

# Plant dispersal N.E.W.S from New Zealand

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Although New Zealand separated from Gondwana during the late Cretaceous (80 million years ago) it shares strong floristic affinities with other Southern Hemisphere landmasses. For 150 years, biogeographers have debated whether these similarities reflect the ancient Gondwanan connection or subsequent dispersal events. Molecular phylogenies are providing new insights into the history of Southern Hemisphere plant groups. These studies show that many plant lineages are recent arrivals in New Zealand, diversifying rapidly and then travelling to other Southern Hemisphere landmasses.

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Almost certainly New Zealand's first flora would have migrated from Gondwana as the ancestral landmass was uplifted along the eastern edge of the supercontinent (Box 1). Although the origins of the earliest colonists seem straightforward, contrasting hypotheses about the significance of geological and climatic change in the New Zealand environment have polarized opinions about the relationships of this first flora and the contemporary assemblage. One hypothesis is that the modern flora represents a Gondwanan relict that is relatively unaltered by dramatic changes in geology and climate (Box 1). Perhaps more importantly, this hypothesis also suggests that the geological isolation of New Zealand acted as a barrier to biotic exchange. That is, lineages in the contemporary flora must have been present when New Zealand separated from Gondwana (Box 1) because, following separation, the distance from potential source areas rules out dispersal. Panbiogeographers have been strong advocates of this view, explaining the entire New Zealand biota in terms of Gondwanan break up and rafting of the fragments to their present-day positions [1]. Long-term geological isolation will certainly have influenced the composition of the New Zealand flora; however, it has been questioned whether the barrier has been impermeable. Indeed, many workers [2–13] have argued that the fossil record [5, 7, 11] and the diverse geographical affinities of the modern assemblage [4, 12, 13] provide evidence for the role of dispersal in establishing the contemporary New Zealand flora. To explain the observed similarities between Southern Hemisphere floras, authors have proposed hypotheses ranging from migration across early Tertiary [65–37 million years ago (mya)] land bridges to long-distance dispersal over vast oceans during the late Tertiary (15–2 mya) and more recently [2–11, 14] (Fig. 1). Although distributional and fossil data [4, 5, 7, 11–13] hint that Gondwanan ancestry cannot be used to fully

explain the extant New Zealand flora, there has been little direct evidence for dispersal. Until recently, the strongest support came from fossil pollen. Comparisons of the palynological records for Southern Hemisphere landmasses show temporal differences in the first appearance of shared taxa, a pattern that could indicate dispersal [2, 5, 7, 11]. Such inferences are suggestive of general patterns; however, the limited taxonomic resolution of the fossil record has prevented the reconstruction of dispersal histories within specific groups. Even with evidence from comparative morphology and contemporary distribution patterns, it is difficult to infer unambiguously dispersal within lineages. For example, in the Australasian apioid Umbelliferae, alternative interpretations of morphological data support opposing hypotheses for the origins of contemporary taxa [15, 16].

Molecular phylogenetic studies both provide an independent test of previous hypotheses and highlight novel insights into the origins and evolution of New Zealand plants. Here, we review recent studies that, with a few exceptions, have focused on large, morphologically and ecologically diverse plant groups of the New Zealand mountains. Often the phylogenetic analyses are consistent with the rapid diversification of the lineage in New Zealand following the onset of late Tertiary mountain building (5–2 mya) and Quaternary climate change [2 mya–14 000 years ago (ya)]. Perhaps more interesting, however, are the insights these studies provide into the relationships between the New Zealand taxa and their Southern Hemisphere relatives. Molecular phylogenies clearly indicate that the patterns of transoceanic dispersal in the southern Pacific are more complex than have previously been envisaged. The results highlight both the dynamic nature of plant evolution and the importance of Southern Hemisphere models for explaining biodiversity.

**Dispersal patterns in the southwestern Pacific**  
A controversial aspect of dispersal hypotheses is the significance of west-wind drift, a meteorological phenomenon that, at high southern latitudes, causes cyclonic weather systems to move progressively eastward. These circumpolar westerly winds and ocean currents were established during the Miocene (23–5 mya) as South America and Australia separated from Antarctica [17]. This eastward flow intensified throughout the late Tertiary but was probably strongest during the Pleistocene glacial

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### Box 1. A brief history of New Zealand

#### Geology

Originally uplifted along the eastern edge of Gondwana 150–140 million years ago (mya) (Fig. 1), tectonic spreading began to isolate New Zealand ~115 mya. A seaway separated the two landmasses by 85 mya, although tectonic movement continued into the Paleocene (65–58 mya) [a]. Throughout the Cretaceous (144–65 mya) and early Tertiary (65–37 mya) steady erosion reduced both the extent and topology of New Zealand, so that during the Oligocene (37–23 mya) only a scattered archipelago of low-lying islands remained. However, activation of the contemporary Pacific–Australian plate boundary (25 mya) resulted in the emergence of a narrow, elongate landmass during the Miocene (23–5 mya) [a,b]. Tectonic activity intensified throughout the Pliocene (5–2 mya), culminating in the rapid uplift of the axial mountain ranges [c]; marine transgressions and volcanism also shaped Pliocene New Zealand. Late Tertiary and Quaternary glaciation (2.5 mya–14 000 ya) affected the geological setting of New Zealand. Many modern landforms result directly from glacial activity or modification of glacial constructions [d].

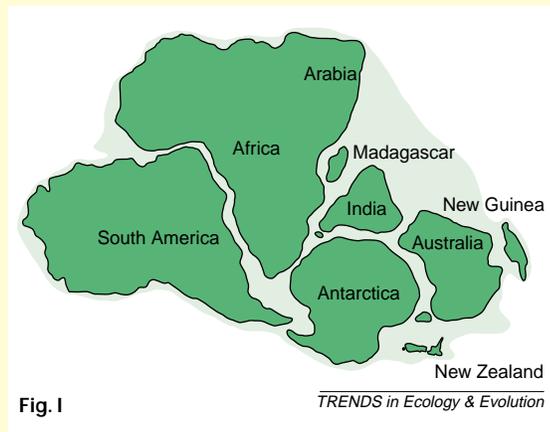


Fig. 1

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#### Climate

Cool temperate climates dominated much of the prehistory of New Zealand [e]. However, extended periods of warming are correlated with both the Eocene (58–37 mya) and Miocene. Cool temperature conditions again dominated by the late Miocene and continued throughout much of the Pliocene before deteriorating further with the onset of glaciation (2.5 mya). Ice-Age New Zealand experienced repeated glacial–interglacial cycles that were characterized by dramatic

climatic fluctuations – alternating between cold, dry glacial maxima and warm, moist interstadials and interglacials [f,g]. The final glacial retreat began 14 000 ya and was followed by a warm, moist thermal optimum before cooler, drier contemporary conditions were established 7000 ya [f].

#### Vegetation

As elsewhere, nonflowering plants dominated Cretaceous assemblages in New Zealand. Although these lineages continued to predominate in early Tertiary floras, angiosperms also featured prominently [e]. The first angiosperm-dominated assemblages appear during the Eocene. Similar to earlier palynofloras, these were uniform in composition; however, from the Oligocene onward, the progressive development of environmental gradients resulted in regional differentiation [e,f]. Late Tertiary and Quaternary glaciation dramatically affected both the composition and distribution of the New Zealand vegetation. During glacial maxima, forests were confined mostly to the far north, with extensive grass and shrubland assemblages dominating the south. During interstadials and interglacials, forest assemblages spread rapidly from the refugia, often re-establishing even in the southernmost areas [f,g]. Following the final glacial retreat (14 000 ya), the thermal optimum supported the rapid, widespread establishment of forests. More recent climate change also affected the composition and distribution of the vegetation [g].

#### References

- a Stevens, G.R. (1985) *Lands in Collision: Discovering New Zealand's Past Geography*, Science Information Publishing Centre, DSIR
- b Pillans, B. *et al.* (1992) The age and development of the New Zealand landscape. In *Landforms of New Zealand* (Soons, J.M. and Selby, M.J., eds), pp. 31–62, Longman Paul
- c Cooper, A. and Cooper, R.A. (1995) The Oligocene bottleneck and the New Zealand biota: genetic record of a past environmental crisis. *Proc. R. Soc. Lond. Ser. B* 261, 293–302
- d Batt, G.E. *et al.* (2000) Thermo-chronological analysis of the dynamics of the southern alps, New Zealand. *Bull. Geol. Soc. Am.* 112, 250–266
- e Mildenhall, D.C. (1980) New Zealand late Cretaceous and Cenozoic plant biogeography: a contribution. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 31, 197–233
- f McGlone, M.S. (1985) Plant biogeography and the late Cenozoic history of New Zealand. *N. Z. J. Bot.* 23, 723–749
- g Markgraf, V. *et al.* (1995) Neogene paleoenvironmental and paleoclimatic change in southern temperate ecosystems – a southern perspective. *Trends Ecol. Evol.* 10, 143–147

periods (2 mya–14 000 ya) [18]. Although the west-wind drift has been less intense during the Holocene (14 000 ya–present), it continues to dominate present-day weather patterns.

One common view is that the distributions of Southern Hemisphere plant groups should reflect the long-term dominance of west-wind drift [4,6,19]. Indeed comparisons of the Australian and New Zealand plant fossil records are consistent with this expectation, indicating that most shared taxa appear first in Australia and only later in New Zealand [2,5,7,11]. Although eastward dispersal seems to account for many plant distribution patterns, several authors have questioned whether west-wind drift can explain the distributions of all plant groups in the southwestern Pacific. In particular, Wardle [8]

has argued that, for several Australasian alpine plant lineages, morphology, chromosome number and species richness suggest dispersal from New Zealand to Australia or New Guinea – events requiring transport in an easterly direction. Perhaps more astonishing is the inference that plants might disperse westward from South America to Australasia [9,22,23], a distance of some 8200 km. Such examples suggest the possibility of dispersal against the prevailing weather systems and ocean currents.

Molecular phylogenetic studies extend our understanding of plant dispersal in the Southern Hemisphere. For many lineages, these studies have confirmed the importance of eastward dispersal. In such analyses, eastward transport is inferred from reconstructed phylogenies when western Pacific

species are basal to those from more eastern locations. For example, in the genera *Hebe* [20] and *Myosotis* [21], phylogenetic trees for the nuclear ribosomal internal transcribed spacer (nrITS) indicate dispersal eastward from New Zealand to South America (Fig. 2a,b). Examples of molecular phylogenetic studies that suggest eastward dispersal are given in Table 1. Although phylogenetic analyses confirm the general importance of eastward dispersal, in several cases they have identified dispersal events that are not favoured by west-wind drift. For example, phylogenetic reconstructions for nrITS sequences (Fig. 2a–c) suggest that successful dispersal events have occurred from New Zealand southwest to the subantarctic islands (*Hebe* [20], *Myosotis* [21] and *Ranunculus* [24]), west to Australia (*Chionohebe* [20], *Myosotis* [21] and *Ranunculus* [24]) and northwest to New Guinea (*Parahebe* [20] and *Myosotis* [21]). Similarly, phylogenetic trees for the chloroplast gene *rbcL* suggest a westward dispersal event from South America to New Zealand for *Tetrachondra* [25] (Fig. 2d). Examples of movements inconsistent with transport by west-wind drift are given in Table 2.

Together, these molecular analyses clearly indicate that westerly marine and air currents have not limited dispersal in the southwestern Pacific, instead plant propagules must have been transported in many directions (Fig. 3). Furthermore, these data highlight the temporal aspect of these dispersal events. In many of the examples molecular dating or observations on the level of genetic divergence between taxa suggest that lineage diversification has occurred since the late Miocene (10–5 mya). It follows that dispersal events involving derivative taxa must also be relatively recent. For example, molecular estimates suggest that the radiation of *Myosotis* in New Zealand is <10 million years old, and so extant taxa, derived from this diversification but now occupying disjunct areas (e.g. Australia, New Guinea, South America and the subantarctic islands), would be younger [21].

#### Dispersal routes and stepping-stones

Even biogeographers who have favoured dispersal are reluctant to accept that plants could, in a single event, travel between Southern Hemisphere landmasses. Instead, intervening regions are often suggested to be stepping stones in such movements. For example, many of the alpine plant lineages of New Zealand might be derived from Northern Hemisphere ancestors that journeyed via the mountains of southeast Asia, New Guinea and Australia [6]. Similarly, plants dispersing between South America and New Zealand might have travelled first to Antarctica or the subantarctic islands [9,10]. Indeed, the discovery of fossilised *Nothofagus* wood in Antarctic deposits of Pliocene (5–2 mya) age makes this route an enticing possibility for all but the most recent migrants [26].

Such hypotheses make specific predictions about the relationships of mainland New Zealand species

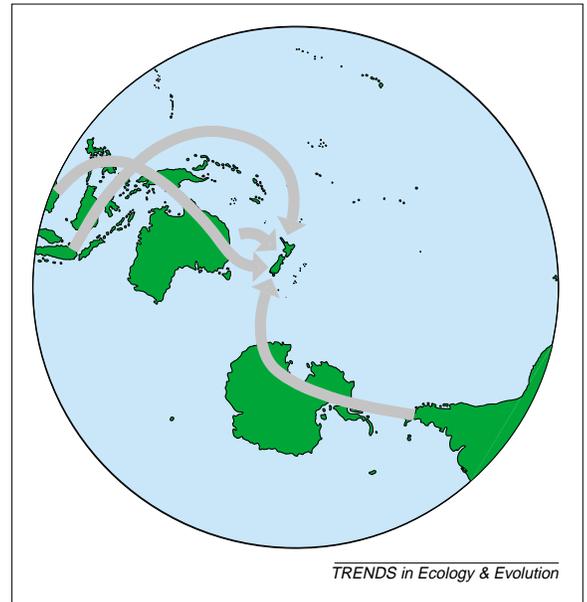


Fig. 1. Hypothesized corridors for plant dispersal into New Zealand as inferred from observations on palynological, morphological and distributional data [2,4–6,9]. Dispersal routes are indicated by arrows.

and their Australian, New Guinean or subantarctic island relatives. For stepping-stone hypotheses, we expect that taxa from intervening areas would be basal to mainland New Zealand species. Alternatively, given direct dispersal, these forms might have arisen from independent long-distance events or might be derived by dispersal from New Zealand. Fossil and distributional data do not differentiate between these predictions, but molecular phylogenies suggest direct long-distance events rather than short-range movements. For example the molecular phylogenies of *Myosotis*, *Ranunculus* and *Parahebe* indicate that, in each case, extant Australian, New Guinean or subantarctic island species originated in New Zealand (Fig. 2a–c).

Although molecular analyses have not favoured stepping-stone hypotheses, we must be cautious about over interpreting phylogenetic trees reconstructed using extant taxa. Given the dramatic nature of Quaternary climate oscillations in temperate regions, and the complete disappearance of vascular plants on Antarctica, it seems likely that inferences of direct long-distance dispersal could be misled by extinction events. For example, if *Myosotis* dispersed from Eurasia to New Zealand by establishing populations in intervening areas, subsequent extinction might result in phylogenies consistent with direct dispersal [21]. Clearly, it is difficult to discount completely missing links based on current molecular evidence. However, improved age estimates for extant Australian, New Guinean and subantarctic island forms with inferred New Zealand origins offer a potential solution. If molecular dates indicated that the contemporary taxa were present during the Quaternary then it would be difficult to explain why only these, and not the stepping-stone forms survived

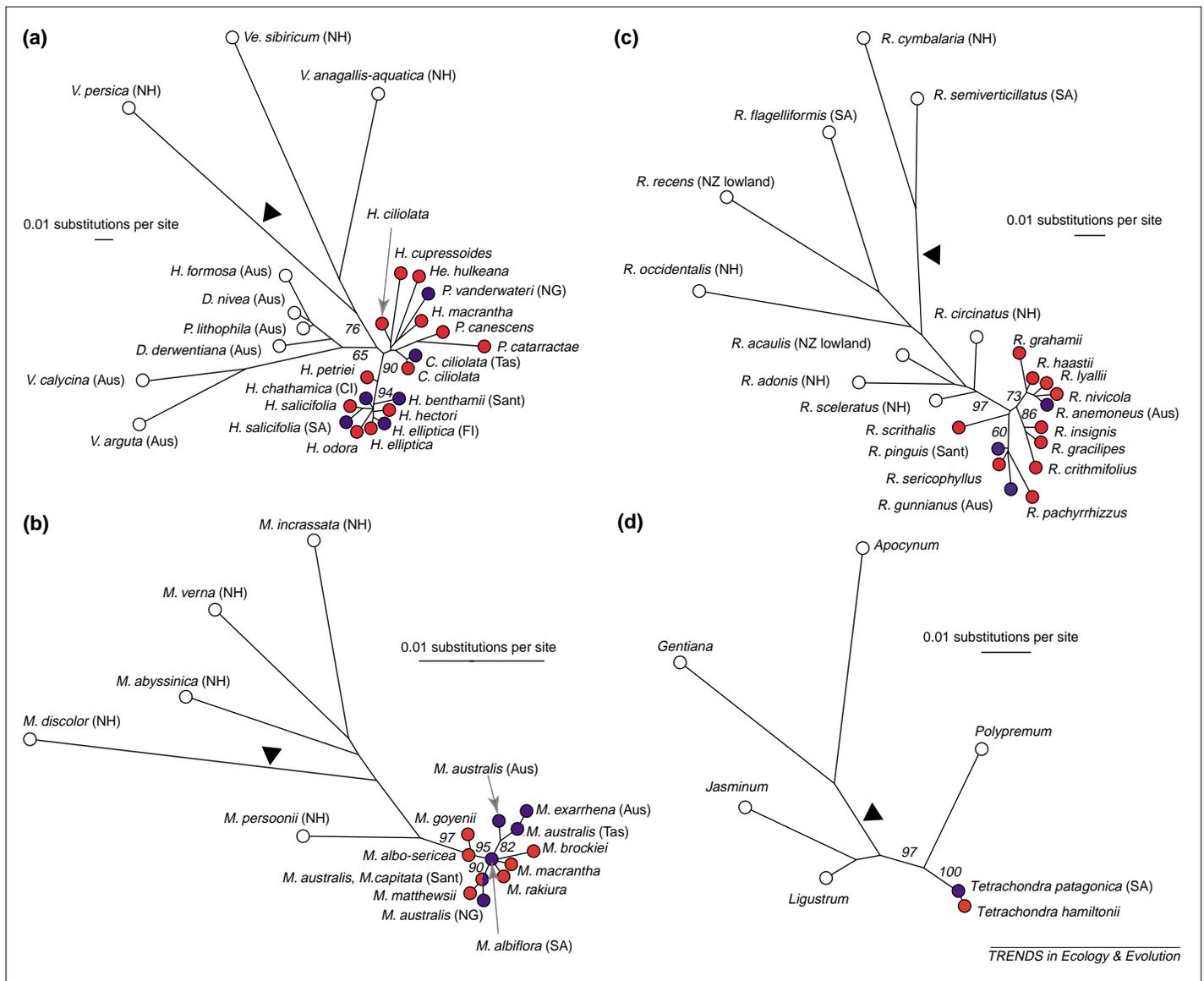


Fig. 2. Unweighted Least Squares trees (with branch lengths estimated from maximum likelihood distances made using a HKY 85 invariable sites model of sequence substitution [50]) for four herbaceous plant groups with transoceanic disjunct distributions in the Southern Hemisphere. Three groups, (a) *Hebe* [20], (b) *Myosotis* [21] and (c) *Ranunculus* [24], have centres of morphological diversity in New Zealand; the fourth (d) *Tetrachondra* [25] is a ditypic genus. Geographical distributions are indicated in two ways: (1) Coloured nodes: red, New Zealand; blue, other Southern Hemisphere landmasses; white, outgroup lineages; (2) Abbreviations: Aus, Australian mainland; CI, Chatham Islands; FI, Falkland Islands; NG, New Guinea; NH, Northern Hemisphere; NZ, New Zealand; Tas, Tasmania; SA, South America; Sant, subantarctic islands. Dispersal is inferred where related taxa occur on disjunct landmasses but are separated by only short branches in the reconstructed graphs (i.e. the short branch lengths suggest that the current distribution could not have arisen by vicariance). In each tree, the midpoint root position is indicated by a black triangle and bootstrap values (1000 iterations) are given for key branches.

the climatic instability. Such a result would suggest that stepping-stone hypotheses are improbable.

**Has establishment limited successful dispersal?** Palynological and molecular evidence offer differing perspectives on dispersal in the southern Pacific. The fossil record suggests transoceanic dispersal occurred throughout the Tertiary [5], whereas molecular analyses indicate that many successful dispersal events have occurred since the late Tertiary. That is, although opportunities for dispersal have existed for

at least the last 65 million years, many Southern Hemisphere plant distributions have arisen only within the last 10 million years. The discordance between the patterns inferred could be explained, in part, by the limitations of the data; the fossil record is limited by temporal and taxonomic resolution and molecular data by the extinction of taxa. However, these observations might also be explained if dispersal was limited by the availability of habitats that were suitable for establishment rather than by opportunities for movement. If so, then the climatic and geological changes of the late Tertiary and Quaternary were probably important determinants of contemporary distribution patterns in the Southern Hemisphere. For example, in New Zealand, the environmental instability of the late Tertiary and Quaternary clearly led to the formation of open habitats (Box 1), environments that could provide increased opportunities for the establishment of dispersed lineages.

As discussed previously, phylogenetic reconstructions for several alpine plant groups

**Table 1. Plant taxa for which phylogenetic reconstructions of molecular data indicate the occurrence of eastward transoceanic dispersal events**

Family	Genus or tribe	Inferred dispersal event	Refs
Apiaceae	<i>Aciphylla</i>	New Zealand → Chatham Islands	[38]
Asteraceae	Gnaphalieae	Australia → New Zealand <sup>a</sup>	[39]
Boraginaceae	<i>Myosotis</i> <sup>b</sup>	New Zealand → South America	[21]
Brassicaceae	<i>Cardamine</i>	Australia → New Zealand	[40]
Coriariaceae	<i>Coriaria</i>	New Zealand → South America	[41]
Corynocarpaceae	<i>Corynocarpus</i>	New Guinea → New Zealand	[42]
Fabaceae	<i>Montigena</i>	Australia → New Zealand	[43]
	<i>Sophora</i>	New Zealand → Pacific islands	[44]
		New Zealand → South America	
		New Zealand → Gough Island (South Atlantic Ocean)	
Myrtaceae	<i>Metrosideros</i>	New Zealand → Pacific islands	[29]
Nothofagaceae	<i>Nothofagus</i>	Australia → New Zealand	[45]
Pittosporaceae	<i>Pittosporum</i>	Australia → New Zealand	[46]
		Australia → Pacific islands	
Scrophulariaceae	<i>Hebe</i> <sup>b</sup>	New Zealand → South America	[20]
Stylidiaceae	<i>Oreostylidium</i>	Australia → New Zealand	[47]
Viscaceae	<i>Korthalsella</i>	Australia → New Zealand	[48]

<sup>a</sup>At least six dispersal events from Australia to New Zealand are indicated by the phylogeny. One event leading to the establishment of the *Anaphalioides*–*Helichrysum*–*Raoulia* clade, three dispersals within the genus *Euchiton*, and one event for both *Craspedia* and *Ozothamnus*.

<sup>b</sup>The molecular phylogeny for this example is illustrated in Fig. 2.

suggest that extant Australian, New Guinean or subantarctic island taxa are derived from New Zealand sources. An interesting possibility is that the radiation of plant groups in the New Zealand mountains during Pliocene and Pleistocene might have pre-adapted these lineages for subsequent establishment in the alpine areas of Australia and New Guinea, as well as on the subantarctic islands. That is, the morphological and physiological traits that adapt these plants to the New Zealand mountains might have also facilitated their establishment following dispersal. Although it seems plausible that adaptation to a given habitat in one location would aid the successful colonization of similar habitats in other areas, this hypothesis requires further investigation.

**Table 2. Plant taxa for which phylogenetic reconstructions of molecular data suggest that dispersal events have occurred in directions that are not explained by the west-wind drift**

Family	Genus	Inferred dispersal event	Refs
Asteraceae	<i>Anaphalioides</i>	New Zealand → New Guinea	[39]
Boraginaceae	<i>Myosotis</i> <sup>a</sup>	New Zealand → Australia	[21]
		New Zealand → New Guinea	
		New Zealand → subantarctic islands	
Gentianaceae	<i>Gentianella</i>	New Zealand → Australia	[49]
		South America → New Zealand	
Fabaceae	<i>Carmichaelia</i>	New Zealand → Lord Howe Island (Tasman Sea)	[43]
Ranunculaceae	<i>Ranunculus</i> <sup>a</sup>	New Zealand → Australia	[24]
		New Zealand → subantarctic islands	
Scrophulariaceae	<i>Chionohebe</i> <sup>a</sup>	New Zealand → Australia	[20]
	<i>Hebe</i> <sup>a</sup>	New Zealand → subantarctic islands	[20]
	<i>Parahebe</i> <sup>a</sup>	New Zealand → New Guinea	[20]
Tetrachondraceae	<i>Tetrachondra</i> <sup>a</sup>	South America → New Zealand	[25]

<sup>a</sup>The molecular phylogeny for this example is illustrated in Fig. 2.

### Dispersal mechanisms

Together, molecular and fossil data provide convincing evidence for the importance of transoceanic dispersal in establishing plant distributions in the southwestern Pacific. However, we have only a limited knowledge of the mechanisms that have transported propagules around the southern Pacific. Our generally poor understanding of long-distance dispersal mechanisms in plants has been, and remains, an obstacle to explaining the transoceanic distributions of plant lineages.

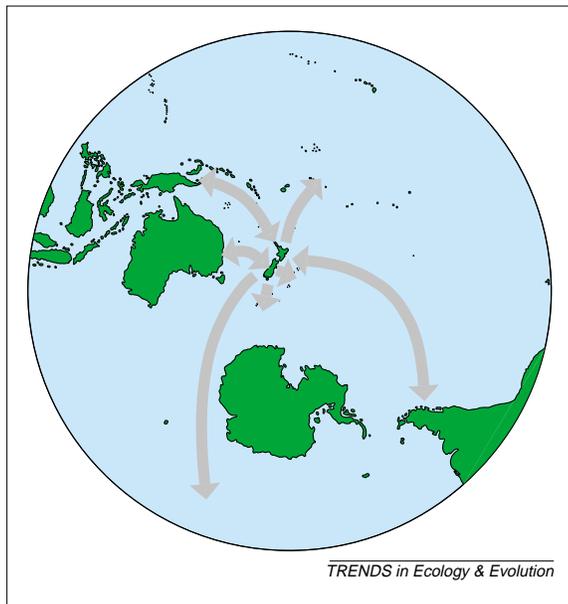
In the southwestern Pacific, wind currents might disperse small, lightweight angiosperm seeds or the spores of nonvascular plants and fungi [28]. Indeed, wind dispersal has been advocated for *Metrosideros* [29], orchids [28] and ferns [30,31], all of which have small propagules. The dominance of west-wind drift at high southern latitudes [6] suggests that wind transport would probably carry propagules eastward, an observation that is consistent with molecular data for *Metrosideros* [29]. However, within individual weather systems, cyclonic airflow might provide opportunities for wind dispersal against the westerly trend [8]. The potential for such movements was recently demonstrated by the first manned balloon flight from New Zealand to Australia [32].

Although some Southern Hemisphere plant distributions can be explained by wind-mediated transport, this mechanism is probably responsible for only a small proportion of successful dispersal events in the southern Pacific [28,33]. In part, this reflects the fact that many lineages produce fruits or seeds that are unsuitable for wind dispersal. However, even for groups that are well adapted for wind transport, the mechanism is strongly distance dependent, suggesting that it is unlikely to be an effective means of crossing the vast southern Pacific Ocean [28,33]. Instead, biotic vectors, especially birds, might be important for mediating plant dispersal [28,30,33]. In the Southern Hemisphere, one potential group of dispersal agents are the transoceanic wanderers (e.g. albatross, petrels and shearwaters) that regularly travel between southern Pacific landmasses. Another important group might be avian migrants, visitors or stragglers, birds that either regularly or more rarely journey across the Pacific [30]. Although bird-mediated transport would probably be affected by the same weather systems that influence wind dispersal, observations suggest that this mechanism can transport propagules over very long distances and in various directions [28,33].

### Conclusion and prospects

There is now compelling evidence for the importance of dispersal in establishing plant distributions in the southwestern Pacific. Although molecular phylogenetic analyses for various plant groups confirm inferences from palynological and distributional data, they also suggest that patterns of Southern Hemisphere dispersal are more complex than was previously recognized. The west-wind drift and circumpolar

Fig. 3. Transoceanic dispersal events inferred from molecular data for New Zealand plant groups. Pathways of dispersal 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. The molecular phylogenetic studies summarized in this illustration are listed in Tables 1 and 2.



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marine currents have not limited plant dispersal in the southern Pacific, instead plant propagules have been carried in many directions. In addition to identifying patterns of dispersal, molecular analyses suggest that many contemporary Southern Hemisphere plant distributions have arisen since the late Tertiary. This observation probably reflects the influence of Pliocene and Pleistocene environmental changes on the lineage extinction and, perhaps more importantly, on the establishment of dispersed lineages.

In spite of important recent advances in our understanding, there are several avenues for further research. We need to test and extend these new

hypotheses for the assembly of contemporary Southern Hemisphere floras with additional, independent molecular markers. In particular, the additional sequence data will be useful for improving age estimates of successful dispersal events. Shared phylogenetic pattern does not necessarily imply temporal congruence [34], and so age information is crucial for identifying periods in which dispersal and rapid diversification have been prominent features of plant evolution. To complement recent molecular studies, further research should be directed towards groups with contrasting distribution patterns. Although the results to date have been important, lineages with differing distributions are now of particular interest, because of their potential to highlight additional patterns of dispersal. Also interesting are groups such as the Araucariaceae, Podocarpaceae and Winteraceae that have long fossil records in New Zealand [5], but for which there is still little molecular data [35,36]. Although dispersal has added many plant lineages to the New Zealand flora, the long record of these taxa suggests an older, perhaps Gondwanan, ancestry.

The significance of conclusions from studies in the southern Pacific area are unlikely to be restricted to just this region as similar questions also arise in Northern Hemisphere floras [37]. In particular, the well-understood prehistory of New Zealand provides a unique opportunity to pursue answers to general questions of plant evolution. Unravelling the complex evolutionary histories of the flora of New Zealand promises important insights into the patterns and processes that shape species radiation and morphological innovation in plants.

#### References

- Craw, R. (1989) New Zealand biogeography: a panbiogeographic approach. *N. Z. J. Zool.* 16, 527–547
- Pole, M. (1994) The New Zealand flora – entirely long-distance dispersal? *J. Biogeogr.* 21, 625–635
- Hooker, J.D. (1853) *Botany of the Antarctic Voyage of H.M. Discovery ships 'Erebus' and 'Terror' in the Years 1831–1843*, Reeve
- Fleming, C.A. (1979) *The Geological History of New Zealand and its Life*, Auckland University Press
- Mildenhall, D. (1980) New Zealand late Cretaceous and Cenozoic plant biogeography – a contribution. *Palaeoogeogr. Palaeoecol.* 31, 197–223
- Raven, P.H. (1973) Evolution of subalpine and alpine plant groups in New Zealand. *N. Z. J. Bot.* 11, 177–200
- Macphail, M.K. (1997) Comment on M. Pole (1994): 'The New Zealand flora – entirely long-distance dispersal?' *Journal of Biogeography* 21, 625–635. *J. Biogeogr.* 24, 113–117
- Wardle, P. (1978) Origin of the New Zealand mountain flora, with special reference to trans-Tasman relationships. *N. Z. J. Bot.* 26, 535–550
- Swenson, U. and Bremer, K. (1997) Pacific biogeography of the Asteraceae genus *Abrotanella* (Senecioneae, Blennospermatinae). *Syst. Bot.* 22, 493–508
- Renner, S.S. *et al.* (2000) Timing transantarctic dispersal in the Antherospermataceae (Laurales): evidence from coding and noncoding chloroplast sequences. *Syst. Biol.* 49, 579–591
- Pole, M. (2001) Can long distance dispersal be inferred from the New Zealand plant fossil record? *Aust. J. Bot.* 49, 357–366
- Cockayne, L. (1967) *New Zealand Plants and their Story* (4th edn), Government Printer
- Dawson, J.W. (1963) Origins of the New Zealand alpine flora. *Proc. N. Z. Ecol. Soc.* 10, 12–15
- Schuettpelz, E. *et al.* (2002) Multiple origins of Southern Hemisphere *Anemone* (Ranunculaceae) based on plastid and nuclear sequence data. *Plant Syst. Evol.* 231, 143–151
- Dawson, J.W. (1971) Relationships of the New Zealand *Umbelliferae*. In *The Biology and Chemistry of the Umbelliferae* (Heywood, V.H., ed.), pp. 43–61, Academic Press
- Webb, C.J. (1986) Breeding systems and relationships in *Gingidia* and related Australasian Apiaceae. In *Flora and Fauna of Alpine Australasia* (Barlow, B.A., ed.), pp. 383–399, CSIRO
- Barker, P.F. and Burrell, J. (1982) The influence upon Southern Ocean circulation, sedimentation, and climate of the opening of Drake Passage. In *Antarctic Geoscience* (Craddock, C., ed.), pp. 377–385, University of Wisconsin Press
- Stewart, R.B. and Neall, V.E. (1984) Chronology of palaeoclimatic change at the end of the last glaciation. *Nature* 311, 47–48
- Close, R.C. *et al.* (1978) Aerial dispersal of biological material from Australia to New Zealand. *Int. J. Biometeorol.* 22, 1–19
- Wagstaff, S.J. and Garnock-Jones, P.J. (2000) Patterns of diversification in *Chionohebe* and *Parahebe* (Scrophulariaceae) inferred from ITS sequences. *N. Z. J. Bot.* 38, 389–407
- Winkworth, R.C. *et al.* The origins and evolution of the genus *Myosotis* L. (Boraginaceae). *Mol. Phylog. Evol.* (in press)
- Bremer, K. (1993) Intercontinental relationships of African and South American Asteraceae – a cladistic biogeographic analysis. In *Biological Relationships between Africa and South America* (Goldblatt, P., ed.), pp. 105–135, Yale University Press
- Bremer, K. and Humphries, C.J. (1993) Generic monograph of the Asteraceae-Anthemideae. *Bull. Nat. Hist. Mus. London Bot. Ser.* 23, 71–177
- Lockhart, P.J. *et al.* (2001) Phylogeny, dispersal and radiation of New Zealand alpine buttercups: molecular evidence under split decomposition. *Ann. Missouri Bot. Gard.* 88, 458–477
- Wagstaff, S.J. *et al.* (2000) Divergence estimates of *Tetrachondra hamiltonii* and *T. patagonica* (Tetracondraceae) and their implications for austral biogeography. *N. Z. J. Bot.* 38, 587–596
- Webb, P.N. and Harwood, D.M. (1993) Pliocene fossil *Nothofagus* (Southern Beech) from Antarctica: phytogeography, dispersal strategies, and survival in high latitude glacial-deglacial environments. In *Forest Development in Cold Climates* (Alden, J. *et al.*, eds), pp. 135–166, Plenum Press

- 27 Lee, D.E. *et al.* (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Aust. J. Bot.* 49, 341–356
- 28 Carlquist, S. (1996) Plant dispersal and the origin of the Pacific island floras. In *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes* (Keast, A. and Miller, S.E., eds), pp. 153–164, SPB Academic
- 29 Wright, S.D. *et al.* (2000) Riding the ice age El Niño? Pacific biogeography and evolution of *Metrosideros* subg. *Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proc. Natl. Acad. Sci. U. S. A.* 97, 4118–4123
- 30 McGlone, M.S. *et al.* (2001) Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. *J. Biogeogr.* 28, 199–216
- 31 Brownsey, P.J. (2001) New Zealand's pteridophyte flora – plants of ancient lineage but recent arrival? *Brittonia* 53, 284–303
- 32 Wallington, J. (2000) West across the Tasman. *Aust. Geogr.* 60, 75–87
- 33 Carlquist, S. (1967) The biota of long-distance dispersal. V. Plant dispersal to the Pacific Islands. *Bull. Torrey Bot. Club* 94, 129–162
- 34 Donoghue, M.J. *et al.* (2001) Phylogenetic patterns in Northern Hemisphere plant geography. *Int. J. Plant Sci.* 162 (Suppl.), S41–S52
- 35 Conran, J.G. *et al.* (2000) Generic relationships within and between the gymnosperm families Podocarpaceae and Phyllocladaceae based on an analysis of the chloroplast *rbcl*. *Aust. J. Bot.* 48, 715–724
- 36 Suh, Y. *et al.* (1993) Molecular evolution and phylogenetic implications of internal transcribed spacer sequences of ribosomal DNA in Winteraceae. *Am. J. Bot.* 80, 1042–1055
- 37 Comes, H.P. and Kadereit, J. (1998) The effect of Quaternary climatic changes on plant distribution and evolution. *Trends Plant Sci.* 3, 432–438
- 38 Radford, E.A. *et al.* (2001) Phylogenetic relationships of species of *Aciphylla* (Apiaceae, subfamily Apioideae) and related genera using molecular, morphological and combined data sets. *N. Z. J. Bot.* 39, 183–208
- 39 Breitwieser, I. *et al.* (1999) Phylogenetic relationships in Australasian Gnaphalieae (Compositae) inferred from ITS sequences. *N. Z. J. Bot.* 37, 399–412
- 40 Mitchell, A.D. and Heenan, P.B. (2000) Systematic relationships of New Zealand endemic Brassicaceae inferred from nrDNA ITS sequence data. *Syst. Bot.* 25, 98–105
- 41 Yokoyama, J. *et al.* (2000) Molecular phylogeny of *Coriaria*, with special emphasis on the disjunct distribution. *Mol. Phylog. Evol.* 14, 11–19
- 42 Wagstaff, S.J. and Dawson, M.I. (2000) Classification, origin and patterns of diversification of *Cornocarpus* (Cornocarpaceae) inferred from DNA sequences. *Syst. Bot.* 25, 134–149
- 43 Wagstaff, S.J. *et al.* (1999) Classification, origins, and patterns of diversification in New Zealand Carmichaelineae (Fabaceae). *Am. J. Bot.* 86, 1346–1356
- 44 Hurr, K.E. *et al.* (1999) Dispersal of Edwardsia section of *Sophora* (Leguminosae) around the Southern Oceans: molecular evidence. *J. Biogeogr.* 26, 565–577
- 45 Martin, P.G. and Dowd, J.M. (1993) Using sequences of *rbcl* to study phylogeny and biogeography of *Nothofagus* species. *Aust. Syst. Bot.* 6, 441–447
- 46 Gemmill, C.E.C. *et al.* (2002) Evolution of insular Pacific *Pittosporum* (Pittosporaceae): origin of the Hawaiian radiation. *Mol. Phylog. Evol.* 22, 31–42
- 47 Laurent, N. *et al.* (1999) Phylogeny and generic interrelationships of the Styliidiaceae (Asterales), with a possible extreme case of floral paedomorphosis. *Syst. Bot.* 23, 289–304
- 48 Molvray, M. *et al.* (1999) Phylogenetic relationships within *Korhalsella* (Viscaceae) based on nuclear ITS and plastid trnL-F sequence data. *Am. J. Bot.* 86, 249–260
- 49 Hagen, K.B. and Kadereit, J.W. (2001) The phylogeny of *Gentianella* (Gentianaceae) and its colonization of the southern hemisphere as revealed by nuclear and chloroplast DNA sequence variation. *Org. Div. Evol.* 1, 61–79
- 50 Swofford, D.L. (2001) *PAUP\*. Phylogenetic Analysis Using Parsimony (\*and Other Methods) Version 4*, Sinauer Associates

# Does parental divergence predict reproductive compatibility?

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Hybridization between populations or species can have either beneficial or detrimental effects on fitness. If these effects could be predicted based on the genetic or geographical distance between parents, this would be of great use to plant and animal breeders, managers and conservation biologists. The relationship between divergence and compatibility is also increasingly relevant to evolutionary biology, because recent work on the genetic architecture of reproductive isolation has fuelled a renewed interest in speciation rates and processes. Many studies have shown a correlation between parental divergence and both pre- and postzygotic isolation, but this relationship is clearly not strong enough to guide management decisions. Although it has been suggested that the speciation clock might tick at similar rates in different taxa, this appears to be far from true, because the divergence times resulting in hybrid vigor, outbreeding depression or partial reproductive compatibility vary widely both within and among taxonomic groups.

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Hybridization between divergent populations or species can result in increased fitness in some cases, but it is generally expected to result in reduced fitness [1]. Concern over these fitness effects is

increasing as the rate of anthropogenically induced hybridizations increases [2–6]. Some of these mixing events are accidental; for example, when farmed salmon (e.g. *Salmo salar*) escape from pens and mate with wild salmon, or when domesticated crop plants (e.g. *Oryza sativa*) cross with their wild relatives. However, other crosses are intentional. Hybridization has been used to induce HYBRID VIGOR (see Glossary) in domesticated plants and animals since before Darwin, and translocation between natural populations is increasingly being proposed as a management tool with which to bolster dwindling population sizes and to prevent INBREEDING DEPRESSION [7–9]. However, enthusiasm for this management method is tempered by concerns about OUTBREEDING DEPRESSION [3–5].

Can the consequences of hybridization be predicted from the degree of divergence between parents? In addition to its importance for conservation biology, this question is central to our understanding of speciation. The relationship between divergence and compatibility might be expected to be stronger if