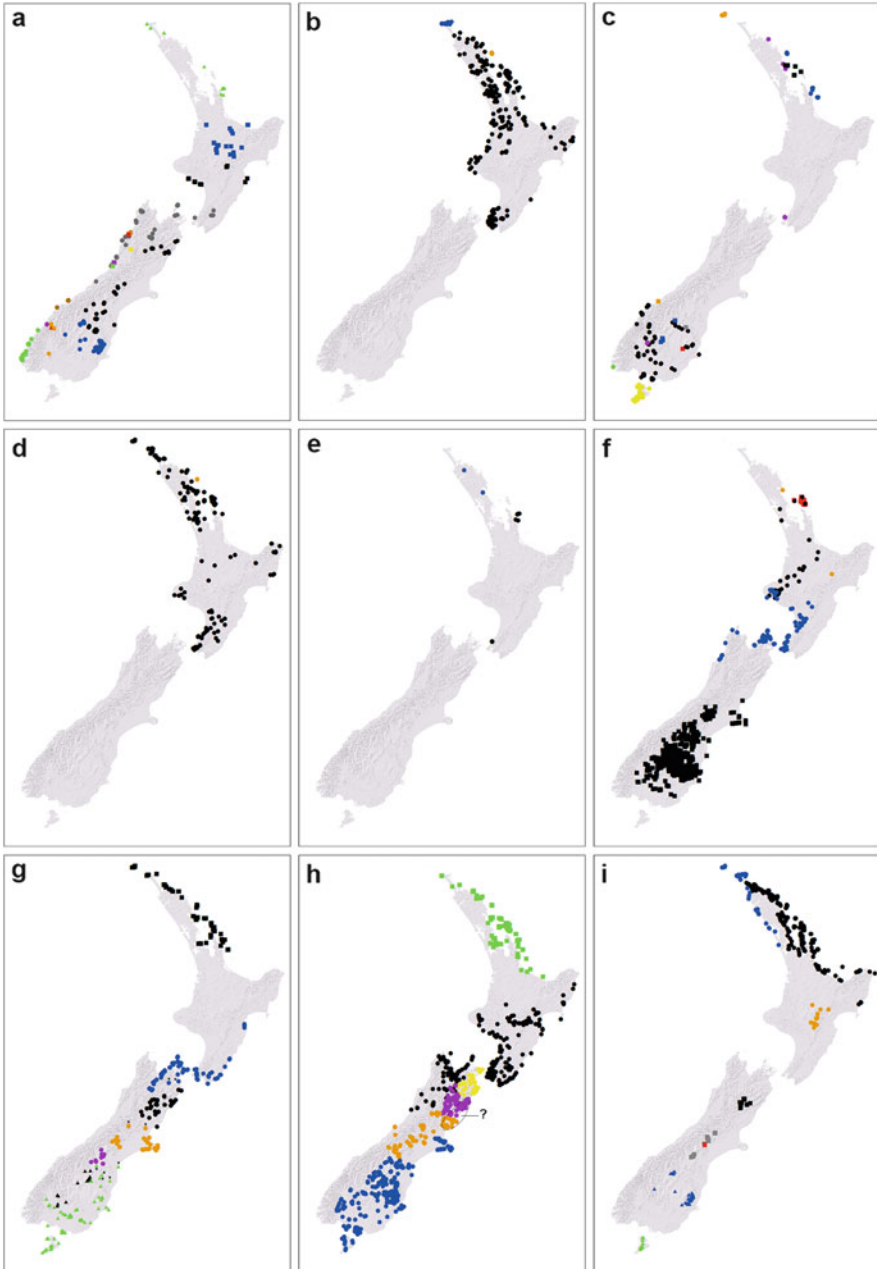


Fig. 5.4 Distribution of New Zealand skink species. The distributional data follows the Department of Conservation BioWeb Herpetofauna database (used with permission from Benno Kappers, Department of Conservation). (a) **Clade 2 + *O. alani***: *O. alani* (green triangles), *O. infrapunctatum* (grey circles), *O. aff. infrapunctatum* 'crenulate' (blue squares), *O. aff. infrapunctatum* 'southern North Island' (black squares), *O. aff. infrapunctatum* 'Alborn' (yellow squares), *O. aff. infrapunctatum* 'Chesterfield' (purple squares), *O. aff. infrapunctatum* 'cobble' (orange square), *O. aff. infrapunctatum* 'Hokitika' (green square), *O. aff. infrapunctatum*

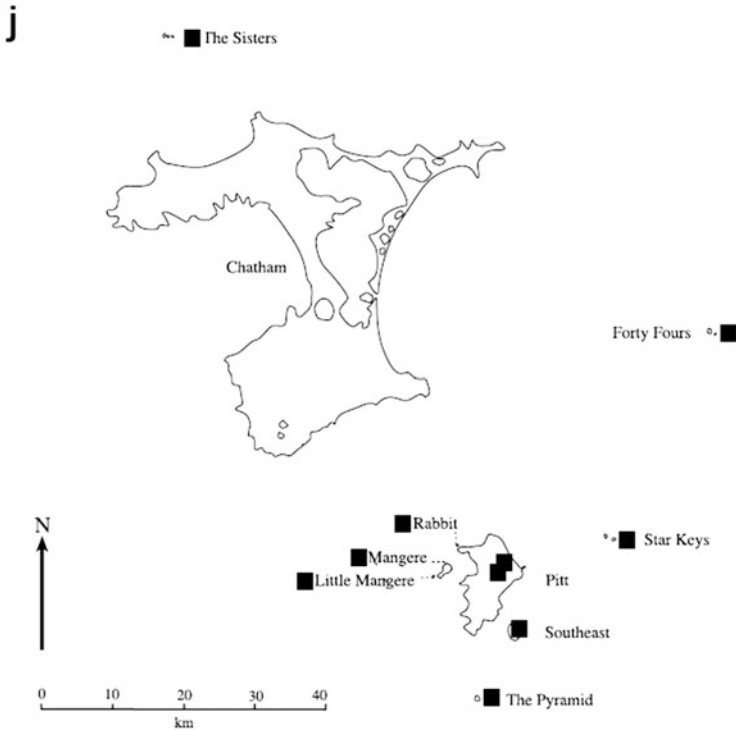


Fig. 5.4 (continued) ‘Westport’ (red square), *O. waimatense* (black circles), *O. otagensis* (blue circles), *O. acrinusum* (green circles), *O. judgei* (orange circles), *O. pikitanga* (purple circles), *O. taumakae* (brown circles), *O. sp.* ‘Homer Tunnel’ (red triangle). **(b) Clade 3:** *O. aeneum* (black circles), *O. hardyi* (orange circles), *O. levidensum* (blue circles). **(c) Clade 4 (part 1) + *O. inconspicuum* complex:** *O. fallai* (orange circles), *O. macgregori* (purple circles), *O. oliveri* (blue circles), *O. townsi* (black squares), *O. burganae* (red squares), *O. inconspicuum* (black circles), *O. notosaurus* (yellow circles), *O. repens* (purple square), *O. tekakahu* (green circles), *O. toka* (blue squares), *O. aff. inconspicuum* ‘North Otago’ (grey squares), *O. aff. inconspicuum* ‘Okuru’ (orange squares). **(d) Clade 4 (part 2):** *O. ornatum* (black circles), *O. roimata* (orange circles). **(e) Clade 4 (part 3):** *O. whitakeri* (black circles), *O. northlandi* (extinct; blue circles). **(f) Clade 5 + *O. maccanni*:** *O. zelandicum* (blue circles), *O. striatum* (black circles), *O. homalonotum* (red squares), *O.* ‘Whirinaki’ (orange circles), *O. maccanni* (black squares). **(g) Clade 6 + *O. lineoocellatum*–*O. chloronoton* complex:** *O. suteri* (black squares), *O. lineoocellatum* (blue circles), *O. aff. lineoocellatum* ‘South Marlborough’ (black circles), *O. aff. lineoocellatum* ‘Central Canterbury’ (orange circles), *O. aff. lineoocellatum* ‘Mackenzie Basin’ (purple circles), *O. chloronoton* (green triangles), *O. aff. chloronoton* ‘West Otago’ (black triangles). The asterisks indicate populations where the taxonomic affinities are uncertain. **(h) Clade 7 + *O. polychroma* complex:** *O. moco* (green squares), *O. polychroma* (black circles), *O. polychroma* clade 2 (yellow circles), *O. polychroma* clade 3 (purple circles), *O. polychroma* clade 4 (orange circles), *O. polychroma* clade 5 (blue circles). Note that the taxonomic affinities of some populations in the Kaikoura area south to Christchurch (as highlighted) are unknown. Clades 4 and 5 may be sympatric in the Lindis Pass–Mackenzie Basin region. **(i) Clade 8 + *O. grande*, *O. stenotis*, *O. longipes* complex:** *O. smithi* (black circles), *O. aff. smithi* ‘Three Kings, Te Pahi, western Northland’ (blue circles), *O. microlepis* (orange circles), *O. grande* (blue triangles), *O. stenotis* (green triangles), *O. longipes* (black squares), *O. aff. longipes* ‘southern’ (grey squares), *O. longipes* ‘Rangitata’ (red squares). **(j) *O. nigriplantare*:** distribution within the Chatham Islands. Note that it does not occur on the main Chatham Island (modified with permission from Liggins et al. 2008b)

Table 5.1 Biogeographic categories for New Zealand skinks and geckos [adapted and modified from Towns et al. (1985)]

Species	Biogeographic category
Skinks (Scincidae: Eugongylinae)	
<i>Oligosoma acrinasum</i> (Hardy, 1977)	17
<i>Oligosoma aeneum</i> (Girard, 1857)	4
<i>Oligosoma alani</i> (Robb, 1970)	3
<i>Oligosoma burganae</i> (Chapple et al. 2011)	19
<i>Oligosoma chloronoton</i> (Hardy, 1977)	16
<i>Oligosoma</i> aff. <i>chloronoton</i> 'West Otago'	15
<i>Oligosoma fallai</i> (McCann, 1955)	1
<i>Oligosoma grande</i> (Gray, 1845)	15
<i>Oligosoma hardyi</i> (Chapple et al. 2008)	1
<i>Oligosoma homalonotum</i> (Boulenger, 1906)	3
<i>Oligosoma inconspicuum</i> (Patterson & Daugherty, 1990)	16
<i>Oligosoma</i> aff. <i>inconspicuum</i> 'North Otago'	15
<i>Oligosoma</i> aff. <i>inconspicuum</i> 'Okuru'	17
<i>Oligosoma infrapunctatum</i> (Boulenger, 1887)	10
<i>Oligosoma</i> aff. <i>infrapunctatum</i> 'Alborn'	11
<i>Oligosoma</i> aff. <i>infrapunctatum</i> 'Chesterfield'	11
<i>Oligosoma</i> aff. <i>infrapunctatum</i> 'cobble'	11
<i>Oligosoma</i> aff. <i>infrapunctatum</i> 'crenulate'	7
<i>Oligosoma</i> aff. <i>infrapunctatum</i> 'Hokitika'	11
<i>Oligosoma</i> aff. <i>infrapunctatum</i> 'southern North Island'	8
<i>Oligosoma</i> aff. <i>infrapunctatum</i> 'Westport'	11
<i>Oligosoma judgei</i> (Patterson & Bell, 2009)	19
<i>Oligosoma levidensum</i> (Chapple et al., 2008)	5
<i>Oligosoma lineoocellatum</i> (Duméril & Duméril, 1851)	10
<i>Oligosoma</i> aff. <i>lineoocellatum</i> 'Central Canterbury'	14
<i>Oligosoma</i> aff. <i>lineoocellatum</i> 'Mackenzie Basin'	14
<i>Oligosoma</i> aff. <i>lineoocellatum</i> 'South Marlborough'	12
<i>Oligosoma longipes</i> (Patterson, 1997)	12
<i>Oligosoma</i> aff. <i>longipes</i> 'Rangitata'	14
<i>Oligosoma</i> aff. <i>longipes</i> 'southern'	14
<i>Oligosoma maccanni</i> (Patterson & Daugherty, 1990)	18
<i>Oligosoma macgregori</i> (Robb, 1975)	9
<i>Oligosoma microlepis</i> (Patterson & Daugherty, 1990)	7
<i>Oligosoma moco</i> (Duméril & Bibron, 1839)	2
<i>Oligosoma nigriplantare</i> (Peters, 1873)	22
<i>Oligosoma notosaurus</i> (Patterson & Daugherty, 1990)	21
<i>Oligosoma oliveri</i> (McCann, 1955)	3
<i>Oligosoma ornatum</i> (Gray, 1843)	4
<i>Oligosoma otagense</i> (McCann, 1955)	15
<i>Oligosoma pikitanga</i> (Bell & Patterson, 2008)	19
<i>Oligosoma polychroma</i> (Patterson & Daugherty, 1990)	10

(continued)

Table 5.1 (continued)

Species	Biogeographic category
<i>Oligosoma</i> aff. <i>polychroma</i> clade 2	12
<i>Oligosoma</i> aff. <i>polychroma</i> clade 3	12
<i>Oligosoma</i> aff. <i>polychroma</i> clade 4	14
<i>Oligosoma</i> aff. <i>polychroma</i> clade 5	16
<i>Oligosoma repens</i> (Chapple et al. 2011)	19
<i>Oligosoma roimata</i> (Patterson, Hitchmough & Chapple, 2013)	1
<i>Oligosoma smithi</i> (Gray, 1845)	2
<i>Oligosoma</i> aff. <i>smithi</i> ‘Three Kings, Te Paki, Western Northland’	2
<i>Oligosoma stenotis</i> (Patterson & Daugherty, 1994)	21
<i>Oligosoma striatum</i> (Buller, 1871)	7
<i>Oligosoma suteri</i> (Boulenger, 1906)	2
<i>Oligosoma taumakae</i> (Chapple & Patterson, 2007)	17
<i>Oligosoma tekakahu</i> (Chapple et al. 2011)	17
<i>Oligosoma toka</i> (Chapple et al. 2011)	19
<i>Oligosoma townsi</i> (Chapple et al. 2008)	3
<i>Oligosoma waimatense</i> (McCann, 1955)	13
<i>Oligosoma whitakeri</i> (Hardy, 1977)	9
<i>Oligosoma zelandicum</i> (Gray, 1843)	10
<i>Oligosoma</i> ‘Whirinaki’	7
<i>Oligosoma</i> sp. ‘Homer Tunnel’	19
Geckos (Diplodactylidae)	
<i>Dactylocnemis pacificus</i> (Gray, 1842)	4
<i>Dactylocnemis</i> ‘Matapia Island’	5
<i>Dactylocnemis</i> ‘Mokohinau’	1
<i>Dactylocnemis</i> ‘North Cape’	5
<i>Dactylocnemis</i> ‘Poor Knights’	1
<i>Dactylocnemis</i> ‘Three Kings’	1
<i>Hoplodactylus duvaucelii</i> (Duméril & Bibron, 1836)	9
<i>Mokopirirakau cryptozoicus</i> (Jewell & Leschen, 2004)	16
<i>Mokopirirakau granulatus</i> (Gray, 1845)	10
<i>Mokopirirakau kahutarae</i> (Whitaker, 1985)	12
<i>Mokopirirakau nebulosus</i> (McCann, 1955)	21
<i>Mokopirirakau</i> ‘Cascades’	17
<i>Mokopirirakau</i> ‘Cupola’	12
<i>Mokopirirakau</i> ‘Okarito’	11
<i>Mokopirirakau</i> ‘Open Bay Islands’	17
<i>Mokopirirakau</i> ‘Roys Peak’	15
<i>Mokopirirakau</i> ‘southern forest’	20
<i>Mokopirirakau</i> ‘southern North Island’	8
<i>Naultinus elegans</i> (Gray, 1842)	6
<i>Naultinus gemmeus</i> (McCann, 1955)	18
<i>Naultinus grayii</i> (Bell, 1843)	5

(continued)

Table 5.1 (continued)

Species	Biogeographic category
<i>Nautinus manukanus</i> (McCann, 1955)	12
<i>Nautinus punctatus</i> (Gray, 1842)	8
<i>Nautinus rudis</i> (Fischer, 1882)	12
<i>Nautinus stellatus</i> (Hutton, 1872)	12
<i>Nautinus tuberculatus</i> (McCann, 1955)	11
<i>Nautinus</i> ‘North Cape’	5
<i>Toropuku stephensi</i> (Robb, 1980)	12
<i>Toropuku</i> ‘Coromandel’	7
<i>Tukutuku rakiurae</i> (Thomas, 1981)	21
<i>Woodworthia chrysosiretica</i> (Robb, 1980)	7
<i>Woodworthia maculata</i> (Gray, 1845)	10
<i>Woodworthia</i> aff. <i>maculata</i> ‘Muriwai’	2
<i>Woodworthia</i> ‘Central Otago’	15
<i>Woodworthia</i> ‘Cromwell’	15
<i>Woodworthia</i> ‘Kaikouras’	12
<i>Woodworthia</i> ‘Marlborough mini’	10
<i>Woodworthia</i> ‘Mount Arthur’	12
<i>Woodworthia</i> ‘Otago/Southland large’	16
<i>Woodworthia</i> ‘pygmy’	14
<i>Woodworthia</i> ‘Southern Alps’	18
<i>Woodworthia</i> ‘southern mini’	15
<i>Woodworthia</i> cf. <i>brunnea</i>	14

The taxonomic authority for described species is provided. The geographic distribution of each species is provided in Figs. 5.3 and 5.4. The 22 biogeographic categories are (1) northern island endemic, (2) northern coastal, (3) northern island relicts, (4) widespread North Island, (5) northern Northland, (6) northern North Island, (7) central North Island, (8) southern North Island, (9) disjunctive relicts, (10) span Cook Strait, (11) West Coast endemic, (12) Nelson/Marlborough endemic, (13) Marlborough/Canterbury, (14) Canterbury endemic, (15) Otago endemic, (16) Otago/Southland, (17) South Westland/Fiordland coastal/island endemic, (18) widespread South Island, (19) southern montane/alpine endemic, (20) Southland endemic, (21) Stewart Island endemic, (22) Chatham Islands endemic

The boundary between Otago and Canterbury is in the Waitaki Valley; all lizard species distributed across this boundary show at least changes in colour. Many pairs of parapatric sister species meet there, but in *O. maccanni*, the boundary is intraspecific between subclades, and in *O. polychroma* and *N. gemmeus*, there is an abrupt change in colour with little or no divergence in neutral genetic markers. The sister taxon relationships across the Waitaki Valley are in contrast to the Taupo line, but as with the Taupo line, their dates of divergence differ considerably, indicating that the processes driving the formation of this zone were not drivers of the original speciation events.

5.3.7 *East–West Splits in Otago*

Active since the late Miocene, the Nevis–Cardrona fault system (delineated by the Cardrona and Nevis rivers) represents the border between eastern and western Otago (reviewed in Waters et al. 2001). Deep genetic breaks are evident across this region in several skink species (*O. grande*, *O. maccanni*, *O. otagense*; Berry and Gleeson 2005; O’Neill et al. 2008; Chapple et al. 2012), and species level breaks are also present in *Woodworthia* geckos (Nielsen et al. 2011). Similarly, tectonic activity in the southern South Island appears to have resulted in several isolated or disjunct species, of Miocene–Pliocene origin, in mountainous regions (Bell and Patterson 2008; Patterson and Bell 2009; Chapple et al. 2011; Nielsen et al. 2011).

5.3.8 *Fiordland*

Fiordland is another centre of endemism, with four of the six species known from Fiordland proper endemic to that region and the other two (*M. cryptozoicus* and *O. judgei*) extending only slightly east to the Takitimu Range. Other species, such as *N. gemmeus*, *W.* ‘Otago/Southland large’, *O.* aff. *polychroma* clade 5, *O. chloronoton* clade 3c and *O. repens* or *O. toka*, are found in the eastern valleys and foothills, but not in the Fiordland ranges proper.

5.3.9 *Stewart Island*

Despite having been connected to mainland South Island by continuous dry land during the last glacial maximum, Stewart Island has an endemic genus (*Tukutuku*) and a surprisingly high number of endemic species (*M. nebulosus*, *O. notosaurus*, *O. stenotis*) or quite deeply divergent intraspecific clades (*O. chloronoton* clade 3d). The boundary for the Stewart Island fauna falls between Stewart Island and the islands of central Foveaux Strait such as the Ruapuke Group Centre and Pig; these islands have a mainland Southland fauna including species such as *Woodworthia* ‘Otago/Southland large’, *O. inconspicuum* and the mainland Southland clade of *O. chloronoton*, which are absent from Stewart Island. Only *O. polychroma* and *N. gemmeus* appear to reflect very recent colonisation from or gene flow with the South Island and span this boundary. Notably, these are the same two species that span the Waitaki Valley.

5.4 Updated Biogeographic Patterns for New Zealand Lizards

The last comprehensive attempt to categorise the distributional and biogeographic patterns of New Zealand lizards was made by Towns et al. (1985). However, at the time, there were only 38 species of lizards (22 skinks, 16 geckos) recognised in New Zealand (Towns et al. 1985). The extensive taxonomic activity over the past three decades, characterised by the splitting of several widespread species into multiple taxa and the discovery of numerous new taxa (Chapple and Ritchie 2013; reviewed in Hitchmough et al. 2016a), has increased the size of the New Zealand lizard fauna ~2.7-fold (Hitchmough et al. 2016b) and led to the existing biogeographic categories becoming seriously out-of-date. Whilst there have been several detailed investigations of the biogeography of New Zealand lizards over the past decade (Jewell 2008; Chapple et al. 2009; Nielsen et al. 2011; Di Virgilio et al. 2014; Pepper et al. In Press), none have proposed an updated list of biogeographic categories for the fauna.

Here we assign the 104 currently recognised extant New Zealand lizard species (61 skinks, 43 geckos) to one of 22 different biogeographic categories (Table 5.1). As with Towns et al.'s (1985) categories, our categories are based on the geographic extent of each species, whether they are endemic to a particular region or exhibit a relictual distribution (e.g. due to introduced mammals or human settlement of New Zealand; Chapple et al. 2008a; see Towns et al. 2016). Although we used Towns et al.'s (1985) categories as a basis for ours, adjustment and expansion of these were required for two key reasons. First, the splitting of previously widespread (composite) species into multiple taxa has necessitated the development of additional categories (as an extreme example, *L. nigriplantare maccanni* is now recognised as 19 distinct species; Chapple 2016). As these new taxa generally do not have overlapping geographic distributions and are often restricted to specific regions of the country, the new categories have been designed to reflect this (e.g. Otago endemic, West Coast endemic; Table 5.1). Indeed, many biogeographic breaks in the South Island correspond to provincial boundaries (Figs. 5.3 and 5.4). Second, most newly discovered species/taxa (see Hitchmough et al. 2016a) are only known from a single locality or restricted region, generally mountainous or remote areas of the South Island. Additional categories have been developed to accommodate these species (Table 5.1).

These changes have substantially decreased the number of widely distributed species recognised in New Zealand (12 in Towns et al. 1985 vs 6 in the present study) and dramatically increased the number of island endemics in the North Island and regional endemics within the South Island (see Table 5.1).

5.5 Conclusions

The foundations have been laid for a golden age of New Zealand lizard biogeography. Increasing field surveys, coupled with the continued development of effective sampling techniques (reviewed in Lettink and Hare 2016), have greatly enhanced our knowledge of the distribution of skinks and geckos in New Zealand. This distributional information maintained in a constantly updated, and publicly accessible, online database (Department of Conservation Atlas of the Amphibians and Reptiles of New Zealand; <http://www.doc.govt.nz/our-work/reptiles-and-frogs-distribution/atlas/>). Importantly, intensive taxonomic work, incorporating molecular studies, has been conducted over the past decade (and is still ongoing), providing enhanced resolution of the true lizard diversity in New Zealand and aiding to delineate species boundaries (reviewed in Hitchmough et al. 2016a). This, for the first time, has provided the essential framework with which to consider the biogeographic patterns evident in the fauna and investigate the processes that have created them. Whilst local extinctions and range contractions, as a result of introduced mammals and human settlement, have been observed, our understanding of prehuman distributions (Worthy and Holdaway 2002; Chapple et al. 2008a), fossil and subfossil evidence has assisted us in reconstructing the previous distributions of several lizard species (Worthy 2016).

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