The New Zealand flora: 'Moa's Ark' or 'Fly-paper of the Pacific'?

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> "New Zealand is an ark, *Moa's Ark*, ... Cast adrift from the ancient continent of Gondwanaland millions of years ago, it has drifted through the ages, preserving aboard many of its ancient features. That is why New Zealand's natural heritage contains so many unique plant and animal forms unknown in the rest of the world: trees mighty enough to have sheltered dinosaurs, ferns which first stood upright 350 million years ago, strange oddities like the tuatara, the amazing black coral of Fiordland, and the national symbol, the kiwi."

So go the notes on the dust jacket of *Moa's Ark: The voyage of New Zealand* by David Bellamy et al. (1990). And similar statements are commonly repeated in books, documentaries and the popular media. The common view has been that New Zealand acted as a refuge for the biota of Gondwana – the southern supercontinent. Because of its isolation in the southern Pacific the plants and animals that inhabited Gondwana were thought to have survived relatively unaltered in New Zealand despite changes in the rest of the world.

Vicariance

Vicariance is a general term used to describe the subdivision of an ancestral distribution range into two or more widely separated areas by the formation of a physical barrier (e.g., oceans or mountains). In the late 1960s our understanding of geological history was transformed by the widespread acceptance of plate tectonics and continental drift. Biologists were quick to realise that these geological events could also be used to explain the distributions of many groups of plants and animals. Accordingly, vicariance hypotheses found favour as the primary explanation for the origins of the New Zealand biota and this is the explanation publicised by Bellamy et al. (1990) and others. In simple terms the story goes something like this. Around 150 million years ago (mya) all the major Southern Hemisphere landmasses were united as part of Gondwana. Then over millions of years tectonic movements caused the supercontinent to break apart and the southern landmasses to drift to their current positions on the globe. New Zealand broke away around 80 mya and with the formation of the Tasman Sea some of the Gondwanan biota became isolated here (Fig. 1A; see Box 1, p. 22). The early isolation of New Zealand and a 2000 km ocean barrier was thought to have buffered its relict biota from the environmental and biotic changes that have occurred over the last 80 million years (my).

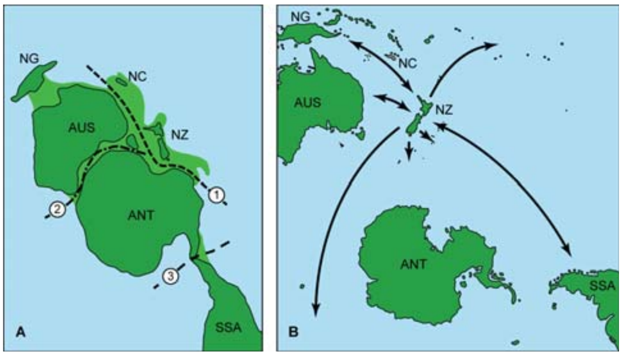

Fig. 1 Changing views on the origins of New Zealand plants: **A,** a paleogeographic reconstruction of Gondwana (approximately 90 mya) showing the sequence of events resulting in the final break-up. 1, separation of New Zealand (NZ) and New Caledonia (NC) from Gondwana, tectonic spreading occurred about 115–58 mya but New Zealand was isolated by about 80 mya. 2, separation of Australia (AUS) and New Guinea (NG) from Antarctica (ANT), tectonic spreading occurred about 95–35 mya but Australia was probably isolated by about 50–45 mya. 3, separation of Antarctica and southern South America (SSA), opening of the Drake Passage occurred about 30–28 mya. (Adapted from Sanmartîn and Ronquist, 2004); **B,** a contemporary map of the southern Pacific showing transoceanic dispersal events inferred from molecular data for New Zealand plant groups (listed in Table 1). Dispersal events shown by arrows: single-headed, to date only dispersal in the direction of the arrow has been inferred; double-headed, dispersal in both directions has been inferred. (Adapted from Winkworth et al., 2002).

Dispersal

Despite the wide acceptance of vicariance, recent research has forced scientists to rethink this point of view. Studies now suggest that *dispersal* was responsible for the arrival of many plant groups in New Zealand. Dispersal is the process plants use to move between geographic locations. It usually involves seeds or other propagules (e.g., fern spores) being carried along by water or wind currents, or by birds and other animals (see Box 2, p. 22). Although it may seem hard to believe, there is now compelling evidence to suggest that the ancestors of many distinctively New Zealand groups were not carried along by the slow tectonic route, but instead have crossed vast marine barriers to reach our shores. Prior to the 1960s acceptance of continental drift, dispersal had often been used to explain the New Zealand biota. The problem was that commonly the timing and mechanism of such events received little or no attention – often only the extreme and rare events were noted. These *ad hoc* explanations involving rare dispersal events quickly lost favour when a single vicariance event could be invoked to explain the entire biota. It has taken more than 30 years for the pendulum to swing back towards dispersal.

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The first of the new insights came from critical examination of plant fossils. In 1994 Mike Pole pointed out that many of the groups that occur commonly in the New Zealand fossil record, covering from just a few thousand years ago (ya) to 80 mya, are not represented in the contemporary flora. And *vice versa*. Pole (1994) interpreted this as reflecting turnover in the flora – the plants that had been important in the New Zealand flora when it split from Gondwana were progressively replaced by new groups. But since New Zealand has been isolated for the last 80 my where did the ancestors of the modern flora come from? The answer appeared to be that the modern New Zealand flora had arrived by dispersal from elsewhere – had the early workers been right after all?

DNA sequencing

Since the 1990s DNA studies have become increasingly important for understanding the evolutionary history of life on earth. The approach uses differences between DNA sequences of living representatives to estimate a 'family tree' (or more correctly a phylogeny) that can then be used to understand how plants have evolved over time. Importantly for our New Zealand story these studies allow scientists to investigate where plant groups lived in the past and also when they lived there. A good many groups in the New Zealand flora have now been examined using molecular approaches and these data provide convincing and independent evidence supporting the importance of dispersal. A review of the molecular studies for species-rich morphologically and ecologically diverse members of New Zealand's alpine flora provides a useful historical snapshot (Winkworth et al., 2002). For all these groups molecular data point to a recent arrival in New Zealand rather than ancient vicariance. Based on the level of difference between DNA sequences and given a calibration point, usually from the fossil record, it is possible to estimate when the local representatives diverged from their overseas relatives. In most cases the genetic data suggest divergence of the alpine flora occurred within the last 20 my (Table 1) – admittedly not at all recent in terms of human lifetimes but certainly much more so than New Zealand's split from Gondwana. And this is the key point: vicariance implies that the New Zealand lineages diverged from their closest relatives about 80 mya, but the molecular age estimates are so much younger that dispersal is the only possible explanation.

Even for some scientists the idea that plant propagules can cross thousands of kilometres of ocean is difficult to accept – perhaps with good reason since such events are likely to be exceedingly rare. But even very rare events become possible given enough time and in New Zealand's case there has been an 80 my timeslot for such rare events to occur. As Pole (1994) summarises "I see oceans not as barriers to plant dispersal but as hurdles which, given enough time, are overcome." Reluctance to accept dispersal appears to have had more to do with the appeal of ancient geological linkages than any failing of dispersal itself. Indeed there is general acceptance that dispersal is the sole explanation for the floras of truly oceanic islands. The Hawaiian Islands are a good example – they are of volcanic origin and have never had direct contact with a continental landmass. Estimates suggest that about 290 dispersal events are required to explain the 970 or so angiosperm species in the Hawaiian flora (Wagner et al., 1990). In New Zealand's case it has conceptually been so much easier to link the origins of the flora to the ancient geological connections of the land than it is to accept that many of the plant lineages in New Zealand today made independent journeys across ocean barriers to get here.

In addition to identifying which lineages have dispersed to New Zealand molecular data also tell us something about patterns of dispersal in the southwest Pacific. As Winkworth et al. (2002) summarise, "many plant lineages are recent arrivals in New Zealand, diversifying rapidly and then travelling to other Southern Hemisphere landmasses." Until molecular data became available it was often assumed that the eastward trend in circumpolar air and water circulation patterns would restrict dispersal direction – dispersal would always be from west to east (i.e., from Australia to New Zealand, from New Zealand to the Pacific Islands). But molecular analyses indicate no such limitation. Instead dispersal patterns are much more complex and plant propagules appear to have been carried in many directions (Fig. 1B). Interestingly, these results are consistent with an observation made in the late 1970s. Based on weather maps Wardle (1978) noted that if an anticyclone passes south of New Zealand a westward airflow is produced over the Tasman Sea providing opportunities for dispersal against the circumpolar trend.

Until very recently molecular studies had tended to focus on herbaceous and shrubby elements in the New Zealand flora. However, we now have molecular data for some of the most biogeographically significant New Zealand trees. For decades, students have been taught that the distribution of the southern beeches (*Nothofagus*) – which includes New Zealand, Tasmania, eastern Australia, New Guinea, New Caledonia, and southwestern South America – is the result of Gondwanan vicariance. Indeed, fossil evidence places *Nothofagus* in Gondwana prior to separation (the earliest *Nothofagus* fossils are about 100 my old) and is at least consistent with the idea that the beeches simply went along for the tectonic ride. However, here again a closer examination of the fossil data raised questions about whether the extant (currently living) New Zealand species really were of Gondwanan age (McGlone et al., 1996). More recent molecular analyses have also added to our understanding of *Nothofagus* evolution. These studies indicate that, like members of the alpine flora, extant Australian and New Zealand species of *Nothofagus* are genetically much more similar to one another than would be expected if they had spent the last 80 my in isolation (Cook and Crisp, 2005; Knapp et al., 2005). The data suggest the split occurred closer to 30 mya meaning that this trans-Tasman link "can only be explained by long-distance dispersal" (Waters and Craw, 2006). While molecular data suggest that perhaps vicariance helped shape the oldest parts of the *Nothofagus* phylogeny, it is clear that the *Nothofagus* in New Zealand today are 'newer' arrivals and not Gondwanan relicts.

Oligocene drowning

One of the most controversial aspects of New Zealand's geological history is the 'Oligocene drowning.' After splitting away from Gondwana the New Zealand landmass was extensively eroded – over a period of about 55 my the ancient landmass was slowly reduced in size. The problem is that we cannot be certain of the full extent of the erosion. Was New Zealand completely drowned or did a few low-lying islands survive until a change in geological activity began to push up what is now modern New Zealand? This is a critical question. As Pole (1994) argues, if the drowning was complete then the entire terrestrial biota would have been lost and must have been replaced by new arrivals. Although molecular data imply dispersal is more important than long-term survival it cannot rule out the possibility that at least some land remained and a few lineages made it through the drowning event.

Like *Nothofagus*, *Agathis* has a Gondwanan distribution and a fossil record that supports an ancient presence in New Zealand. However, unlike *Nothofagus*, the level of genetic difference between the New Zealand kauri, *A. australis*, and its nearest relatives suggest this species has been isolated in New Zealand for a longer period of time. Stöckler et al. (2002) concluded their genetic data provided "the strongest evidence to date that New Zealand was not completely submerged during the Oligocene". This view was later corroborated by age estimates showing that the *A. australis* lineage diverged from the remainder of *Agathis* prior to the Oligocene (Knapp et al., 2007). However suggestive these data are we must still be somewhat cautious about the inference of any ancient presence in New Zealand. The problem with the molecular data is that it does not exclude alternative explanations involving dispersal and extinction. A similar phylogeny would also be expected if the *A. australis* lineage had arisen elsewhere, dispersed to New Zealand post-Oligocene, and then become extinct in its homeland (Waters and Craw, 2006; Knapp et al., 2007). While the *Agathis* story is not fully resolved it remains a candidate for the title of Gondwanan relict. And we cannot rule out the possibility that among groups with long fossil records in New Zealand (e.g., Podocarpaceae and Winteraceae) there are other examples of long-term survival.

Conclusion

In his recent and aptly entitled article *Goodbye Gondwana* (2005), Matt McGlone concludes:

> "… this supposed ancient, unchanging Gondwanic heritage is an important cultural icon. But there is no reason why a dispersalist universe, with a much diminished role for Gondwana, cannot be as appealing, with each taxon having its unique history and the biota as a whole having a complex network of relationships reaching across the entire globe. Nevertheless, for New Zealanders in particular, abandoning 'Time Capsule of the South Seas' for 'Fly-paper of the Pacific' will be a wrench."

Although scientists are changing the way they view the origins of the New Zealand flora, these new perspectives have been much slower to filter through to the general public. Certainly it will be difficult to give up the idea of ancient linkages, but perhaps the importance of dispersal in the assembly of our biota is an ironic twist since New Zealanders are themselves the product of 'long-distance dispersal'.

Acknowledgements

This article is based in part on the review papers of McGlone (2005), Waters and Craw (2006), and especially Winkworth et al. (2002). We are grateful to the publisher, Elsevier, for permission to adapt portions of Winkworth et al. (2002), and we thank Matt McGlone and Steve Wagstaff for their helpful comments on the preparation of this article.

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Box 1 Prehistory of New Zealand (adapted from Winkworth et al., 2002)

Geology
New Zealand was originally uplifted along the eastern edge of Gondwana some 150 mya. About 115 mya tectonic spreading began to isolate the New Zealand landmass (Fig. 1A), a seaway separated the two landmasses by 80 mya, although the Tasman Sea continued to widen until the Paleocene (65–58 mya). Erosion throughout the Cretaceous (144–65 mya) and early Tertiary (65–37 mya) steadily reduced both the extent and topology of New Zealand, and for part of the Oligocene (37–23 mya) it is unclear whether parts of New Zealand remained above sea level or not. Activation of the modern Pacific–Australian plate boundary (some 25 mya) resulted in renewed uplift of land during the Miocene (23–5 mya) and Pliocene (5–2 mya), and led to the rapid uplift of the axial mountain ranges. Marine inundations and volcanism also shaped Pliocene New Zealand while many landforms are the result of Pleistocene (2 mya–14,000 ya) glaciation.

Climate
For much of its prehistory New Zealand has experienced cool temperate climates. However, periods of warmer conditions occurred during the Eocene (58–37 mya) and Miocene. Around 2.5 mya the onset of a global Ice Age led to a marked deterioration of climates in New Zealand. Pleistocene New Zealand was characterised by dramatic climatic fluctuations – the climate repeatedly alternating between colder, drier glacial maxima and warmer, moister interglacials. The final glacial retreat began around 14,000 ya and after a brief warm spell, climates like those experienced today were established about 7000 ya.

Vegetation
Non-flowering plants dominated the Cretaceous vegetation of New Zealand; angiosperms only began to feature prominently in the early Tertiary. The first angiosperm-dominated assemblages appeared during the Eocene. These gradually increased in diversity and from the Oligocene onward there was regional differentiation of floras as environmental gradients developed. Glacial climates affected both the composition and distribution of vegetation in New Zealand. During glacial maxima forests were largely confined to the far north, with grass- and shrub-dominated vegetation dominating the south. In the warmer intervals forests spread rapidly, often re-establishing even in the southernmost areas. Rapid and widespread establishment of forests followed the last glacial retreat although the modern forest types did not become established until the climate stabilised about 7000 ya.

Box 2 Plant dispersal in the southern Pacific (adapted from Winkworth et al., 2002) *(continued over page)*

Molecular and fossil data provide convincing evidence for the importance of transoceanic dispersal in establishing plant distributions in the southwestern Pacific. Several general dispersal mechanisms are recognised:

Water
For seeds and fruits (and perhaps also viable vegetative material) capable of surviving long periods immersed in seawater, ocean surface currents provide a means of dispersing propagules potentially thousands of kilometres. At high southern latitudes the Antarctic Circumpolar Current (ACC), the strongest marine current system, dominates circulation. Flowing eastward it links the Atlantic, Indian, and Pacific oceans. In the Pacific, the South Pacific Gyre dominates circulation patterns to the north of the ACC. This surface system results in water moving north along the west coast of South America, turning westward as it nears the equator, and finally circulating south past Australia and New Zealand.

Mangroves (e.g., *Avicennia* spp. and *Rhizophora* spp.) and coconut (*Cocos nucifera*) are well-known examples of species adapted to dispersal in ocean currents. Studies have also shown that *Sophora* (kowhai) seeds, with their hard seed coats, float and may remain viable in seawater for many years. Obviously only a small proportion of plants produce fruits or seeds adapted to water dispersal. This implies that the mechanism is unlikely to account for more than a small fraction of dispersal events. However, observations suggest that vegetation rafts may increase the number of distributions that are the result of water dispersal. Vegetation rafts consist of aggregations of debris and perhaps also soil that are washed out to sea usually from rivers. These have been found floating hundreds of kilometres from the nearest land and it is assumed they could act as dispersal vectors, allowing propagules that would not normally be suitable for water dispersal to be transported by this mechanism.

Wind
Wind currents may disperse small, lightweight seeds or the spores of ferns, mosses, and fungi. As in the oceans, atmospheric currents at high southern latitudes are dominated by an eastward-flowing system – the West-Wind Drift (WWD) – and it had been assumed that dispersal at these latitudes would be exclusively eastward due to the influence of the WWD. However, it now appears that the cyclonic nature of individual weather systems provides opportunities for wind dispersal against this trend.

Wind dispersal across the Pacific has been advocated for *Metrosideros* and the orchid family, both of which have minute seeds. Among the orchids there are several confirmed cases of Australian native species that (despite not having been previously recorded) have suddenly been found growing wild in New Zealand. These 'vagrant' orchids are suspected of having arrived via wind transport from Australia in very recent times.

Although the distribution of some plants may be explained by wind dispersal, this mechanism is probably responsible for only a small proportion of successful dispersal events. As for water dispersal this at least partly reflects the fact that many plants have fruits and seeds unsuitable for wind dispersal. However, even for those that are well adapted, wind dispersal is strongly distance dependent; most propagules fall close to the parent plant and very few are dispersed more than a few kilometres. This pattern suggests that for most species wind is unlikely to provide an effective means of crossing the vast Southern Pacific Ocean.

Birds and other animals

Many plants have fruits or seeds that are adapted to transport by biotic vectors. Some plants produce fleshy fruits that are an attractive food source. In this case the seeds are carried internally. It is assumed that at least some of the seeds will pass intact through the animal's digestive system and at the same time will be carried away from the parent plant. The alternative is external transport. Some propagules are covered with hooks or a sticky coating that allow them to adhere to the outside of the animal. Here the expectation is that the propagule will be carried for some distance before being dislodged.

Biotic vectors seem likely to have been important for mediating Southern Hemisphere plant dispersal. One group of potential vectors are the 'transoceanic wanderers' – birds such as albatrosses, petrels, and shearwaters that regularly travel vast distances across the Southern Ocean. Although unlikely to act as vectors for fleshy-fruited plants (due to diet), they may well be an important means of external transport. Another important group may be migrants, visitors, and stragglers. Depending on the species, these birds may be regular travellers around the Pacific or alternatively be rare arrivals perhaps carried in by a storm system. For example, various Australian bird species have been recorded in New Zealand, and while they do not usually establish breeding populations, they may be an important means of transport. Like other mechanisms biotic transport requires some element of luck – an ocean-going bird would need to make an unusual stop so that the seeds would be deposited on land or a forest bird blown out to sea would need to have recently fed so that it was carrying seeds or other plant propagules. Bird-mediated dispersal is likely to be influenced by prevailing weather systems; however, observations suggest that this mechanism can transport propagules over very long distances and in various directions, which is consistent with the pattern suggested by current data (Fig. 1B).

Table 1 New Zealand plant taxa for which molecular phylogenetic analyses suggest recent origins, recent diversification, and/or involvement in dispersal within the Southern Hemisphere (adapted from Winkworth et al., 2002, 2005).

Taxon	Estimated number of New Zealand species	Inferred origins	Age estimate for the New Zealand lineage (my)	Dispersal events inferred within the Southern Hemisphere. Inferred direction of dispersal is indicated by arrows, dashes indicate an uncertain direction of dispersal
Apiaceae: *Apioid* genera	60	Northern Hemisphere	–	New Zealand → Chatham Islands
				New Zealand – Australia
Asteraceae: *Abrotanella*	10	Southern Hemisphere	<20	New Zealand → Australia
				New Zealand → New Guinea
				New Zealand → subantarctic islands
				South America → New Zealand
Asteraceae: *Brachyglottis*	30	equivocal	–	New Zealand → Australia
Asteraceae: Gnaphalieae	75	equivocal	–	Australia → New Zealand
				New Zealand → New Guinea
Atherospermataceae: *Laurelia–Laureliopsis*	1	equivocal	57–33	South America → New Zealand
Boraginaceae: *Myosotis*	34	Northern Hemisphere	<15	New Zealand → South America
				New Zealand → Australia
				New Zealand → New Guinea
				New Zealand → subantarctic islands
Brassicaceae: *Cardamine*	7	equivocal	–	New Zealand →Australia
				New Zealand → South America
Brassicaceae: *Pachycladon*	9	Northern Hemisphere	1–3.5	Australia – New Zealand
Caryophyllaceae: *Scleranthus*	3	Northern Hemisphere	<8	Australia – New Zealand
Coriariaceae: *Coriaria*	8	Indo-Pacific	<63	New Zealand → South America
Corynocarpaceae: *Corynocarpus*	1	Indo-Pacific	<55	New Caledonia → New Zealand
Fabaceae: *Carmichaelia*	23	Australia	–	New Zealand → Lord Howe Island
Fabaceae: *Montigena*	1	Australia	–	Australia → New Zealand
Fabaceae: *Sophora* sect. *Edwardsia*	8	equivocal	<30	New Zealand → Pacific islands
				New Zealand → South America
				New Zealand → Gough Island
Gentianaceae: *Gentianella*	30	Northern Hemisphere	<5	South America → Australasia
				New Zealand → Australia
Gunneraceae: *Gunnera*	5	equivocal	–	New Zealand – Australia
Myrtaceae: *Metrosideros*	12	equivocal	–	New Zealand → Pacific islands
Nothofagaceae: *Nothofagus*	4	Southern Hemisphere	<60	South America → Australasia
			<33	New Zealand – Australia
Plantaginaceae: *Hebe* and relatives	100	Northern Hemisphere	<4	New Zealand → South America
				New Zealand → Australia
				New Zealand → New Guinea
				New Zealand → subantarctic islands
Plantaginaceae: *Ourisia*	12	South America	–	South America → Australasia
Ranunculaceae: *Psychrophila*	1	South America	–	South America → Australasia
Ranunculaceae: *Ranunculus*	43	Northern Hemisphere	6	New Zealand → Australia
				New Zealand → subantarctic islands
Santalaceae: *Korthalsella*	3	Indo-Pacific	–	Australia → New Zealand
Stylidiaceae: *Forstera* and *Phyllachne*	7	equivocal	6	South America – Australasia
				Australia – New Zealand
Stylidiaceae: *Oreostylidium*	1	Australia	2	Australia → New Zealand
Tetrachondraceae: *Tetrachondra*	1	South America	2.5	South America → New Zealand