Review

Evolution of New Zealand's terrestrial fauna: a review of molecular evidence

Julia Goldberg[1,*], Steven A. Trewick[2] and Adrian M. Paterson[3]

[1]Allan Wilson Centre for Molecular Ecology and Evolution, Institute of Molecular Biosciences, Massey University, Private Bag 11-222, Palmerston North 5301, New Zealand
[2]Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11-222, Palmerston North 5301, New Zealand
[3]Bio-protection and Ecology Division, Lincoln University, PO Box 84, Lincoln 7647, New Zealand

New Zealand biogeography has been dominated by the knowledge that its geophysical history is continental in nature. The continental crust (Zealandia) from which New Zealand is formed broke from Gondwanaland *ca* 80 Ma, and there has existed a pervading view that the native biota is primarily a product of this long isolation. However, molecular studies of terrestrial animals and plants in New Zealand indicate that many taxa arrived since isolation of the land, and that diversification in most groups is relatively recent. This is consistent with evidence for species turnover from the fossil record, taxonomic affinity, tectonic evidence and observations of biological composition and interactions. Extinction, colonization and speciation have yielded a biota in New Zealand which is, in most respects, more like that of an oceanic archipelago than a continent.

Ke words:

be taken as evidence of a dominant role of continental drift in the origination of the biota. Unfortunately, it is just this supposition that is widely made. The addition of timing of divergence is necessary to choose between the three meanings of Gondwanan.

a young oceanic island and/or a high level of extinction. Isolation ensures that only a subset of nearby continental faunas will be represented on the islands and the lack of great age of the island would account for the low diversity levels. Very commonly, the New Zealand biota is described as 'unique' and unlike anything elsewhere. Diamond (1997) described the biology as 'the nearest approach to life on another planet'. In fact, the nature of the biota is inconsistent with the process to which it is frequently ascribed because,

(i) physical isolation does not equate to biological isolation,
(ii) all biotas are unique,

> Islands resemble one another in that each is unique
>
> (Quammen 1996)

(iii) species endemicity is usually high on oceanic islands,

> New Zealand ranks alongside island groups like Hawaii and the Galápagos Islands for its levels of endemism.
>
> (Gibbs 2006, p. 12)

(iv) distinctive taxa are common products of evolution on islands, and
(v) disharmonic biotas are best and usually explained as resulting from stochastic colonization and extinction (Carlquist 1965).

> Trans-oceanic dispersal by air and water from neighbouring continental areas and islands was thought to have played quite an important role at all times in New Zealand's history in assembly of the disharmonic fauna and flora of the Archipelago
>
> (Gaskin 1975, p. 87).

If New Zealand was isolated since 80 Ma, we would expect it to support the descendants of a Zealandian biota with high diversity, complex coevolutionary associations, endemicity at deeper taxonomic/phylogenetic levels and a more complete faunal composition.

(b) *Ancient lineages and living fossils*

Several 'ancient' lineages have been identified within the New Zealand biota. For example, the tuatara (Sphenodon

(Baker *et al.* 1995; Burbidge *et al.* 2003). Moa are inferred as speciating after the Oligocene, even though calibration assumed that moa ancestors have been in New Zealand since isolation from Australia (Baker *et al.* 2005).

(ii) *Harvestmen*

The Pettalidae family of morphologically conserved harvestmen are found in leaf litter and have a classic Gondwanan distribution (Boyer & Giribet 2007). Despite finding that most groups within this family form monophyletic continental clades, New Zealand is home to three different lineages represented by the genera *Neopurcellia*, *Rakaia* and *Aoraki* (Boyer & Giribet 2007). Contrary to the inference of a vicariant history to explain this pattern, the levels of molecular divergence among the pettalid lineages are too low to be consistent with an ancient origin, unless there has been a very substantial taxon specific change in mutation rate. Diversity and spatial structuring on South Island mountains that are *ca* 5 Ma old suggest an arrival within the past few million years.

(iii) *Other examples*

In recent years, other examples of purported 'ancient Gondwanan lineages' have been shown to have

New Guinea and Lord Howe) (Suter 1916; Ponder *et al.* 2003). Despite the fact that most of these islands emerged from beneath the ocean, this distribution has

(Raven 1973), Antarctica (Hooker 1860), or northern boreal habitats) and (ii) radiation and adaptation in New Zealand during the Pleistocene glacial epoch. A third alternative can be added: evolution in New Zealand in response to the development of an alpine zone on mountain ranges that emerged during the Pliocene. In the North Island, the ranges are less extensive and even younger (*ca* 1 Ma) than those in South Island. The to the presence of Pliocene islands that subsequently united to form Northland, New Zealand. Carnivorous snails of the Rhytididae have an intriguing distribution that encompasses Gondwanan landmasses as well as Pacific archipelagos. The subfamily Paryphantinae contains four genera, including the kauri snails, *Paryphanta*, is almost entirely limited to Northland and some offshore islands in this region and is among taxa that might have experienced population subdivision during the Pleistocene (Fleming 1979). Spencer *et al.* (2006) found that speciation probably did happen in the Pliocene, but they failed to find spatial patterns consistent with Pliocene vicariance events. A similar complex pattern, developed since the Pliocene, exists among *Oligosoma* skinks in the region (Hare *et al.* 2008).

(ii) *Tree weta*

The New Zealand tree weta *Hemideina thoracica* is an arboreal herbivore. It is flightless like all other Anostostomatidae (Orthoptera) species in New Zealand, and it is confined to North Island. Analysis of mitochondrial DNA sequences revealed higher genetic diversity in northern populations of *H. thoracica* than in the south of the island (Morgan-Richards *et al.* 2001) and indicated that genetic diversity, genetic distances, spatial distribution of mitochondrial lineages and chromosome races are consistent with simultaneous formation of at least five isolated populations on Pliocene islands in northern New Zealand (figure 6).

(iii) *Other examples*

Several New Zealand insect groups have distributions that extend from North Island into northern South Island, which are indicative of recent range expansion (e.g. *Clitarchus* stick insects: Trewick *et al.* 2005; tree weta: Trewick & Morgan-Richards 2005). Such range shifts probably reflect [illegible] islands (Daugherty et al

phases of Zealandian and New Zealand geophysical history ought to provide the basis for rather more sophisticated hypotheses about which periods were most evolutionarily influential. Major events since separation of Zealandia include K/T asteroid impact, Oligocene submergence, Miocene and Plio-Pleistocene climate change, Pliocene orogenics and Pleistocene volcanics.

4. C C

To advance our understanding of the evolutionary history of New Zealand, we especially need more molecular studies, in an appropriate taxonomic framework linking New Zealand fauna to their counterparts in other parts of Australasia, the Pacific and the world. There are relatively few such studies of terrestrial animals but rather more to date on plant taxa. The presumption that the New Zealand fauna is captive and thus monophyletic is untenable and inappropriate as a starting point, if meaningful inferences of biological

Breitwieser, I. & Ward, J. M. 2003 Phylogenetic relationships and character evolution in New Zealand and selected Australian Gnaphalieae (Compositae) inferred from morphological and anatomical data. Bot. J. Linn. Soc. **141**, 183–203. (doi:10.1046/j.1095-8339.2003.00141.x)

Brown, B., Emberson, R. M. & Paterson, A. M. 1999 Phylogeny of "Oxycanus" lineages of hepialid moths from New Zealand inferred from sequence variation in the mtDNA COI and II gene regions. Mol. Phylogenet. Evol. **13**, 463–473. (doi:10.1006/mpev.1999.0662)

Buckley, T. R. & Simon, C. 2007 Evolutionary radiation of the cicada genus Maoricicada Dugdale (Hemiptera: Cicadoidea) and the origins of the New Zealand alpine biota. Biol. J. Linn. Soc.

spo1416.e7(k)0(1i[(do)1ss.)1625561.2(er).5(s(i)1.7270.37(79)5829.63)16.7(3)8(4:)2(389)TT)3125.0198 -Mo3(y(l3.175040(E9.538((v)1983.l)14.1(c)0

Duthie, C., Gibbs, G. & Burns, K. C. 2006 Seed dispersal by weta. *Science* **311**, 1575. (doi:10.1126/science.1123544)
Ecroyd, C. E. 1996 The ecology of *Dactylanthus taylorii* and threats to its survival. *New Zeal. J. Ecol.* **20**, 81–100.
Emerson, B. C. & Kolm, N. 2005 Species diversity can drive speciation. *Nature* **434**, 1015–1017. (doi:10.1038/nature03450)

Kishino, H., Thorne, J. L. & Bruno, W. 2001 Performance of a divergence time estimation method under a probabilistic model of rate evolution. *Mol. Biol. Evol.* **18**, 352–361.

Knapp, M., Stöckler, K., Havell, D., Delsuc, F., Sebastiani, F. & Lockhart, P. J. 2005 Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (southern oxidase 1 gene. *Mollusc. Res.* **23**, 159–178. (doi:10.1071/MR03001)

Pratt, R. C., Morgan-Richards, M. & Trewick, S. A. 2008 Diversification of New Zealand weta (Orthoptera: Ensifera: Anostostomatidae) and their relationships in Australasia. *Phil. Trans. R. Soc. B* **363**, 3427–3437. (doi:10.1098/rstb.2008.0112)

Quammen, D. 1996 *The song of the dodo: island biogeography in an age of extinctions*. New York, NY: Scribner.

Raven, P. H. 1973 Evolution of subalpine and alpine plant groups in New Zealand. *New Zeal. J. Bot.* **11**, 177–200.

Robertson, A. W., Kelly, D., Ladley, J. J. & Sparrow, A. D. 1999 Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). *Conserv. Biol.* **13**, 499–508. (doi:10.1046/j.1523-1739.1999.97471.x)

Robertson, A. W., Ladley, J. J. & Kelly, D. 2005 Effectiveness of short-tongued bees as pollinators of apparently ornithophilous New Zealand mistletoes. *Austral Ecology* **30**, 298–309. (doi:10.1111/j.1442-9993.2005.01474.x)

Roelants, K. & Bossuyt, F. 2005 Archaeobatrachian paraphyly and Pangaean diversification of crown-group frogs. *Syst. Biol.* **54**, 111–126. (doi:10.1080/10635150590905894)

Sanmartin, I. & Ronquist, F. 2004 Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Syst. Biol.* **53**, 216–243. (doi:10.1080/10635150490423430)

Sanmartin, I., Wanntorp, L. & Winkworth, R. C. 2007 West Wind Drift revisited: testing for directional dispersal in the Southern Hemisphere using event-based tree fitting. *J. Biogeogr.* **34**, 398–416. (doi:10.1111/j.1365-2699.2006.01655.x)

Shepherd, L. D. & Lambert, D. M. 2007 The relationships and origins of the New Zealand wattlebirds (Passeriformes, Callaeatidae) from DNA sequence analyses. *Mol. Phylogenet. Evol.* **43**, 480–492. (doi:10.1016/j.ympev.2006.12.008)

Sinclair, B. J., Worland, S. M. & Wharton, D. A. 1999 Ice nucleation and freezing tolerance in New Zealand alpine