A giant eagle swoops on moa.
Credit: John Megahan

Vicars & Vagrants

BY STEVE TREWICK

DNA studies of New Zealand's birds are causing a rethink of the importance of colonisation events in the evolution of its endemic species.

Many of the species found on an island do not occur anywhere else in the world. The number of these "endemic" species indicates how long that island's animal and plant life have been isolated, but the significance of endemicity is difficult to judge from looks alone. DNA sequence data are helping to solve this mystery.

The islands of New Zealand provide an especially intriguing case. Most islands are formed by undersea volcanoes, so we know that they initially supported no life. However, New Zealand is different. It was formed from continental crust that was previously part of the supercontinent Gondwana, so it is possible that some land has been above water and supporting life since Zealandia broke away from Gondwana.

For that reason it is often supposed that New Zealand's biota evolved in isolation over a long time. However, analysis of genetic data have changed this view and shown that New Zealand is not a museum of old species but a vibrant if enigmatic evolutionary system.

Most striking have been the revelations concerning New Zealand's birds. The closest living relative of the world's largest eagle is the Australian little eagle, and the giant wingless moa have emerged as relatives of much smaller flying birds, the tinamou of Central America. Such discoveries are rendered even more remarkable by the fact that the giant eagle and all species of moa are extinct, and their evolutionary narrative has been relayed through DNA remnants retrieved from fossil bones.

Populations that are sufficiently isolated can evolve into distinct species, so it is no surprise that most islands harbour endemic species (as famously observed by Charles Darwin in the Galapagos). Endemicity at deeper taxonomic levels tends to take longer to evolve.

If Zealandia's biota ~80 million years ago had remained confined and separate from other biotas we might expect the New Zealand fauna and flora to be dominated by endemic species, with most belonging to families found nowhere else in the world. Indeed, some examples do exist among the birds. For instance moa, kiwi, New Zealand wrens, adzebill and wattlebirds are all endemic families. These could be the biogeographic "vicars" of New Zealand's avifauna, originating from ancient vicariance (see *Vicariance and Dispersal* on following page).

However, many less-distinctive taxa are only endemic at the genus or species level. Indeed New Zealand actually shares some species with other countries, such as the swamphen and boobok owl in Australia.

Other New Zealand birds have their closest relatives in the region. For example, relatives of New Zealand parakeets are in Norfolk Island and New Caledonia, the kingfisher occurs from Pacific islands to Indonesia, and the extinct merganser (*Mergus australis*) was far removed from the usual range of this bird group in the Northern Hemisphere.

Thus some of New Zealand's birds appear evolutionarily distinct but many are very close relatives of birds found elsewhere in the world.

A long-established but isolated biota on a relatively large archipelago like New Zealand might also be expected to have a high level of local diversity in each endemic family or genus. These species radiations are even prominent on smaller oceanic islands of smaller area. For example, there are 15 species of Galapagos "finch" and 20 Hawaiian honeycreepers.

However, the predominant pattern in New Zealand is for only a few species per lineage even when taking into account extinctions that have occurred since the arrival of humans. For example, New Zealand had two owls (Australia has seven), one kingfisher (Australia has eight), three falcon/eagles (Australia has 24) and two honeyeaters (Australia has 74). The most extensive New Zealand bird radiations are the ~10 moa, five kiwi, five wrens and three wattlebirds.

Molecular Studies

Comparison of DNA sequence data allows testing of species relationships independently of morphological or behavioural characteristics that can make species appear more or less related than they really are.

For instance, among the ground-living rail family (Rallidae) there are a number of wholly flightless species on New Zealand and other islands. Some New Zealand rails were initially treated as endemic genera but have since been shown to belong within widespread genera.

Flightless species often look very different from their flying relatives but similar to one another. Phylogenetic analysis of DNA sequences, however, indicates that each island rail species evolved independently from a flying colonist ancestor rather than from another flightless rail. In most cases the ancestral colonist is now extinct.

New Zealand and nearby islands have thus assembled at least 10 species of endemic rail not by species radiation in the normal sense but by accumulation following a sequence of colonisation events (Fig. 1). This cumulative process may well be more important in the development of New Zealand's birds and biota than has been recognised.

Molecular data also make it possible to estimate the time since evolutionary separation of species, and this provides evidence for the pace of morphological change. The now-extinct New Zealand giant eagle, which had a massive wingspan of ~3 metres, was assumed to have evolved in ancient times to feed on moa, and

Zealandia Past and Present

As New Zealand formed from part of Zealandia, it is reasonable to suppose that the ancestry of New Zealand's plants and animals could be traced to the formation of Zealandia, but most of this continent is now beneath the sea.

Reconstructions from geological data (left) indicate that Zealandia originated as a strip on the eastern margin of Gondwana about 90 million years ago. After it rifted away, Zealandia was stretched and thinned over ~60 million years and submerged, where most of it remains today (right).

New Zealand as we recognise it today started to form about 25 million years ago following activation of the Australian/Pacific continental plate boundary. Indeed, geologists tell us that if the current level of tectonic activity at the plate boundary was not pushing new crust to the surface, New Zealand would subside into the ocean.

While the numerous earthquakes experienced by New Zealanders are unsettling and often destructive, they are also the reassuring signal that land-building processes are operating.

LEFT: Gondwanan palaeogeography at ~100 Ma showing the inferred position of Zealandia.
RIGHT: Zealandia is now mostly beneath the sea.
Modified from originals by Nick Mortimer of GNS Science, New Zealand.

Figure 1. The flightless takahe *Porphyio hochstetteri* (top left) and flying swamphen or pukeko *P. porphyrio* (bottom right; image credit Juan Carlos Ramirez) are related, but molecular and fossil evidence indicates that the swamphen arrived in New Zealand about 300 years ago and probably from Australia – after the takahe evolved. It is likely that in some earlier time a separate swamphen colonisation provided the takahe ancestor, and probably in yet another event the ancestor of a second extinct species of takahe, *Porphyrio mantelli* (top right). Curiously, takahe plumage is more similar to the swamphen *P. madagascariensis* from Africa (bottom left; image credit Juan Sagardia) than the one from Australia, implying a shared ancestry that is also supported by molecular data.

was placed in its own endemic genus. However, while it certainly hunted moa, DNA data indicate that the giant eagle is best placed in the same genus as its nearest living relative, the little eagle of Australia (~1.2 metre wingspan). Their common ancestor probably lived just 1–2 million years ago.

Furthermore, our understanding of the history of the giant eagle's prey has recently changed. Moa are large, literally wingless walking birds long thought to be "vicars" originating during the separation of Zealandia from Gondwana. Molecular studies of DNA collected from fossil bones up to 4000 years old have shown that taxonomists originally described too many species – more than 30 – based on their morphology. In fact, many of these were members of the same species collected in different parts of New Zealand or were males and females of the same species (females were about twice as heavy as males).

It is now thought that radiation of the 10 species of moa now recognised occurred less than 5 million years ago, and that the closest living relatives of moa are not other large flightless ratites like ostrich and emu but a group of smaller flying palaeognaths called tinamou that today live in South America. However, New Zealand's other small ratites, kiwi, appear to be most closely related to the Australian emu despite their very different size and ecology.

Molecular data have revealed other curiosities, including evidence that the New Zealand wrens (Acanthasittdae) may be the sister group to all other songbirds in the world. This hints at an ancient ancestry of the family, and it is tempting to assume that this ancestry originated in Zealandia. However, molecular phylogenies cannot prove this, and there are too few fossil song-birds to confirm that closer relatives of these wrens have not become extinct in other parts of the world relatively recently.

Just as evolutionary trees built from molecular data do not show directly where a lineage has existed before the present, they do not show when traits evolved. For example, even though New Zealand has a temperate climate it unusually has several endemic species of parrot. Particularly odd are kea that live in the alpine zone and kakapo that are even stranger and are placed in an endemic tribe of their own.

Kakapo have this taxonomic distinction because of their combi-nation of large size, nocturnal habit, lack of flight and unusual

Vicariance and Dispersal

Vicariance (left) occurs where geophysical processes split existing populations, and is usually assumed for continental areas. *Dispersal* (right) is required for oceanic islands where the biota has only come from immigrating species.

However, vicariance and dispersal are just different perspectives on the same process. Both scenarios involve the expansion of species range followed by isolation of the populations to enable their independent evolution or extinction.

Under vicariance, species move to occupy habitat that is subsequently subdivided by a geophysical mechanism such as continental drift. The populations are divided, and differentiation will occur if gene flow between populations is sufficiently low.

Similarly, infrequent dispersal and establishment events result in the occupation of separate habitat patches (e.g. volcanic islands emerging in the ocean). Independent evolution is the outcome if subsequent gene flow is infrequent.

Evolution by via natural selection and/or stochastic genetic drift (different morphs of black creatures in the figure), in concert with colonisations (grey dashed arrows) and extinctions (grey creatures), dictate the composition of regional biotas.
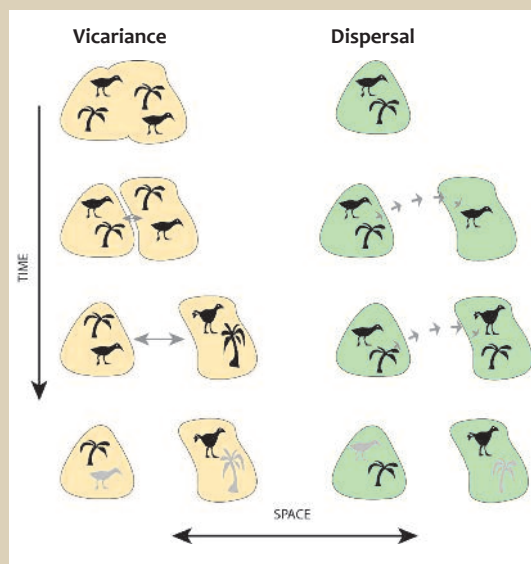
breeding system, where males attract mates with vocal displays but provide no paternal care. Although kakapo look and behave unlike other parrots, and molecular phylogenetics shows their lineage arose early among the parrot family, we cannot tell how far back in the past their peculiar traits evolved.

Very distinctive species like this and the burly, turkey-sized adzebill, which has no near relative living in the world, are the most difficult to interpret biogeographically.

Enough Is Enough

The modern islands of New Zealand cover about 270,000 km² and lie some 1500 km from Australia. About 245 species of breeding birds were present when people first arrived ~700 years ago. Many of these are wide-ranging seabirds, which naturally move between land areas as they feed at sea.

Species found only on offshore islands also contribute to the New Zealand bird count, so the main islands actually supported only about 95 species of native breeding non-marine birds. As we have seen, these are an eclectic mix from highly distinctive species to those that are also found in other countries. The pace of evolution is erratic, so although some of the more distinctive forms might be vicars descended from the Zealandian biota, many are descended from "vagrants".

The importance and rapidity of over-sea colonisation in other parts of the world is obvious from the diverse terrestrial life that exists on volcanic islands such as the Hawaiian archipelago (>4000 km from continental land) and from observations of islands formed in recent human history (e.g. Krakatau, Indonesia; Surtsey, Iceland). The rapid arrival of plants, animals and their propagules on such islands shows that there is a fairly constant rain of potential immigrants. Most of them probably die in the sea, or upon reaching land find the habitat unsuitable or competition from existing occupants too intense. Habitats already occupied by other species will be less easily colonised by vagrants, so their evolutionary importance often goes unnoticed.

It has been commonplace to attribute New Zealand's distinctive biology to its supposed ancient isolation. One reason for this is that dispersal is usually thought to be rare because actual dispersal events are rarely observed.

However, there are other ways to estimate dispersal frequency. We know, for instance, that during the past 150 years at least 10 species of bird have colonised New Zealand and established breeding populations. This equates to a rate of more than 66,000/million years, from which we can extrapolate that 1.65 million successful bird establishments could have occurred in the past 25 million years since tectonic activity started the formation of New Zealand.

Ornithologists have also recorded 137 vagrant species (without established populations) in New Zealand. This conservative estimate of the number of times that foreign birds have reached New

Pukeko have successfully colonised New Zealand in recent times.

Zealand indicates a dispersal rate over 900,000/million years, or 22.5 million potential dispersals in the past 25 million years.

Considering there are only about 9000 species of bird in the world today, it is clear that the potential rate of dispersal and colonisation is very high. Thus dispersal is unlikely to be limiting colonisation opportunities, and although colonisation is less frequent (about 1/13th in this case) it nevertheless indicates a formidable capacity for the development of a biota.

It would seem likely that the colonisation potential of different types of birds and other organisms depends on factors affecting their likelihood of dispersing (e.g. abundance, storms) and becoming established (e.g. habitat availability). However, among the recent successful New Zealand colonists are the pukeko, a large (1 kg) ground bird with ungainly and seemingly weak flight found in swamps and grassland, and the silvereye, a tiny (11 g) songbird of scrub and forest. The success of both implies that the frequency of dispersal is sufficiently high to facilitate the colonisation of diverse types of bird even if the process is largely a lottery.

Conclusion

The assembly of New Zealand's avifauna appears to have been more strongly influenced by recent evolutionary processes than previously thought. Colonisation and speciation have occurred in geologically recent time, and new species continue to arrive.

We know that human colonisation of New Zealand led to the extinction of many bird species, and also modified the environment in ways that provided opportunity for colonist birds. However, it is not just humans that modify the environment, and habitat availability has likely been influenced over a longer time frame by changing land area, topography, climate and catastrophic events. These will have caused extinction, but also provided novel evolutionary opportunities for surviving lineages and new arrivals – for vicars and vagrants alike.

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