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RESEARCH ARTICLE

The Cenozoic history of New Zealand temperate rainforests: comparisons with southern Australia and South America

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ABSTRACT
The temperate rainforests of southern hemisphere continents share Gondwanan antecedents, but subsequent trajectories exhibit divergent patterns. We review the Cenozoic history of major forest elements (c. 30 genera/families) of the temperate rainforests of New Zealand and compare these with South America and southeast Australia. From macro- and microfossil evidence, the major structural components of temperate rainforests in New Zealand have lineages dating back almost continuously to the Eocene or earlier. These include the tree ferns (*Cyathea* and *Dicksonia*), *Agathis*, all but one of the podocarps, Nothofagaceae and other broadleaved genera such as Lauraceae and Cunoniaceae. Collectively these taxa contribute approximately 50% of current biomass in New Zealand temperate forests. However, several previously important groups in the Cenozoic such as *Araucaria*, the *Brassospora*-type beeches, and Casuarinaceae became extinct in New Zealand in the Miocene to Pleistocene. Patterns of extinction are broadly similar in New Zealand and South America (mostly late Miocene to Pleistocene) in response to climate cooling along steepened environmental gradients whereas in southern Australia taxa became extinct later (Pleistocene) reflecting limited suitable habitat during glacials. The deep-time continuity evident in the composition of New Zealand temperate rainforests was not influenced by the decrease in land area during the maximum marine transgression in the late Oligocene (c. 25–24 million years ago). Forest canopy dominants and emergents appear to have remained remarkably stable, perhaps reflecting community resilience. However, new subcanopy and open habitat lineages arrived as forest taxa were extirpated and climates cooled, reducing potential forest habitats.

Introduction

The southern hemisphere, and particularly New Zealand, has played a significant part in disentangling the role of evolutionary, ecological and biogeographical processes involved in the formation of terrestrial ecosystems. Although isolated by more than 1500 km from other landmasses for much of the Cenozoic, New Zealand temperate rainforests share

many plant lineages with southeast Australia and South America, reflecting a common Gondwanan heritage (Wardle 1991). However, recent perspectives on the antiquity and assembly history of New Zealand temperate rainforests have been influenced by the suggestion that the New Zealand landmass may have been completely submerged at some time in the Oligocene/early Miocene (Pole 1994, Landis et al. 2008). Although there is evidence of Neogene long-distance dispersal for some plant groups (Pole 1994; Jordan 2001; Sanmartin & Ronquist 2004), mostly from Australia or South America, the cumulative geological evidence overwhelmingly supports persistent terrestrial environments throughout the Cenozoic (Lee et al. 2014; Mildenhall et al. 2014b). Focus on the period of maximum marine inundation in New Zealand has, in our view, overemphasised area as an important extinction or bottleneck filter in forest development but overlooks other potentially critical abiotic factors influencing the composition of modern forests. Understanding the roles of vicariance, climate, geography, extinction and diversification is essential for explaining forest biome evolution in New Zealand during the Cenozoic.

Our knowledge of the Cenozoic history of temperate rainforests in New Zealand has improved with the investigation of new sites containing leaves with cuticular preservation (and occasionally flowers with in situ pollen, fruits, seeds and wood) (e.g. Ferguson et al. 2010; Lee et al. 2012; Conran et al. 2014). This, when combined with the excellent New Zealand Cenozoic palynological record (Raine et al. 2011; Mildenhall et al. 2014b and references therein), makes it possible to reconstruct the composition of forest vegetation through time with an accuracy rarely available elsewhere over macro-evolutionary time-scales. Similar advances in southeast Australia and South America enable us to compare trajectories of rainforest assembly across these southern continents. The fossil record shows high levels of persistence of woody flowering plants within continental landmasses through the Cenozoic globally (Xing et al. 2015), in particular of Gondwanan rainforest plant lineages, with different lineages culled in different places (Kooyman et al. 2014). Though plant molecular phylogenies are yielding new perspectives on the origin and diversification of floras, they show large potential errors for the timing of significant events and often having a systematic 'young bias' for many plant clades (Wilf & Escapa 2014). We therefore focus on the fossil record.

These southern hemisphere temperate rainforests contrast with counterparts in the northern hemisphere, occupying smaller and more discrete landmasses strongly influenced by oceanic conditions, continental breakup and orogenic activity. Although global climate cycles were important in the evolution of all contemporary forests, lineage composition and diversification patterns (Leslie et al. 2012), physiological tolerances (Bannister 2007), and inter-hemisphere biotic interchange (Morley 2000; Sniderman & Jordan 2011) have all contributed to understanding modern vegetation differences in forests of northern and southern hemispheres. However, much is still to be learned about the relative contribution of all of these processes in assembling the New Zealand biota.

In this review, we focus on southern hemisphere temperate rainforests in three geographic regions: New Zealand, southeast Australia/Tasmania and South America (Figure 1). Biogeographically these areas share many forest lineages but have divergent geographic and climatic histories, providing a suite of different scenarios for the evolution of their biotas. New discoveries of well-dated plant fossils and recent advances in phylogenetic analyses of some major plant groups enable a more thorough understanding of
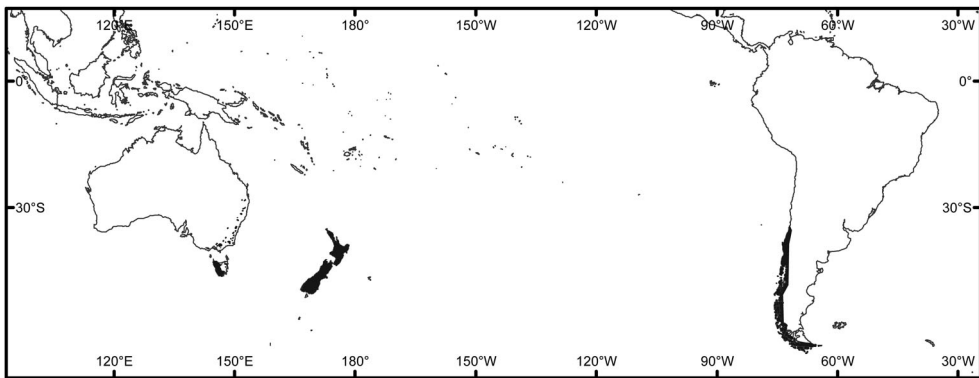
Figure 1. Distribution of temperate rainforest in New Zealand, South America and southeastern Australia.

forest evolution in these regions than was previously possible. The aim is to determine and compare factors influencing continuity and change in the formation of modern temperate rainforests, and how these forests have responded to contrasting settings in these three regions. The comparison across three continents was undertaken to understand the role of contingent factors in the evolution of extant New Zealand temperate rainforest. Historically, these rainforests have experienced a range of climatic conditions, including periods of marginally subtropical environments, particularly from the Eocene to the mid-Miocene.

For this study we investigate the history of c. 30 selected key forest families/genera of plants that represent important components of extant southern forests (Table 1; Figure 2), using evidence from the fossil record. These groups also have fossil records since at least the Eocene in the form of clearly identifiable pollen, leaves with cuticular preservation, wood and/or fruits. The integration of pollen and macrofossil data provides the most comprehensive fossil-based overview possible of vegetation change.

Temperate rainforest

Temperate rainforests grow in areas characterised by annual rainfall in excess of 800–1000 mm and a mean annual temperature between approximately 5 °C and 15 °C with variable seasonality. Because different terminologies for rainforest are used in the three regions, we will consider that the temperate rainforests of New Zealand are comparable to the latitudinally equivalent temperate forests of Australia and South America. Temperate rainforests occur throughout New Zealand today; they are dominated in northern New Zealand by *Agathis* and a range of emergent podocarps, and many broadleaved taxa such as *Beilschmiedia* and *Dysoxylum* (Wardle 1991). These northern rainforests have the greatest species diversity in New Zealand today. *Nothofagus* forests are widespread in cooler and drier regions, often extending to the treeline, especially in the South Island, and are typically species poor in comparison to the northern lowland forests. Conifers are present, and a fern understorey is common, with few grass or herb species (Wardle 1991) apart from sedges. New Zealand temperate rainforests are extremely vulnerable to fire, and regeneration generally follows cyclonic and tectonic disturbance.

Table 1. Cenozoic time ranges for selected temperate rainforest taxa in New Zealand, South America and southeastern Australia based on micro- and macrofossil records.

Ferns		
Cyatheaceae	NZ	Triassic to Recent
	South America	Cretaceous to Miocene
	SE Australia	Cretaceous to Recent
Dicksoniaceae	NZ	Jurassic to Recent
	South America	Cretaceous to Recent
	SE Australia	Cretaceous to Recent
Lygodium	NZ	Paleocene; late Eocene to Recent
	South America	Paleocene to late Oligocene
	SE Australia	Cretaceous to Recent
Lophosoria	NZ	Cretaceous to Palaeogene
	South America	Cretaceous to Recent
	SE Australia	Cretaceous to Pleistocene
Araucarians		
Araucaria	NZ	Cretaceous to Miocene
	South America	Cretaceous to Recent
	SE Australia	Cretaceous to Pleistocene
Agathis	NZ	Cretaceous?; Oligocene to Recent
	South America	Palaeocene to Eocene
	SE Australia	Cretaceous?; Eocene to Pliocene
Dilwynites pollen type	NZ	Cretaceous to Miocene
	South America	Palaeocene to Eocene
	SE Australia	Cretaceous to Miocene
Podocarps		
Dacrycarpus	NZ	Palaeocene to Recent
	South America	Palaeocene to Miocene
	SE Australia	Eocene to Pleistocene
Dacrydium	NZ	Late Cretaceous to Recent
	South America	Late Cretaceous to Miocene
	SE Australia	Eocene to Miocene
Halocarpus	NZ	Eocene to Recent
	South America	no record
	SE Australia	Palaeocene to Miocene
Lagarostrobos	NZ	Cretaceous to Miocene
	South America	Late Cretaceous to Miocene
	SE Australia	Cretaceous to Recent
Lepidothamnus	NZ	Palaeocene to Recent
	South America	Pleistocene to Recent
	SE Australia	Eocene
Microcachrys	NZ	Cretaceous to Pleistocene
	South America	Cretaceous to Miocene
	SE Australia	Cretaceous to Recent
Phyllocladus	NZ	Eocene to Recent
	South America	no confirmed record
	SE Australia	Cretaceous to Recent
Podocarpus	NZ	Eocene? to Recent
	South America	Cretaceous to Recent
	SE Australia	Eocene to Recent
Prumnopitys	NZ	Palaeocene to Recent
	South America	Recent
	SE Australia	Eocene to Recent
Selected angiosperms		
Nothofagaceae		
Subgenus *Fuscospora*	NZ	Late Cretaceous to Recent
	South America	Late Cretaceous to Recent
	SE Australia	Late Cretaceous to Recent
Subgenus *Lophozonia*	NZ	Eocene to Recent
	South America	Late Cretaceous to Recent
	SE Australia	Late Cretaceous to Recent
Subgenus *Brassospora*	NZ	Eocene to Pleistocene
	South America	Paleocene? to Miocene

Table 1. Continued.

Ferns		
	SE Australia	Paleocene? to Pleistocene
Subgenus *Nothofagus*	NZ	Eocene to Miocene
	South America	Late Cretaceous to Recent
	SE Australia	Palaeocene to Miocene
Atherospermataceae *Laurelia*	NZ	Eocene to Recent
	South America	Eocene to Recent
	SE Australia	no record
Casuarinaceae *Gymnostoma/Allocasuarina*	NZ	Palaeocene to Pleistocene
	South America	Palaeocene to Eocene
	SE Australia	Palaeocene to Recent
Cunoniaceae *Weinmannia*	NZ	Oligocene to Recent
	South America	Palaeocene to Recent
	SE Australia	Oligocene to Miocene?
Lauraceae	NZ	Eocene to Recent
	South America	Paleocene to Recent
	SE Australia	Palaeocene to Recent
Meliaceae *Dysoxylum*	NZ	Oligocene to Recent
	South America	no record
	SE Australia	Eocene to Miocene
Myrtaceae *Eucalyptus*	NZ	Miocene to Pleistocene
	South America	Eocene
	SE Australia	Eocene to Recent
Onagraceae *Fuchsia*	NZ	Oligocene to Recent
	South America	Miocene to Recent
	SE Australia	Oligocene to Miocene
Paracryphiaceae *Quintinia*	NZ	Palaeocene to Recent
	South America	Oligocene to Pliocene
	SE Australia	Eocene to Recent
Winteraceae		
Pseudowintera	NZ	Palaeocene to Recent
Drimys	South America	Eocene to Recent
Tasmannia	SE Australia	Palaeocene to Recent

Temperate forests in South America occur in a narrow fringe along the Andean region of Argentina and Chile, from 38°30'S to 55°30'S. The rainforest region includes both evergreen (Valdivian, North Patagonian and Subantarctic) and deciduous forests. These forests are structurally complex, with an uncommonly high presence (for temperate forests) of woody vines and climbing shrubs (Arroyo et al. 1996). The Valdivian rainforest, mainly developed in Chile between 37°S and 43°S, with some extensions in western Argentina, is characterised by tree species of *Nothofagus*, *Laureliopsis*, *Weinmannia*, *Saxegothaea*, *Drimys* and *Podocarpus* (Cabrera & Willink 1973; Arroyo et al. 1996). In the understorey, there are several species of bamboo (*Chusquea*), diverse ferns and vines (Cabrera & Willink 1973; Arroyo et al. 1996; Roig 1998). North Patagonian (43°–47°S) and Magellanic (47°–55°S) rainforests are less diverse and simpler versions of the Valdivian rainforest (Arroyo et al. 1996). The deciduous forests develop at higher altitudes within the evergreen forests and at the eastern margins of the Andes where precipitation is less. They constitute open and discontinuous stands composed mainly of *Nothofagus antarctica* and *Nothofagus pumilio*, with *Austrocedrus chilensis* in the northern part (between 40 and 41°S) forming xerophytic forests.

The temperate rainforests of southeastern Australia (Tasmania, Victoria and New South Wales) are markedly species poor, mostly being dominated by *Nothofagus*
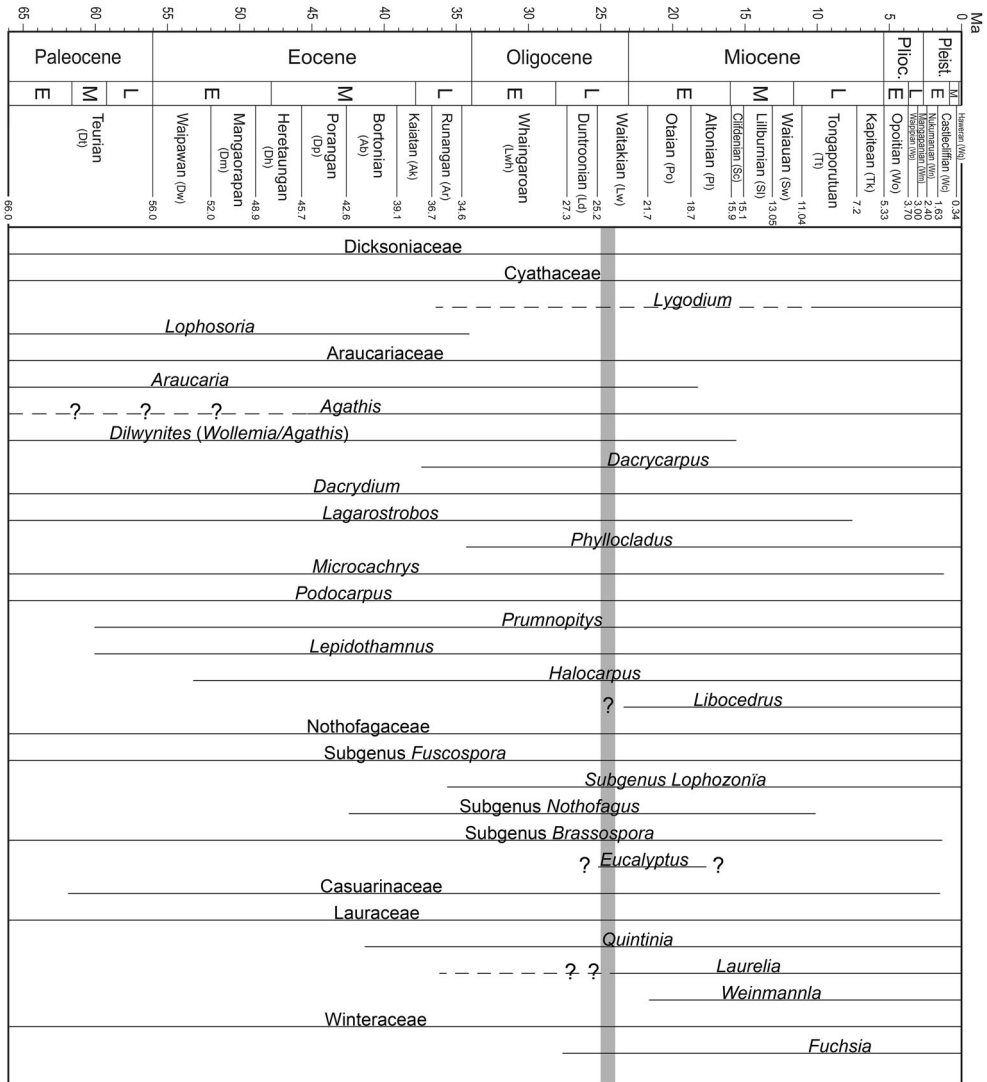
Figure 2. Cenozoic time ranges for selected temperate rainforest taxa in New Zealand based on micro- and macrofossil records. The grey bar indicates the period of minimum land area in the late Oligocene.

cunninghamii or *Atherosperma moschatum* with a small but disparate set of other species (such as *Phyllocladus*, *Eucryphia*, some Ericaceae, some Proteaceae). The richest temperate rainforests in terms of both species numbers and phylogenetic diversity are conifer-dominated forests that are mostly restricted to high-altitude areas of western Tasmania. This paucity of rainforest species may be related to climatically driven extinctions over the Pleistocene (Jordan 1997). However, there are also extensive areas of fire-dependent mesic forests dominated by *Eucalyptus* species with understoreys of rainforest species and/or specialist 'wet sclerophyll' species especially from *Acacia*, Asteraceae, Rhamnaceae, Ericaceae and Rutaceae.

Modern forests in New Zealand

Today, indigenous rainforests cover 23% of the land surface of New Zealand (Wardle 1991), although they are much reduced following the arrival of humans about 700 years ago (Wilmshurst et al. 2008). Although tree species typically have broad ecological tolerances (Wardle 1991), these forests can be subdivided into five major groups: (1) broadleaved-conifers (c. 39% of total extant forest); (2) beech-broadleaved (20%); (3) beech–broadleaved–conifers (c. 17%); (4) beech (14%), and (5) broadleaved (10%) (Richardson et al. 2009).

Conifers—New Zealand is a recognised centre of diversity of southern hemisphere conifers, with 10 genera and 21 species in the modern flora, many of which are ecological dominants (Wardle 1991). It includes one genus of Araucariaceae (*Agathis*), one of Cupressaceae (*Libocedrus*) and eight of Podocarpaceae (*Dacrycarpus*, *Dacrydium*, *Halocarpus*, *Lepidothamnus*, *Manoao*, *Phyllocladus*, *Podocarpus* and *Prumnopitys*). All species and two of the genera (*Halocarpus* and *Manoao*) are endemic: five of the genera include multiple, closely related species. However, debate continues as to whether New Zealand conifers are relicts of an ancient, more diverse conifer flora, or relatively recent arrivals (Jordan et al. 2011; Kooyman et al. 2014).

Broadleaved angiosperms—Broadleaved species characteristically form forest canopies throughout New Zealand. Lauraceae (*Beilschmiedia*), *Hedycarya* (Monimiaceae), *Laurelia* (Atherospermataceae) and *Dysoxylum* (Meliaceae) are common in warmer, northern forests, while *Weinmannia* (Cunoniaceae), *Metrosideros* (Myrtaceae), *Melicytus* (Violaceae) and *Pseudopanax* (Araliaceae) are found throughout New Zealand.

Nothofagus—The most widespread beech species is *Nothofagus menziesii* (subgenus *Lophozonia*), followed by the *Fuscospora* species (*Nothofagus fusca*, *Nothofagus solandri* and *Nothofagus truncata*). All are canopy-forming in either monodominant forests, congeneric mixtures, or with broadleaved and conifer species (Wardle 1984).

Ferns—New Zealand is well known for its abundance and variety of ferns which, including several tree ferns, comprise about 7.5% of the indigenous vascular flora (Brownsey & Perrie 2013) and form a major component of the understorey in our temperate rainforests (Brownsey & Smith-Dodsworth 2000).

The genera and families included in this study are listed in Table 1 and Figure 2. Collectively, the taxa listed that are extant in New Zealand represent about 50% of the living biomass and individual stems in a modern, systematic sample of New Zealand temperate rainforests (Peltzer et al. 2009; Richardson et al. 2009). All have well-documented fossil records in New Zealand, South America and/or southeastern Australia. A few other small trees such as *Fuchsia* (Onagraceae) and *Pseudowintera* (Winteraceae) are included because of their fossil record and biogeographical importance. We omit other widespread small trees such as *Melicytus* and *Pittosporum* as their fossil record is poorly understood.

Cenozoic fossil records in New Zealand, South America and southeastern Australia

Ferns: tree ferns

The extant New Zealand tree ferns (seven species of *Cyathea*—one of which extends to Australia and another to several Pacific Islands—and three *Dicksonia* species, all

endemic) are distinctive components of forests throughout New Zealand (Large & Braggins 2004). Both genera now occur in Australia and South America, and have fossil records (mostly of spores, but also some macrofossils) extending well back into the Mesozoic (Large & Braggins 2004).

Recent work on fern fossils from sites such as the late Eocene Pikopiko Fossil Forest (Homes et al. 2015) suggests that tree ferns (and other ferns) have been important in New Zealand rainforests throughout the Cenozoic. The flora includes the spore *Cibotiidites tuberculiformis*, which has affinities to *Dicksonia squarrosa* and a continuous record in New Zealand from the Jurassic to Recent (Raine et al. 2011). Similar spores have been found in situ in a fossil frond fragment of *Dicksonia*, from the early Oligocene Little Rapid River site in Tasmania (Jordan et al. 1996). Such spores also occur in southern Australia throughout the Cretaceous and Palaeogene and are produced by species still present in subtropical to tropical Australia. They occur in South America until the Miocene. *Matonisporites ornamentalis*, the spore with affinities to the Australian tree fern, *Dicksonia antarctica*, is present in the New Zealand Palaeogene (Raine et al. 2011) and occurs widely in South America until the Miocene (Kooyman et al. 2014, and references therein). Similarly, macrofossils of *Dicksonia* occur in early and middle Eocene sites in Patagonia (Carvalho et al. 2013).

Cyathidites minor, which has a Triassic to Neogene record in New Zealand, is likely to represent Cyatheaceae (Cieraad & Lee 2006; Raine et al. 2011). Fossil evidence from Patagonia reports *Cyathea* megafossils (*Cyathea cyathifolia*) from the Early Cretaceous (Archangelsky et al. 2003). Cenozoic reports of Cyatheaceae are restricted to spores. Several species of *Cyathidites* that resemble spores of extant Cyatheaceae are widely documented from the Late Cretaceous to the Miocene (Kooyman et al. 2014, and references therein). *Cyathea* spores are present from the Cretaceous to today in Australia (Dettmann 1994; Macphail et al. 1994).

Lygodium *and* Lophosoria

Two other distinctive fossil ferns with records from all three regions are *Lophosoria* (Dicksoniaceae) and *Lygodium* (Lygodiaceae). *Lygodium articulatum* is the only climbing fern in New Zealand, where it occupies an altitudinal range from sea level to 950 m (Brownsey & Perrie 2014). Macrofossils of *Lygodium* are known from the Palaeocene of New Zealand (Rozefelds et al. 1992; Pole 2012). Spores resembling *Lygodium articulatum* have been reported from the late Eocene (Edwards 1991), and more certainly from late Miocene to present day (Mildenhall & Suggate 1981). In southeastern Australia *Lygodium* is represented in the early and middle Eocene as macrofossils with in situ spores (Rozefelds et al. 1992; Carpenter et al. 2012) and spores (Macphail et al. 1994). In southern South America the genus is represented by macrofossils from the Palaeocene (Iglesias et al. 2007) and spores from late Oligocene sites (Barreda 1997a; Barreda et al. 2003).

Lophosoria quadripinnata (Lophosoriaceae) is a dominant forest floor fern from Patagonia to Central America but is absent outside the Americas. However, this is the only extant species that produces spores comparable to *Cyatheacidites annulata* (Dettmann 1986), which has a record in New Zealand from the Cretaceous to Palaeogene. This spore type is common in Patagonia from the Cretaceous to latest Miocene (Kooyman et al. 2014, and references therein) and in a highly broken range in Australia–Late

Cretaceous, and then from the Oligocene (Hill et al. 2001) to the early Pleistocene (Sniderman 2011).

Gymnosperms—Araucariaceae, Podocarpaceae and Cupressaceae

Araucariaceae—Wood, foliage, leaves with cuticle preserved and two pollen types attributable to Araucariaceae occur at many fossil sites throughout New Zealand. The wind-dispersed pollen grains of extant Araucariaceae (*Agathis*, *Araucaria* and *Wollemia*) are morphologically similar and difficult to distinguish (Pocknall 1981; Macphail & Carpenter 2013), a problem exacerbated by degradation (Kershaw & Wagstaff 2001; Dettmann & Clifford 2005). *Araucariacites australis* is a ubiquitous araucarian pollen type that has been noted in New Zealand, South America and Australia from the Cretaceous to Recent (Raine et al. 2011). *Dilwynites granulatus*, possibly associated with *Wollemia*, is recorded in New Zealand from the Cretaceous through to the early Miocene (Cantrill & Raine 2006; Raine et al. 2011), as well as in Australia. In Patagonia, *Dilwynites* pollen is only recorded from the late Palaeocene–middle Eocene, coinciding with the records of *Agathis* macrofossils (Macphail et al. 2013; Wilf et al. 2014). The earliest record of pollen attributed to modern *Agathis australis* is from various Pliocene and Pleistocene sites in the Coromandel (Mildenhall 1985).

Putative records of *Agathis* in New Zealand have been the subject of much debate (Knapp et al. 2007), with Hill & Brodribb (1999) excluding all fossil *Agathis* species from New Zealand. However, Lee et al. (2007) subsequently identified well-preserved leaves from the late Oligocene–early Miocene site in the Gore Lignite Measures at Newvale Mine, Southland, as *Agathis* although Wilf et al. (2014, 159) considered that they may possibly represent 'a species of Araucariaceae outside of *Agathis*'.

Distinctive araucarian foliage is commonly present in Late Cretaceous floras at Shag Point, Kaitangata (Pole & Douglas 1999), Pakawau (Ettingshausen 1891) and Roa Mine near Greymouth. A log with well-preserved wood identified as araucarian occurs at a Palaeocene site in Otago (Lindqvist 1986), and silicified araucarian logs are present in the late Oligocene. Araucarian bark is preserved at the Eocene Pikopiko Fossil Forest site (Lee et al. 2012), and leaves with cuticular preservation assigned to *Araucaria* s.s. were described by Pole (2008) from various Eocene and Miocene sites. *Araucaria* appears to have become extinct in the region in the late Miocene.

In Patagonia, the family first appears in the early Jurassic and reaches its maximum diversity and geographic extent in the Early Cretaceous (Panti et al. 2012). From the Late Cretaceous to the present day Araucariaceae began to decline in abundance, diversity and geographic distribution. Macrofossils represented by leaves and reproductive structures are also widely distributed in both northern and southern Patagonia (Panti et al. 2012, and references therein). The presence during the Eocene of *Araucaria* section *Eutacta*, today restricted to Australia, New Caledonia and New Guinea, is noteworthy. *Agathis* was also present in the early and middle Eocene (Wilf et al. 2014).

Although neither *Araucaria* nor *Agathis* are extant in southern Australia, both genera have long and rich fossil records in the region. Araucarian wood is present in the Jurassic (Bromfield et al. 2007), and Araucariaceae pollen occurs as far back as the Early Cretaceous (Macphail et al. 1994), disappearing finally in the early Pleistocene (Sniderman 2011). Macrofossils of *Agathis* occur from the middle Eocene (or more contentiously, the Late

Cretaceous) to the early Miocene (Hill & Brodribb 1999). Macrofossils of a diverse range of *Araucaria* species occur from the Cretaceous to the early Miocene and at least one extinct genus of the family was present (Hill & Brodribb 1999).

Podocarpaceae—New Zealand has a long and extensive fossil record of podocarps, mainly based on pollen, but including well-preserved macrofossils at a number of sites. A few taxa are now regionally extinct (e.g. *Microcachrys* and *Lagarostrobos*) but others are still major components of New Zealand forests. For example, the late Oligocene–early Miocene Newvale fossils include foliage with cuticular preservation of at least six genera and nine species of podocarps. These include the first macrofossil record of the New Zealand endemic genus, *Halocarpus*, as well as species of *Dacrycarpus*, *Dacrydium*, *Microcachrys*, *Phyllocladus* and *Podocarpus* (Ferguson et al. 2010; Carpenter et al. 2011; Jordan et al. 2011). In addition, the same leaf bed has yielded 12 conifer pollen types consistent with *Phyllocladus*, *Dacrycarpus*, *Dacrydium*, *Microcachrys* and *Podocarpus* and/or *Prumnopitys*. Only *Lagarostrobos franklinii* is not yet represented by macrofossils.

Dacrycarpus, which today has nine species ranging from New Zealand to New Caledonia, Fiji and New Guinea to south China, first appears in the New Zealand pollen record in the late Eocene (c. 37 Ma) (DC Mildenhall, pers. comm. 2015). Characteristic *Dacrycarpus* foliage is present at Newvale Mine (Jordan et al. 2011) and in the early Miocene Manuherikia Group (Pole 2012). Pole & Vajda (2009) reported *Dacrycarpus*-like cuticles in the Palaeocene. In Australia, the genus had a diverse and geographically extensive fossil record of both pollen and macrofossils from the Eocene through to the Miocene, and disappeared in the Pleistocene (Hill & Brodribb 1999). In South America, *Dacrycarpus* pollen is known from the Palaeocene to Miocene (Barreda & Palazzesi 2007; Kooymann et al. 2014). Macrofossils occur from the Eocene to early Miocene (Panti et al. 2008; Falaschi et al. 2012; Wilf 2012, and references therein).

The current distributions and fossil records of *Dacrydium* are similar to those of *Dacrycarpus*. *Dacrydium* first appears in the New Zealand pollen record in the Late Cretaceous (DC Mildenhall, pers. comm. 2015), and is present as foliage in the late Oligocene. The genus has a geographically extensive fossil record of both pollen and macrofossils from the Eocene through to the Miocene in Australia (Hill & Brodribb 1999). Pollen is common through the Palaeogene to Miocene in South America (Barreda & Palazzesi 2007; Del Fueyo et al. 2007).

Phyllocladidites mawsonii, the pollen attributed to the Tasmanian endemic genus *Lagarostrobos*, had a very long record in New Zealand, first appearing c. 93 Ma in the Late Cretaceous, and disappearing in the late Miocene. This pollen type is more or less ubiquitous in Late Cretaceous and Palaeogene assemblages across the southern hemisphere. However, there is a question mark about the closeness of the link between this pollen and *Lagarostrobos*. The extant species of *Lagarostrobos*, *Lagarostrobos franklinii*, is ideal for preservation—the foliage is strikingly over-represented in modern riverine litter samples and occurs abundantly in Pleistocene sediments (Jordan 1992). However, there are no pre-Pleistocene macrofossils of this genus even in assemblages that contain both *Phyllocladidites mawsonii* at high levels (often up to 50% of the pollen count) and many macrofossils of other conifers. A single macrofossil record attributed to *Lagarostrobos* is likely to be *Manoao*, and was described as *Lagarostrobos* only because the description was made before *Manoao* was recognised as a genus (Hill & Brodrib 1999).

In New Zealand, pollen of *Phyllocladus* first appears near the Eocene–Oligocene boundary whereas the earliest record of leaves is in the late Oligocene. In Australia, fossil pollen attributed to *Phyllocladus* ranges from Late Cretaceous to present, and macrofossils are common from the mid- to late Eocene to the Pleistocene (Jordan 1995; Hill & Brodribb 1999). There are no confirmed records of *Phyllocladus* in South America.

As with *Lagarostrobos*, the pollen of the ancient Tasmanian relict *Microcachrys* occurs widely in late Mesozoic and Palaeogene sediments across the southern hemisphere (Mildenhall & Byrami 2003; Barreda & Palazzesi 2007). Foliage of *Microcachrys* from the late Oligocene Newvale Mine site provides the oldest and first extra-Australian macrofossils (Carpenter et al. 2011). Based on pollen, several species probably lived in New Zealand from the early Cretaceous through the Cenozoic, finally becoming extinct locally in the early Pleistocene (Mildenhall & Byrami 2003).

The pollen and macrofossil records of the large genus, *Podocarpus*, are slightly problematic because of some ambiguity about their identity. This can partly be attributed to the apparently convergent similarity of *Podocarpus* and *Prumnopitys* pollen (Macphail et al. 1994), as molecular data and morphology indicate that these genera belong to different major clades in the family (Leslie et al. 2012). However, some fossils are clearly attributable to *Podocarpus*, and some are ambiguous. In this context *Podocarpus*-type pollen (e.g. *Podocarpidites ellipticus*) first appears in the New Zealand record in the Cretaceous and extends to the present (Raine et al. 2011). *Podocarpus-type* pollen is recorded from the Maastrichtian to the present in South America (Kooyman et al. 2014), and fossil leaves related to *Podocarpus* are present from the Eocene to the Miocene (Césari et al. 2015 and references therein). Large leaves that resemble modern Queensland species were present briefly in the early Miocene (Pole 1993b). *Prumnopitys* pollen was first identified from the Palaeocene of New Zealand at 60 Ma (DC Mildenhall, pers. comm. 2015). Reliable macrofossil records from Australia commence in the early Eocene (Carpenter et al. 2012) and extend to the present. However, there are numerous unpublished records of *Podocarpus*-like leaves.

Lepidothamnus pollen has been identified in New Zealand from the Palaeocene (c. 60 Ma). The genus is recorded once in Australia from the middle–late Eocene in Tasmania (Hill & Brodribb 1999), and from the Pleistocene in South America (Heusser et al. 1995).

The first macrofossils of *Halocarpus* appear at the late Oligocene Newvale site but pollen is present in the New Zealand record from the early Eocene (c. 55 Ma) (DC Mildenhall, pers. comm. 2015). The Australian record includes pollen that may belong to *Halocarpus* ('*Halocarpus bidwillii*-type') from the Palaeocene to early Miocene (Macphail et al. 1994).

In summary, all of the extant New Zealand podocarp genera except *Manoao* are now represented in the local fossil record as pollen and/or as macrofossils (leaves with cuticle) by the Eocene to late Oligocene (Jordan et al. 2011); the apparent absence of *Manoao* could be an artefact as the pollen of this species is morphologically similar to both *Podocarpus* and *Prumnopitys* and is only segregated from those taxa in Quaternary samples. In addition, several podocarp genera such as *Lagarostrobos* and *Microcachrys* that had a long history in New Zealand are now locally extinct.

Cupressaceae—The only member of the Cupressaceae living in New Zealand today is *Libocedrus*, native to New Zealand and New Caledonia and closely related to the South American genus *Pilgerodendron* (Leslie et al. 2012). Dispersed cuticle attributed to *Libocedrus* is recorded in New Zealand from the early Miocene Gore Lignite Measures (Pole

2007). Southern Australia has a rich record of macrofossils of Cupressaceae, including *Libocedrus* (e.g. Hill & Brodribb 1999). The southern South American macrofossil record includes *Papuacedrus* (now only in New Guinea) from the Eocene and *Athrotaxis* (now only in Tasmania) from the Late Cretaceous (Del Fueyo et al. 2008; Wilf et al. 2009). The fossil pollen record is problematic because of a lack of differentiation in pollen types across the family, and also poor preservation of this fragile pollen.

Nothofagus

Nothofagus pollen is recorded in New Zealand from the Campanian to present day. Further investigation is needed to unravel the pollen records of the various subgenera, but *Nothofagidites senectus* 'ancestral-type') first appears in New Zealand in the early Campanian and various as yet undescribed *Nothofagidites* species with generalised '*fusca*-group' morphology are present in the Late Cretaceous (JI Raine, pers. comm. 2015). The record of *Nothofagidites asperus* (subgenus *Lophozonia*) extends from the late Eocene, and the first appearance of pollen of *Nothofagidites flemingii* (subgenus *Nothofagus*) is mid Eocene (JI Raine, pers. comm. 2015). The *Brassospora*-type beeches appear at a similar time, but if *Nothofagidites kaitangataensis* is indeed an early *Brassospora* type, then the New Zealand record extends back to the mid-Campanian. Leaves of *Brassospora* beech with cuticular preservation occur at Newvale Mine (Carpenter et al. 2014), and others resembling modern New Caledonian species occur at a new Miocene–Pliocene site near Auckland. *Brassospora*-type pollen disappears in the Pleistocene.

Subgenus *Nothofagus* is recorded in southern South America from the Maastrichtian to present with a marked increase in abundance and species number during the late Eocene–early Miocene (Romero & Zamaloa 1997). Subgenus *Fuscospora* is recorded in Patagonia from the Maastrichtian to Miocene on the basis of pollen (*Nothofagidites saraensis*); *Nothofagus alessandri* (the only extant South American representative of *Fuscospora*) is today restricted to central Chile. Subgenus *Lophozonia*, although scarce, is recorded from Maastrichtian to present (Romero & Zamaloa 1997). Subgenus *Brassospora* was represented from the Palaeocene to the early Miocene (Romero & Zamaloa, 1997; Barreda et al. 2012). Macrofossils (leaf impressions) indicate the presence of large-leaved Nothofagaceae in the Palaeocene (Iglesias et al. 2007) and three of the four extant subgenera (*Lophozonia*, *Fuscospora*, *Nothofagus*) in the Eocene, Oligocene and Miocene of southern Patagonia where the family dominates the austral forests (Brea 1993; Gandolfo 1994; Pujana 2009b; Brea et al. 2012; Césari et al. 2015; Pujana et al. 2015).

Macrofossils of all four subgenera of *Nothofagus* occur in the Oligocene and Miocene of Tasmania (Hill 2001) and pollen of all four groups from the Late Cretaceous (Dettmann 1994). Two of the subgenera (*Lophozonia* and *Fuscospora*) still persist in Tasmania, and one (*Lophozonia*) extends to mainland Australia. Subgenus *Brassospora* disappeared from southern Australia in the early Pleistocene (Sniderman 2011), and the South American subgenus, *Nothofagus*, is last known from the Miocene (Hill 2001).

Myrtaceae—Eucalyptus

Myrtaceae pollen is abundant across New Zealand, Australia and South America throughout the Cenozoic. However, there is low differentiation among pollen types of the different

members of the family (Thornhill et al. 2012), and pollen can only rarely be assigned with confidence to *Eucalyptus*, although such pollen is present in Australia from the early Eocene (Macphail et al. 1994). Leaves and reproductive structures that resemble *Eucalyptus* are present in the early Miocene of Central Otago (Pole 1993a, 2012). Fossil leaves, infructescences, capsules and flower buds of *Eucalyptus* from the early Eocene of Patagonia represent the oldest macrofossil record of *Eucalyptus* and the sole evidence of this genus outside Australasia (Gandolfo et al. 2011). Pollen grains of Myrtaceae have been widely reported in southern South America during the Cenozoic, but none can be related to any extant genus with confidence. *Eucalyptus* macrofossils are surprisingly rare in Australia, partly for preservational reasons (Carpenter & Horwitz 1988). There are macrofossils that may be *Eucalyptus* both from sediments that are likely to be early Eocene of Queensland (not in southern Australia), and from middle Eocene sediments in central Australia: more compelling macrofossils occur from the latest Oligocene (Rozefelds 1996).

Casuarinaceae

Casuarinaceae, today confined to Australia, some Pacific Islands and South East Asia, had a much wider past geographic distribution in former Gondwana landmasses. Pollen evidence indicates that this family was widespread in New Zealand from the early Palaeocene to Pleistocene (Raine et al. 2011), with abundant *Gymnostoma*-like 'cones' present in some Oligocene–Miocene deposits (Campbell & Holden, 1984) and *Allocasuarina* from the Miocene of Lake Manuherikia (Pole 2012). Macrofossil stems assigned to *Gymnostoma* are common at Newvale (Ferguson et al. 2010).

Pollen grains of Casuarinaceae (*Haloragacidites harrisi*) were reported in southern and central Patagonia from the late Maastrichtian to Eocene (Archangelsky 1973; Zamaloa & Andreis 1995; Barreda et al. 2012), with Eocene records from central and southern Chile (Doubinger & Chotin 1975; Palma Heldt 1980). Macrofossils of Casuarinaceae originally reported by Frenguelli (1943) from the Eocene Laguna del Hunco locality were assigned to *Casuarina patagonica*. New collections indicate that these fossils are related to extant *Gymnostoma*, and Zamaloa et al. (2006) defined three fossil species on the basis of infructescences, staminate inflorescences and leaves.

Casuarinaceae is common in Australian fossil assemblages, with a conspicuous pattern emerging from the macrofossil record: *Gymnostoma*, which is mostly a rainforest clade, is common from the Palaeocene to the Oligocene and is then replaced by *Allocasuarina* or *Casuarina* (Scriven & Hill 1995). Although these genera can occur in very wet climates, they are more conspicuous in dry climates, have the xeromorphic feature of encrypted stomata (Hill 1994) and typically occur in open vegetation usually with fire.

Lauraceae

Most species in this largely tropical family of trees and shrubs belong to the large genera *Beilschmiedia*, *Litsea*, *Cryptocarya* and *Cinnamomum*. In New Zealand today, Lauraceae comprise just five species in three genera, two of which are leafless hemiparasitic vines. The fossil record is primarily of leaves because the pollen is small, fragile and rarely preserved (Bannister et al. 2012). However, recent study of the remarkable early Miocene flora

preserved at Foulden Maar demonstrates that Lauraceae were once much more diverse locally with at least 10 species in three genera dominating the vegetation in one small area (Bannister et al. 2012). Lauraceae leaves, including some with preserved cuticle, are present at many Eocene and Oligocene localities, suggesting that the family formerly played a much more important role in the New Zealand rainforest flora.

The presence of Lauraceae in southern South America is confirmed during the Palaeogene and early Neogene by the presence of abundant fossil leaves in both Argentina and Chile (Troncoso et al. 2002; Iglesias et al. 2007; Césari et al. 2015, and references therein). Similarly, Lauraceae leaves or cuticles are almost ubiquitous in southeastern Australian macrofossil assemblages from the Palaeocene to early Pleistocene, although many are undescribed. These include a diverse range of forms and are likely to represent multiple genera.

Paracryphiaceae—Quintinia

Quintiniapollis psilatispora, the pollen of *Quintinia*, a genus of about 20 evergreen trees or shrubs native to New Zealand, Malesia, New Caledonia and Australia, ranges from the middle Eocene to the present day in New Zealand (Mildenhall & Pocknall 1989). *Quintiniapollis* is recorded in late Oligocene to Miocene sequences of southeastern Patagonia (Barreda 1997b; Barreda & Palamarczuk 2000) and in the Oligocene–early Pliocene Forest Bed in the Falkland Islands (Macphail & Cantrill 2006). In Australia similar pollen is reported from ?Eocene to present (Martin 1973). Fossil *Quintinia* leaves occur in early Pleistocene sediments in Tasmania, and, remarkably, are more closely allied to the New Zealand species than to the subtropical–tropical Australian species (Jordan 1997).

Atherospermataceae—Laurelia

Atherospermataceae is a small family that occurs today in temperate and tropical rainforests of New Zealand, Australia, New Caledonia, New Guinea and Chile. *Laurelia* today contains just two species, one endemic to New Zealand and the other to Chile. Recently, fruits and leaves with cuticular preservation assigned to a new species of *Laurelia* were described from the early Miocene Foulden Maar site (Conran et al. 2013). *Laurelia/Laureliopsis* leaf impressions were reported from the Eocene Laguna del Hunco and Río Pichileufú sites (Berry 1935; Knight & Wilf 2013). Fossil woods of Atherospermataceae (*Laurelites doroteaensis*) were reported from the late Oligocene in southern Patagonia (Pujana 2009a) and the mid Cenozoic of southern Chile (Nishida et al. 1992).

Cunoniaceae—Weinmannia

Weinmannia is a large genus of about 200 species distributed from Madagascar and Malesia to New Zealand. and from Mexico to Chile (Dawson & Lucas 2011). *Weinmannia* is the most widespread canopy forest tree in New Zealand today and has a macrofossil record dating back to at least the earliest Miocene (JM Bannister, pers. comm. 2015).

In Australia, fossil *Weinmannia* leaves have been found in late Eocene and Oligocene sites (Barnes et al. 2001), and tricolporate Cunoniaceae pollen consistent with the genus (and others) occurs from Palaeocene to present. Similar pollen occurs in South America

from the Palaeocene, Miocene and Holocene in southern South America (Zetter et al. 1999; Villagrán & Hinojosa 2005). There are also reports of Cunoniaceae macrofossils from the Palaeocene and Eocene of Patagonia, including woods (*Weinmanoxylon*) and fruits: some have close similarities with extant *Weinmannia* (Petriella 1972; Raigemborn 2008; Wilf et al. 2014).

Winteraceae

This family comprises aromatic evergreen trees or shrubs whose wood lacks vessels (Heywood et al. 2007), and with a disjunct southern hemisphere distribution from Madagascar, Malesia, New Caledonia, Australia, South America and New Zealand. It has a long fossil record extending back to the Late Cretaceous (Doyle 2000). Three closely related genera are geographically distributed in present day South America (*Drimys*), southern Australia (*Tasmannia*) and New Zealand (*Pseudowintera*).

The distinctive pollen of Winteraceae (*Pseudowinterapollis*) first appears in New Zealand in the Late Cretaceous (Mildenhall & Crosbie 1979 [1980]). Leaves of *Pseudowintera* with excellent cuticular preservation are present in the earliest Miocene Foulden Maar, together with other genera of Winteraceae now restricted to New Caledonia (Pole 1996; JM Bannister, pers. comm. 2015).

The oldest records of this family in southern Patagonia are Albian pollen tetrads of *Walkeripollis* (related to Winteraceae) (Barreda & Archangelsky 2006). Pollen grains related to *Drimys* (*Pseudowinterapollis couperi*) are common in Patagonia from the Eocene to Miocene particularly in the south (Barreda 1997a; Olivero et al. 1998; Zamaloa 2000). Macrofossil records are restricted to leaves (*Drimys patagonica*) from the Eocene of northern (Berry 1938) and southern (Hunicken 1967) Patagonia. *Pseudowinterapollis* also has a long record in southern Australia, first appearing in the Campanian and continuing until today (Macphail et al. 1994).

Onagraceae (Fuchsia)

Fuchsia today has an unusual biogeographic pattern. Four species, including the tree fuchsia, occur in New Zealand, one in Tahiti, while the remaining c. 100 species are endemic to South and Central America. The distinctive diporate pollen has a continuous record in New Zealand from the late Oligocene to the present, and recently macrofossils were discovered at the earliest Miocene Foulden Maar site (Lee et al. 2013). Pollen grains of *Fuchsia* (*Crassiorites australis*) were reported from the Miocene to Holocene in southwestern Patagonia, but in low frequencies (Markgraf 1983; Zamaloa & Romero 1990). Fossil pollen is reported from the Oligocene and Miocene of Australia (Macphail 1999; Martin, 2003) where the genus is now extinct.

New Zealand temperate rainforests through time

Since it drifted away from the eastern margin of Gondwana about 83 million years ago, the New Zealand landmass has undergone major changes in land area, physiography, isolation and climate, which profoundly influenced the composition and richness of the vegetation and flora (Lee et al. 2001). The most significant of these are, first, the gradual reduction in

land area from c. 500,000 km^2 in the Palaeocene–Eocene, to a series of large islands with a minimum area of c. 20,000 km^2 (larger than New Caledonia today) at the peak of marine transgression in the late Oligocene, followed by an increase during the Miocene to near its present size of 270,000 km (Lee et al. 2014).

Second, isolation increased following final severance of probable land connections to northeastern Australia about 55 Ma, although volcanic and other islands continued to provide intermittent connections northward to New Caledonia (e.g. Ladiges & Cantrill 2007). Third, topographic relief became subdued as the landmass slowly subsided, resulting in weathered, perhaps infertile soils. Following inception of the new Pacific–Australian plate boundary in the late Oligocene, the landscape became topographically more varied with increasing tectonism (including localised volcanism) resulting in mountain-building reaching elevations of 1000 m by the late Miocene and 3000 m in the Pliocene. Finally, for much of this period, until the late Miocene, the climate was warm temperate to marginally subtropical, but always oceanic and mesic. Apart from localised, post-Pliocene rain shadows in eastern areas, New Zealand has retained mesic climates (Lee et al. 2001).

From the Palaeocene through to the Pleistocene, New Zealand had extensive rainforest: evidence for this comes from the continuous and geographically representative palynological record (Mildenhall 1980; Raine et al. 2011; Mildenhall & Raine 2012, and references therein) and from macrofossil records mainly from extensive swamps of late Eocene to mid Miocene age, and lake deposits (Lee et al. 2012; Pole 2012, and references therein).

Palaeocene to Eocene

Common angiosperm components of the early–middle Eocene vegetation of New Zealand included *Nypa*, (mangrove palm), Casuarinaceae, Cupaniae, *Bombax*, *Anacolosa*, numerous Proteaceae pollen types, Myrtaceae and Sapotaceae (Pocknall 1990). Pocknall (1989) noted that in the late Eocene and Oligocene angiosperm floras were dominated by Casuarinaceae, many Proteaceae, *Nothofagus* subgenus *Brassospora*, palms and myrtaceans; Lauraceae and Nothofagaceae are common at macrofossil sites. A diverse range of conifer pollen is present throughout.

Late Oligocene to mid Miocene

New Zealand has an exceptionally strong record of forest vegetation for the late Oligocene to mid Miocene, preserved in swamps, maar lake deposits (Foulden Maar) and the large inland palaeolake Manuherikia. A recent investigation of the palynoflora at a c. 24 Ma coastal site contemporaneous with late Oligocene marine transgression (Conran et al. 2014) listed more than 100 taxa including Araucariaceae and Podocarpaceae (*Dacrydium*, *Dacrycarpus*, *Lagarostrobos*, *Microcachrys*, *Phyllocladus* and *Podocarpus*) and 16 ferns including *Cyathea and Dicksonia*. The angiosperm palynoflora included numerous eudicots including Casuarinaceae, Cunoniaceae, Euphorbiaceae, Loranthaceae, Malvaceae, *Myrtaceae*, Nothofagaceae, Proteaceae and Strasburgeriaceae. The predominance of rainforest tree pollen and fern spores suggests a regional warm temperate to marginally subtropical coastal forest and high rainfall.

Similarly, the 100,000 year long pollen record from the earliest Miocene Foulden Maar core (Mildenhall et al. 2014a) shows that vegetation immediately after maximum marine

transgression consisted of forest trees dominated by *Nothofagus* (*Brassospora*, *Fuscospora* and *Lophozonia*), Casuarinaceae, podocarps (*Dacrycarpus*, *Dacrydium*, *Phyllocladus*, *Microcachrys* and *Podocarpus/Prumnopitys*), araucarians, Myrtaceae, Proteaceae, Loranthaceae, Aquifoliaceae—*Ilex* with records of many other taxa including Arecaceae, Araliaceae, Euphorbiaceae (*Euphorbia* and *Mallotus/Macaranga*), Meliaceae, Monimiaceae (*Hedycarya*), Onagraceae (*Fuchsia*), Sapindaceae (*Cupania*) and Sapotaceae. The Foulden pollen record is complemented by thousands of leaves, 40% of which are Lauraceae (not represented in the pollen record; Bannister et al. 2012) as well as *Podocarpus travisiae* (Pole 1993b), Cunoniaceae, Elaeocarpaceae, Meliaceae, Myrsinaceae, Myrtaceae, Sapindaceae and Winteraceae (Pole 1996) and Proteaceae (Carpenter et al. 2012).

However, it is worth noting that non-rainforest vegetation also occurred in New Zealand in this period, with *Eucalyptus*, *Acacia*, *Banksia*, non-rainforest Casuarinaceae, *Persoonia* and the open-vegetation conifer *Microcachrys* (Carpenter et al. 2010a, 2010b, 2011; Pole 1993a, 2007, 2012). In particular, the presence of amphistomatic Proteaceae (a strong indicator of open vegetation; Jordan et al. 2014) is clear evidence for some open vegetation at the Newvale site.

Late Miocene

By the late Miocene to Pliocene, many of the rainforest and other warm climate trees had vanished from New Zealand. They include *Araucaria*, the *Dilwynites* source tree, several palms, *Ephedra*, *Lagarostrobos*, large-leaved *Podocarpus*, *Cryptocarya*, *Cupania*, Sapotaceae, Aquifoliaceae—*Ilex*, *Macaranga/Mallotus*, and most of the once numerous Proteaceae.

Pliocene to Pleistocene

During the 20 or so glacial–interglacial climate cycles that characterised the Pleistocene, temperate rainforests in New Zealand probably became restricted to the northern North Island and to local refugia in the South Island. Most information about the Pliocene to Pleistocene floras is derived from pollen (Newnham et al. 2013). A few rainforest groups with a long fossil record were extirpated in the Pleistocene (e.g. *Microcachrys*, Casuarinaceae, *Eucalyptus*, the last *Brassospora* beeches, and some Proteaceae such as *Beauprea*; Carpenter et al. 2012). Range expansion and contraction during this period seem to have caused few additional extinctions of forest trees.

South American temperate rainforests through time

The Cenozoic development of South American plant lineages was originally studied by Menéndez (1971), Romero (1993) and more recently by Barreda & Palazzesi (2007) and Palazzesi et al. (2014), among others.

Palaeocene to Eocene

The Palaeocene–early Eocene was characterised by warm-temperate climates; the sea level was high and key areas of southern South America were flooded. Pollen and macrofossils indicate that highly diverse rainforests were widespread in southern South America: they

were dominated by Araucariaceae and Podocarpaceae, but included both Australasian (e.g. *Agathis*, *Acmopyle*, *Dacrycarpus*, *Eucalyptus*, *Gymnostoma*) and Neotropical (e.g. Arecaceae, *Cupania* (Sapindaceae), Rubiaceae, Pandanaceae) taxa. The late Eocene, characterised by a progressive decrease in temperature, involved expansion of *Nothofagus* forests.

Oligocene–Miocene

The pronounced temperature decline in the latest Eocene–early Oligocene triggered the expansion of cool temperate floras in wide areas of Patagonia. Important components of these floras were Podocarpaceae, Araucariaceae, Nothofagaceae and Proteaceae (Césari et al. 2015, and references therein). The understorey would have been dominated by ferns (Polypodiaceae, Lophosoriaceae, Schizaeaceae) and herbs supporting a high rainfall regimen and cool-temperate conditions. The late Oligocene–early/middle Miocene was characterised by new warming episodes, and marine transgressions flooded wide areas of Patagonia. The Andean uplift began to produce a rain shadow leeward of the Andes, and the first xerophytic halophytic shrubby/herbaceous communities began to develop in coastal environments. However, forests were still widespread in extra-Andean Patagonia. During the late Miocene the Andean range reached its maximum height, promoting rain shadow effects on the eastern side of the Andes with continentality and arid conditions in inland Patagonia. This induced substantial changes in the Patagonian vegetation, particularly the extinction of several forest taxa (e.g. *Dacrycarpus*, *Dacrydium*, *Lagarostrobos*, *Microcachrys*) from eastern Patagonia) and the expansion of xerophytic lineages. Rainforest taxa of Nothofagaceae, Podocarpaceae and ferns were present in western Patagonia, but discontinuous patches of Araucariaceae may have developed on mainland areas (Barreda & Palazzesi, 2007, 2014; Palazzesi et al. 2014).

Pliocene to Pleistocene

Pliocene aeolian records in northeastern Patagonian sequences suggest drier climates. The present eastern Patagonian desertification probably occurred during the last 6 Ma, following glaciation of the southern Andes, Antarctic ice sheet expansion, and changes in the atmospheric circulation patterns with the establishment of strong westerly winds (Palazzesi et al. 2014). The distribution of the Pleistocene and Holocene vegetation would have shifted repeatedly across latitudinal and/or altitudinal gradients in response to these changing parameters (Markgraf 1983).

Southern Australian temperate rainforests through time

The history of the Australian rainforests is discussed by Hill (2004). Some of the key features of this history are described.

Palaeocene to Eocene

This is widely considered to represent a period of high moisture and warm climates under which rainforest flourished in southern Australia, even though the region was at high

latitudes (c. 65°S for Tasmania in the early Eocene) (Carpenter et al. 2012). Macrofossils show few floristic links to the current cool temperate rainforest flora, with most taxa representing groups now associated with subtropical or tropical environments (Carpenter et al. 1994; Christophel 1994; Carpenter et al. 2012). In contrast, fossil pollen shows stronger links with the cool temperate forests, with the temperate groups of Nothofagaceae, conifers such as *Lagarostrobos* and ferns being prominent (e.g. Carpenter et al. 2012).

Oligocene to Miocene

The Oligocene to Miocene is generally considered to be a period of cooling and drying, resulting from global climate changes (Zachos et al. 2001) partially ameliorated by drift northwards. The forest flora changed in ways expected under such climate change— with the extensive loss or reduction of clades that now have tropical affinities or clades of poorly known affinity (such as numerous Proteaceae pollen types), and increases in temperate elements (Macphail 2007). Hence, both macrofossil and pollen floras tend to be dominated by some mix of mesic conifers, Nothofagaceae, Proteaceae and Cunoniaceae in the Oligocene and early Miocene. Fires (as evidenced by charcoal) become more important through this time and this is associated with general increases in the fire-associated flora (such as eucalypts). There is an almost complete absence of plant fossil evidence from that time until the Pliocene, which may reflect dry climates causing a paucity of wet environments.

Pliocene to Pleistocene

The Pliocene and early Pleistocene have a moderately well represented array of macrofossil and fossil pollen floras. These clearly show a decrease in diversity of rainforest floras involving high levels of extinction of both rainforest and sclerophyll species (Jordan 1997; Sniderman 2011; Sniderman et al. 2013). Fossil charcoal is common in almost all fossil assemblages through this time, and indeed right up to the present day. The glacial interglacial cycles induced major cycles in the vegetation with a typical pattern of open vegetation (often with grasses, daisies and saltbushes) alternating with forest vegetation. Rainforest is likely to have contracted to multiple small refugia in each of the cold and dry glacials.

Discussion

In this study we provide a deep-time perspective on the biogeography of southern hemisphere temperate rainforests, with the main focus on New Zealand. We recognise that the fossil record in all three regions is incomplete, with gaps in both the pollen and more especially the macrofossil record. However, it is most parsimonious to assume a continuous presence for most of the rainforest clades following their first appearance rather than extinction and recolonisation (Table 1; Figure 2). Similarly, the oldest fossil records are very unlikely to represent the actual first appearance of a taxon in these regions and these taxa may well have longer histories within the region than indicated by fossils (Heads 2005).

Through the Cenozoic New Zealand shows a persistence of a wide range of mesic lineages, presumably reflecting temperate to marginally subtropical, but constantly mesic conditions regionally throughout this period. One of the 30 genera considered here is now exclusive to New Zealand—the small tree or shrub *Halocarpus*. At least eight other taxa that are important in modern New Zealand rainforests (*Cyathea*, *Dicksonia*, *Prumnopitys*, two subgenera of *Nothofagus* (*Fuscospora* and *Lophozonia*), Lauraceae and Winteraceae (albeit as separate genera) have near continuous records through the Cenozoic in New Zealand, South America and Australia (although, in Australia, *Prumnopitys* is now only in the tropics). Three of the prominent extant New Zealand conifer taxa now only survive elsewhere in the world in tropical and subtropical areas (*Agathis*, *Dacrycarpus* and *Dacrydium*). Five other taxa have survived in New Zealand and South America through this period (*Lygodium*, *Laurelia*, *Weinmannia* and *Fuchsia*). *Phyllocladus* persists today in New Zealand, Tasmania and Malesia.

Podocarpus presents a case in which the fossil evidence for persistence of the modern New Zealand clade is weaker. As noted in the results, identification of fossil pollen and leaves of the genus is difficult. More seriously, along with *Podocarpus gnidioides* from New Caledonia and *Podocarpus lawrencei* from Tasmania, the extant New Zealand species form a small clade that is nested within this large (100 species) genus (Leslie et al. 2012). The species of this clade are uniformly small leaved, even the tropical species, *P. gnidioides*, whereas many of the fossil leaves are more similar to other clades.

Since the late Miocene, New Zealand has lost significant forest taxa, particularly conifers, including *Araucaria*, the *Dilwynites* pollen source tree—*Wollemia/Agathis*, *Lagarostrobos* and *Microcachrys*—but also two *Nothofagus* subgenera (*Nothofagus* and *Brassospora*) as well as Casuarinaceae and *Eucalyptus* (Lee et al. 2001). Interestingly, many of the same groups also became extinct in South America: *Agathis*, *Eucalyptus* and Casuarinaceae last appear in the Eocene; *Dacrycarpus* and *Dacrydium*, *Lagarostrobos*, *Microcachrys* and *Brassospora* beeches in the Miocene, and *Quintinia* in the Pleistocene. The similarities in the patterns of extinction in New Zealand and South America may in part reflect steep climatic gradients associated with mountain-building. In contrast, the extinctions in southeastern Australian rainforests commonly took place in the Pleistocene (e.g. *Dacrycarpus*, *Dacrydium* and *Brassospora* beeches), apparently in response to the drying climate and extreme restriction of suitable habitat during glacials (Jordan 1997).

Extinction in New Zealand has been a gradual process with several taxa, notably warmth-loving taxa such the *Brassospora* beeches and *Agathis*, initially retreating to northern refugia as the climate cooled from the late Miocene to Pleistocene (Lee et al. 2001). During the Pleistocene, limited land at low latitudes meant that the once diverse *Brassospora* beeches eventually died out, and once locally extinct, were unable to return from refugia in New Caledonia and New Guinea. Furthermore, the relative lack of first appearances of rainforest tree taxa argues that the extreme isolation of New Zealand for the past 40 million years has limited recolonisation possibilities for forest taxa.

We see no evidence that a decrease in land area and change in land configuration had any impact on extinction rates of forest taxa (Figure 2). This contradicts a perception derived mainly from popular literature (e.g. Campbell & Hutchins 2007) that the New Zealand temperate rainforests underwent striking changes following maximum marine transgression ('catastrophic Oligocene inundation' of Campbell & Hutchins 2007), with post-Oligocene forests being repopulated by long-distance dispersal from Australia and

elsewhere. In contrast, the major extinctions began 10 million years after maximum marine transgression in the later Miocene through to the Pleistocene, when the New Zealand land area was close to its present size (Lee et al. 2001). Hence, the extinctions of the New Zealand tree taxa discussed here were caused mainly by climatic cooling and limited access to warm northern refugia. However, immigration of smaller trees and shrubs (e.g. *Coprosma*, *Myrsine*, *Kunzea*) has occurred in New Zealand (Lee et al. 2001; Papadopulos et al. 2011), mostly during warmer conditions in the early to mid Miocene and in groups that included both forest and open habitat taxa.

In summary, in the early to middle Cenozoic, the main components of New Zealand's temperate rainforests were shared with other southern hemisphere landmasses. Continental similarities diverged post-Eocene, due mainly to differential extinctions on all three landmasses. New Zealand and South America experienced a similar level of taxonomic loss especially during the Miocene across conifer and some broadleaved groups. What is remarkable in New Zealand is the near-absence of immigrant forest-forming taxa replacing the vacant niches left by the late Miocene extinctions, which may have left opportunities exploited through the well-known radiations in some taxa in rainforest understoreys such as *Coprosma* and *Pittosporum* (Wardle 1991).

Disclosure statement

No potential conflict of interest was reported by the authors.

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