In northeastern New Guinea, the ongoing collision of the Finisterre and Sarawaged ranges with the Bismarck volcanic arc causes uplift of the north coast of the Huon Peninsula at averaged rates of 1–3 mm/yr. Study of raised coral terraces on the peninsula has yielded a high-quality record of fluctuations in sea level during the Late Quaternary. At the same time the Finisterre mountain mass rides southward and causes the down-warping of the northern end of the Papuan peninsula, which is subsiding at rates of up to 5 mm/yr.

In eastern New Guinea, active sea floor spreading in the Woodlark Basin is advancing westward and causing north-south extension of the mainland and adjacent islands. One result is the emergence in the Pliocene of domes and half-domes of metamorphic rocks by low-angle extensional faulting. Another is the opening of small rift basins offshore. Spreading within the last 1.2 million years has caused the separation of Misima Island from a position adjacent to Woodlark (Muyua) Island (152.8° E).

ECONOMIC ASPECTS

Oil is produced from Miocene reefs in the Salawati Basin. A 17-trillion cubic foot reserve of gas beneath Bintuni Bay is being developed for export as liquefied natural gas (LNG). In Papua New Guinea oil and gas are produced from structures in the fold belt. Copper and gold are produced from major mines at Grasberg and Ok Tedi, and gold from Porgera and Lihir Island. In the eastern Bismarck Sea (Manus Basin), gold and base metal sulfide mineralization on the sea floor is associated with active spreading ridges.

SEE ALSO THE FOLLOWING ARTICLES

Earthquakes / New Guinea, Biology / Plate Tectonics / Pocket Basins and Deep-Sea Speciation

FURTHER READING

Cloos, M., B. Sapiie, A. Quarles van Ufford, R. J. Weiland, P. Q. Warren, and T. P. McMahon. 2005. *Collision delamination in New Guinea: the geotectonics of subducting slab breakoff.* Special Paper 400. Boulder, CO: Geological Society of America.

Dow, D. B., G. P. Robinson, U. Hartono, and N. Ratman. 1988. *Geology of Irian Jaya*. Indonesia: Geological Research and Development Centre.

Hill, K. C., and R. Hall. 2003. Mesozoic–Cenozoic evolution of Australia's New Guinea margin in a west Pacific context. , in *Evolution and dynamics of the Australian plate.* R. R. Hillis and R. D. Müller, eds. Special Paper 372. Boulder, CO: Geological Society of America, 265–290.

Hope, G. S., and K. P. Aplin. 2007. Paleontology of Papua, in *The ecology of Papua: Part 1.* B. M. Beehler and A. J. Marshall, eds. Singapore: Periplus Editions, 247–254.

Parris, K. 1996. Central Range Irian Jaya Geology Compilation 1:500,000 scale geological map. Jakarta: P. T. Freeport Indonesia.

Pieters, P. E., C. J. Pigram, D. S. Trail, D. B. Dow, N. Ratman, and R. Sukamto. 1983. The stratigraphy of western Irian Jaya. *Bulletin of the Geological Research and Development Centre, Bandung, Indonesia* 8:14–48.

Pigram, C. J., and H. L. Davies. 1987. Terrranes and the accretion history of the New Guinea orogen. *BMR Journal of Australian Geology and Geophysics* 10:193–211.

Visser, W. A., and J. J. Hermes. 1962. *Geological results of the exploration for oil in Netherlands New Guinea.* Verhandelingen, Geologische Serie 20. The Hague: Koninklijk Nederlands Geologisch Mijnbouwkundig Genootschap.

REFERENCES

Satellite Geodesy, Scripps Institute of Oceanography. 2008. *Global topography.* http://topex.ucsd.edu/marine_topo/mar_topo.html.

Smith, W. H. F., and D. T. Sandwell. 1997. Global seafloor topography from satellite altimetry and ship depth soundings. *Science* 277: 1957–1962.

NEW ZEALAND, BIOLOGY

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New Zealand, spanning more than 1400 km of latitude on the southwest edge of the Pacific Ocean, supports a distinct assemblage of plant and animal groups. Species-level endemism in the wet temperate forests and alpine habitats is high; however, compared to many other oceanic islands, species diversity is not. New Zealand is a small part of a large continent, Zealandia, that sank beneath the surface of the sea after separation from Gondwanaland and is thus often considered a continental island. Whether any of the New Zealand biota originated in Zealandia is uncertain, but a number of animals that lack close living relatives elsewhere in the world may have arrived in that way. As with true oceanic islands, New Zealand biodiversity is dominated by speciation in relatively recent geological time, mostly from overseas colonists.

GEOLOGICAL HISTORY AND GEOGRAPHIC SETTING

New Zealand is composed of continental crust; a property it shares with just a few other islands, including New Caledonia and Madagascar. In fact, the geological histories of New Zealand and New Caledonia are closely linked, as both are small, emergent parts of an otherwise submerged continental fragment, Zealandia. The continent of Zealandia was somewhat larger than India when it rifted from Gondwana starting about 85 million years ago. During the following 60 million years the continental crust of Zealandia stretched, thinned, and sank, so that today 93% of its area is beneath the sea. Subsequently, parts of Zealandia have re-emerged as a result of local tectonic activity to form islands, and these include New Caledonia, the Chatham Islands, and most if not all of New Zealand.

The New Zealand archipelago lies in the southwest Pacific Ocean and has a total area of about 270,000 km^2. The nearest continent, Australia, is about 1,500 km to the west. New Zealand consists of three main islands: North Island and South Island separated by the Cook Strait, and the rather smaller Stewart Island separated by Foveaux Strait (Fig. 1). There are a number of other smaller inhabited islands: the Chatham Islands (963 km^2) about 800 km east and the islands of Waiheke and Great Barrier in the Hauraki Gulf of North Island, plus numerous uninhabited islands near the mainland coast that share a recent biological history, because they were connected when sea level was lower in the Pleistocene (Fig. 2). In contrast, the more distant islands to the north (Poor Knights, Three Kings), south (sub-Antarctic islands), and east (Chatham Islands) have been isolated longer or were never linked to mainland New Zealand. Diversity and endemicity are not homogeneous even across the main islands; distinct zones of higher endemicity are particularly conspicuous among the flora (Fig. 2). The climate is predominantly temperate but ranges from cool temperate in the south (latitude 47°) to subtropical in the north (latitude 34°). A large proportion of New Zealand can be classified as mountain land (60% of South Island and 20% of North Island), and this contributes to habitat diversity. The majority of alpine habitat is on the Southern Alps, which run the length of South Island, but there are smaller ranges and a number of volcanic mountains in North Island (Fig. 1). The Southern Alps reach to ~3000 m above sea level (the highest, Mt. Aoraki/Cook, is 3753 m), but the treeline in New Zealand is relatively low (averaging 1300 m above sea level), so the alpine zone is a relatively large and important ecotone.

For students of island biogeography, New Zealand is an enigma. The biology has features reminiscent of both continental lands and oceanic islands. For example, the absence of native terrestrial mammals is typical of an island fauna, but the presence of an endemic order of reptiles (tuatara; Sphenodontia), two endemic orders of birds (moa and kiwi), and an endemic family of amphibians (frogs; Leiopelmatidae) is seen as more continental in nature. Recognition that New Zealand is a continental island, and that fragmentation of Gondwanaland played an important role in its geological formation, has strongly influenced interpretation of its biogeography. In contrast to dispersal origination of biota on true oceanic islands, the biota of New Zealand have been widely treated as elements of an ancient, continental "ark." There has been an overemphasis on inferring biogeographic origins from distribution patterns rather than recognizing the role of speciation in New Zealand biology.

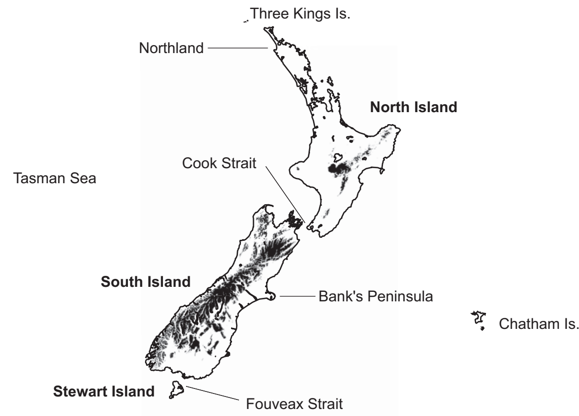

FIGURE 1 The islands, straits, and and other locations in modern New Zealand, with the distribution of montane land (1000 m) indicated (black), formed largely since the Pliocene (5 million years ago).

PATTERNS OF SPECIES DIVERSITY

Prior to human arrival the natural vegetation over about 85% of New Zealand was mixed temperate rain forest, with southern beech (*Nothofagus*), tree ferns (*Cyathea, Dicksonia*), and species of the Southern Hemisphere gymnosperm family Podocarpacea being prominent features of the forests. The biggest New Zealand tree is the endemic kauri (*Agathis australis*), the only representative of this genus in New Zealand. Kauri belongs to a group of ancient conifers Araucariaceae, which has most of its diversity in subtropical and tropical Oceania.

New Zealand plants tend not to have prominent, showy flowers; instead, a large proportion of angiosperms have small, often pale or white flowers pollinated by generalists, including flies, rather than specialist butterflies and bees. Among the few flamboyant flowering trees are kowhai (*Sophora*), with large yellow flowers, and pohutakawa or Christmas tree (*Meterosidros*), which produces abundant scarlet inflorescences in December; both have close relatives elsewhere through the southern hemisphere and Pacific.

Like the flora, New Zealand's birds are not showy; native forest birds tend to have cryptic plumage, many are nocturnal (21%), and there is also little sexual dimorphism in plumage. For example, New Zealand species of *Petroica* robins are monomorphic and monochrome, whereas male Australian *Petroica* robins have bright pink or scarlet chests. However, several New Zealand birds show traits indicative of resource partitioning, including pronounced beak dimorphism in the huia (*Heteralocha acutirostris,* extinct) and probably also, but to a lesser extent, the Chatham Island rail (*Gallirallus modestus,* extinct) and kaka parrot (*Nestor meridionalis*), and size dimorphism in some moa that was so extreme that bones from males and females were initially identified as belonging to different species.

The alpine habitat is rather youthful in New Zealand, probably largely developed during the last 5 million years as the mountain ranges formed and the climate cooled in the late Pliocene. Nevertheless there are many alpine specialists, including snow tussock grass (*Chionochloa*), cushion-forming herbs such as "vegetable sheep" (*Haastia* and *Raoulia*), buttercups (*Ranunculus*), alpine daisies (*Celmisia*), skinks, geckos, birds including the rock wren (*Xenicus gilviventris*), and the world's only alpine parrot, the kea (*Nestor notablis*). Specialist alpine invertebrates are numerous and include cicadas (*Maoricicada*), a black ringlet butterfly (*Percnodaimon*), short-horned grasshoppers (e.g., *Sigaus*), cockroaches (*Celatoblatta*), and weta. Some insects, including the alpine species of weta (*Hemideina* and *Deinacrida*), grasshoppers (*Sigaus Brachaspis*), and cockroaches (*Celatoblatta*), are tolerant of freezing and over-winter under snow and ice as adults and juveniles (Figs. 3–6). These alpine-adapted species all belong to recent radiations that include alpine and lowland representatives.

ASSEMBLY OF THE BIOTA

The New Zealand biota has been described as ill-balanced because of the variance in diversity and endemicity exhibited among different plant and animal groups, and this has frequently been attributed to New Zealand's supposed long isolation in the Pacific. However, the composition is broadly consistent with other island assemblages and indicative of long-standing (albeit intermittent) interactions with other biotas. Its geographic position, hundreds of kilometers from other land for some millions of years, has inevitably restricted successful migration of plants and animals, but not precluded it. As a result, a large proportion of species in many groups are endemic to New Zealand, but endemicity above this level is much lower. For example, New Zealand

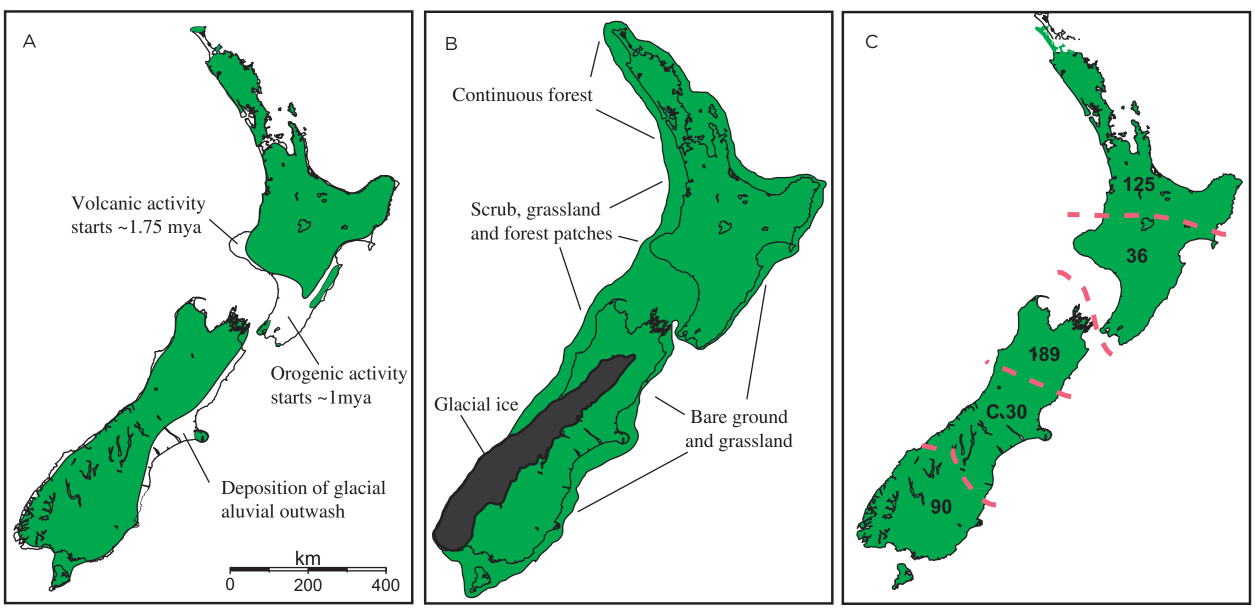

FIGURE 2 The changing shape of New Zealand and its biota. Changes in the distribution, extent and topography of land during the last 5 million years are thought to have influenced the distribution of endemism within New Zealand. (A) During the early Pleistocene (1.8 million years ago) there were two major islands separated more than today. A number of smaller islands were subsequently joined to the mainland (for example, Bank's Peninsular and the Northland archipelago, which still have endemic species). Estimated outline of land during the early Pleistocene (green) is superimposed on the present shoreline. (B) During glaciation sea level fell, and at the last glacial maximum (0.02 million years ago) a single major island would have existed (green). During this time glaciers extended across the Southern Alps (black) (McGlone 1985). (C) Five broad zones of plant endemicity have been identified among plants (dashed lines, values indicate numbers of endemic species) (Wardle 1963). Not surprisingly, the land areas with fewest endemics are those that are youngest or most disturbed during the late Pleistocene. The extent of forests was much reduced during glacials.

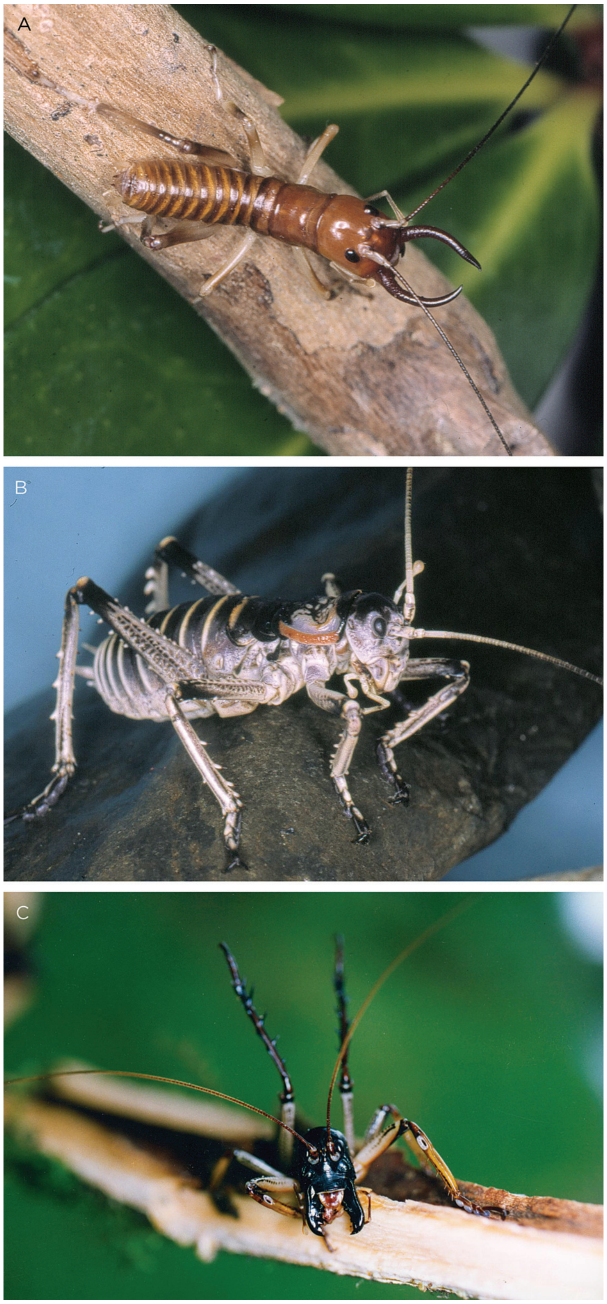

FIGURE 3 Biodiversity patterns in New Zealand, exemplified by anostostomatid weta. The Anostostomatidae are a relatively diverse group of orthopterans in New Zealand, expressing a range of biological features characteristic of the biota generally. The tusked weta (A) have their closest relatives in New Caledonia. The (B) giant (*Deinacrida*) and (C) tree (*Hemideina*) weta of New Zealand are unique among Anostostomatidae for eating leaves, fruit, and flowers. Secondary sexual characteristics such as enlarged heads and jaws in males have evolved in *Hemideina* tree weta, and a similar evolutionary path has resulted in the tusks of male tusked weta (A).

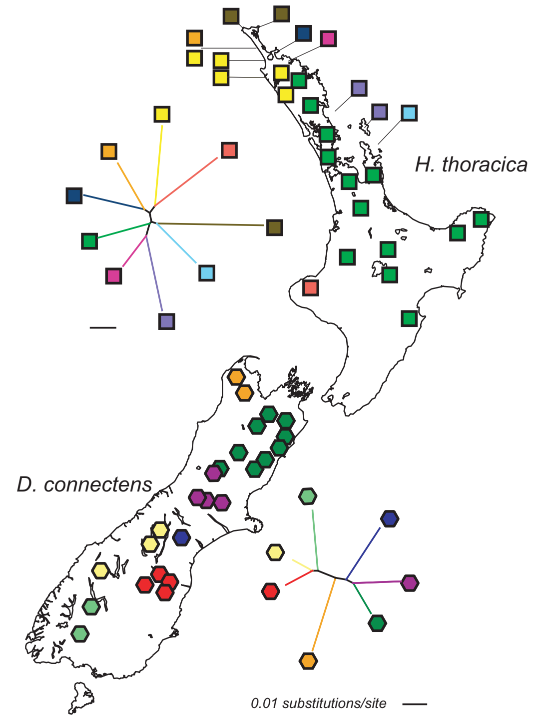

FIGURE 4 Biodiversity patterns in New Zealand, exemplified by anostostomatid weta. Genetic structure within two widespread species of weta in New Zealand. The Auckland tree weta (*Hemideina thoracica*) in North Island has greatest genetic diversity in the far North, where islands exisited during the Pliocene and where forests grew even during Pleistocene glacial cycles and after the volcanic eruptions of the central North Island. The giant scree weta (*Deinacrida connectens*) in South Island is fragmented on mountain peaks, but during glacial cycles its distribution would have been more continuous at a lower altitude. Genetic diversity within this species dates to uplift of the southern mountains.

has more than 20,000 endemic invertebrate species (95% endemism at species-level) but just five endemic invertebrate families, and 2000 endemic species of vascular plants but no endemic families.

New Zealand is subjected to a prevailing westerly wind and circumpolar oceanic current, and some animals are regular visitors. For instance, many seabirds regularly traverse the oceans but nest in New Zealand (e.g., sooty shearwater, *Puffinus griseus*); cuckoos (*Chrysococcyx lucidus, Eudynamys taitensis*) travel to and from islands in the Pacific Ocean; and godwits (*Limosa lapponica*) migrate to breed in Alaska.

For other taxa, migration is less frequent, but among the landbirds there are many post-human colonists (see the section "Human Contact"), and Australian species that arrived before recording began (e.g., the pukeko *Porphyrio porphyrio,* the harrier *Circus approximans,* the fantail *Rhipidura fuliginosa,* and the owl *Ninox novaezealandiae*), in addition to endemic species that have a close affinity (genus level) to

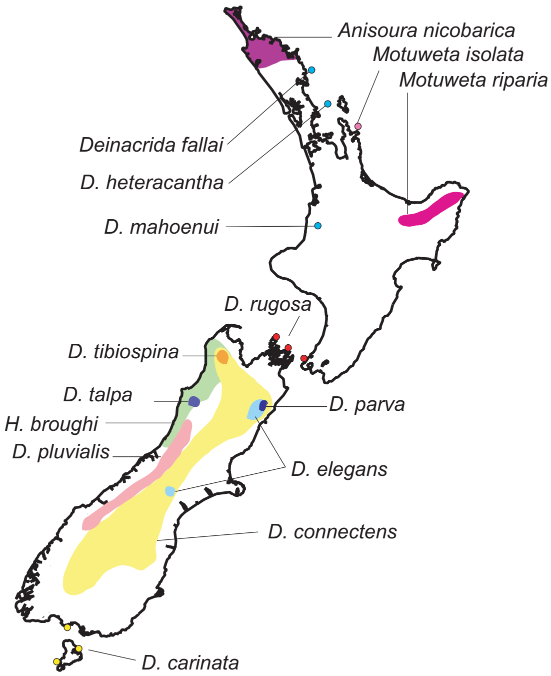

FIGURE 5 Biodiversity patterns in New Zealand, exemplified by anostostomatid weta. The distribution of tusked and giant weta in New Zealand. The greatest diversity of *Deinacrida* is in the habitat-diverse South Island mostly associated with the mountains. The three tusked weta species are restricted to northern North Island.

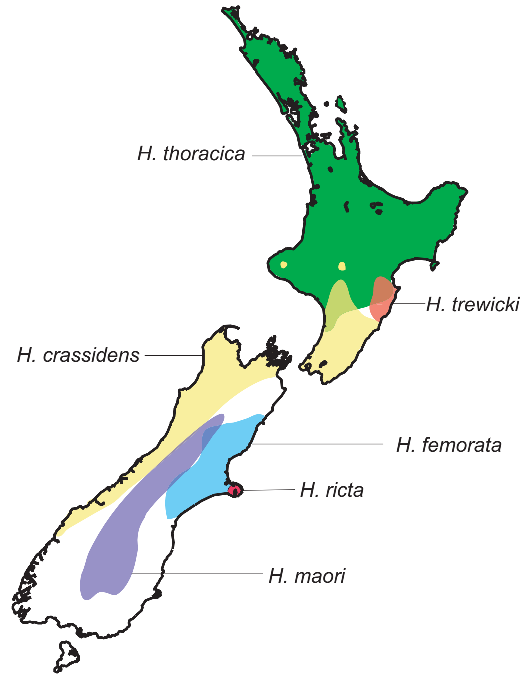

FIGURE 6 Biodiversity patterns in New Zealand, exemplified by anostostomatid weta. The distribution of tree weta reveals broad regional allopatry and evidence for range expansion following climate change. *H. thoracica* extend its range south probably after the last glacial maximum, excluding the cold-adapted *H. crassidens* from lowland forests of central North Island but leaving isolated populations of *H. crassidens* marooned in the subalpine zone of mountains in the region.

taxa elsewhere (e.g., *Petroica* robins in Australia). In many instances, New Zealand species have extraordinary forms compared to their nearest (frequently Australian) counterparts. For example the large, endemic flightless takahe (*Porphyrio hochstetteri*) shares a common ancestor with the smaller, flying purple swamphen or pukeko (*P. porphyio*), and the giant extinct eagle (*Harpagornis moorei*) shares a recent (Plio-Pleistonce) ancestor with the Australian little eagle (*Aquila morphnoides*). However, New Zealand also has taxa that have been classified as distinct at higher levels (e.g., bird families including wrens Acanthisittidae, kiwis Apterygidae).

In the freshwater realm, the fish are either themselves diadromous or are related to diadromous taxa. Eels are common (*Anguilla*) and have been an important food resource of people. Other native fish in New Zealand lakes and streams include species of *Galaxias, Neochanna,* and *Gobiomorphus,* most of which are endemic, but the genera also occur elsewhere, including Australia. Endemic freshwater invertebrates include two species of crayfish (*Paranephrops*) (related taxa exist among the more diverse Parastacidae fauna of Australia) and a number of insects with unusual life histories, such as caddis flies and dragonflies with semi-terrestrial larvae. Freshwater invertebrates tend to be highly distinctive (e.g., 20 of 21 genera of stoneflies, Plecoptera, are endemic), although there is a species of freshwater crab that also occurs in Australia. An analogous pattern is evident in the terrestrial flora too, with endemism high at species level (80%) but less so at higher taxonomic levels. The flora, and other elements of the biota, have been subjected to substantial change over time. There is evidence for bouts of diversification associated with geophysical events in New Zealand's prehistory, including significant changes in area, habitat diversification, and climate fluctuation. During and since the Miocene, changing diversity has resulted from extinction (e.g., *Eucalyptus* gum trees disappeared from New Zealand), colonization (e.g.; *Fuscospora* beech arrived), and speciation (e.g., *Coprosma*).

Many elements of the biota are described as "Gondwanan." Such taxa are simply those that have a distribution largely restricted to modern land areas that originated from the breakup of Gondwanaland: Africa (usually just southern Africa), Madagascar, South America, India, Australia, and New Caledonia. It is often assumed that a Gondwana distribution is evidence of a vicariant Gondwanan origin, and this concept has been a central tenet in New Zealand biogeography since the acceptance of continental drift in the early 1970s. A broad range of New Zealand taxa are attributed to this origin, including moa and kiwi (ratite birds), southern beech trees (*Nothofagus*), weta (anostostomatid crickets), land snails (Punctidae, Charopidae), and peripatus (Onychophora or velvet worms). Following a form of reciprocal illumination, some biogeographers have confounded the apparent evidence from Gondwana biological distributions with geological evidence for the Gondwanan origin of the continental crust from which New Zealand is formed and concluded that the biology of New Zealand is first and foremost Gondwanan. That is, that the biota of New Zealand has evolved in isolation since separation by continental drift from Gondwana some 62–80 million years ago. A stream of recent evidence from molecular studies in particular reveal that this is, in fact, far from true. A prime example comes from *Nothofagus* beech, an iconic Gondwanan taxon, long assumed to be incapable of transoceanic dispersal. Yet, recent research has revealed that extant New Zealand beech arrived after separation of Zealandia from Gondwana. In a similar vein, although the presence of peripatus (Onychophora) in New Zealand is consistent with a vicariant Gondwanan origin, this is not the only explanation. There are also peripatus in Jamaica (an emergent Miocene island more than 600 km from a continent). Similarly, weta (Anostostomatidae), which have a largely Gondwanan distribution (i.e., Southern Hemisphere), also occur in Japan, and speciose land snail families (Charopidae, Punctidae) are well represented on oceanic Pacific islands. It may remain useful to describe some of these as Gondwanan in terms of distribution (extant and fossil), but not necessarily in terms of the process that led to their current distribution. Gondwanan taxa are essentially southern hemisphere taxa and these are the most likely to arrive in southern lands.

For most plants and for almost all terrestrial animals, the fossil record in New Zealand is, as yet, too patchy to be highly informative about timing of origin and persistence in the biota. Birds and some insects and plants are represented by fossils in caves, middens, swamps, and sand dunes; such sites often have abundant material, but because they are of Holocene age, they are informative about the last few thousand of years of New Zealand's prehistory and not the preceding millions. Recent discoveries of rich Miocene fossil sites in southern South Island will no doubt open important windows into the past biology. Already a small mammal, a crocodile, and a community of now-extinct aquatic birds are known to have existed 18 million years ago and reveal much about the turnover of the New Zealand biota.

FEATURES OF THE BIOTA

Eclectic Mix

There are no living snakes, land turtles, or crocodiles in New Zealand, and lizards belong to just two groups (geckos and skinks), but the tuatara is the only living representative of the sphenodontid reptiles anywhere in the world. Among invertebrates, many orders are missing (e.g., Scorpionida, Embioptera, Zoraptera), and others are poorly represented (e.g., Mecoptera, one species; Formicidae, 12 species, compared to ~1300 in Australia). Similarly, within orders, representation is patchy even in comparison to neighboring land areas. For example, Orthoptera have high endemicity and diversity among the Rhaphidophoridae (18 genera, ~50 species), Anostostomatidae (five genera, ~70 species), and to a lesser extent Acrididae (four endemic and two native genera, ~16 species, mostly associated with alpine habitat), fewer still in Tettigonidae (two Australian katydids), Gryllidae (two endemic and one Australian species), and Gryllotalpidae (one endemic), while others are absent (e.g., Gryllacrididae).

Curious Endemics

Among the birds, the large parrot kakapo (*Strigops habaproptilus*) is exceptional in its combination of life history characteristics and is unique among parrots for any one of these characteristics: lek breeding, nocturnal, and flightless. The sporadic breeding cycle of the kakapo is linked to the masting of forest trees.

The New Zealand avifauna included some 16 ratites (all endemic genera), including five of the smallest living members of the group, the kiwi (*Apteryx*). Kiwi invest all their reproductive effort into a single, very large (up to 450 g) egg per nesting. They are predominantly nocturnal and are the only birds with nostrils at the tip of the bill. Olfactory cues are important to kiwi, which forage on the ground at night, but it was recently discovered that kiwi have vibration sensors in the bill tip like those of wading birds (Scolopacidae), which are used when probing for prey.

New Zealand amphibian diversity consists of just four extant frogs, belonging to an endemic family (Leiopelmatidae). New Zealand frogs lack ears, pass through the tadpole stage in their eggs, and have paternal care of froglets.

The only recent native mammals are three species of bat. The long-tailed bat (*Chalinolobus tuberculatus*) probably arrived from Australia in the Pleistocene. The two short-tailed bats (one now extinct) belong to an endemic family (Mystacinidae), and *Mystacina tuberculate* is unusual in having evolved the ability to move efficiently on the ground, where they forage on insects, fruit, pollen, and nectar. The largest known eagle in the world (*Harpagornis moorei*) hunted moa (as revealed by talon marks in Holocene fossil moa hip bones), had a wingspan of 2.5 m, and had evidently evolved to exploit this large prey. Two genera of New Zealand weta (*Deinacrida* and *Hemideina*) are unusual in having adopted a largely herbivorous diet (Fig. 3). They feed primarily on green leaves or fruit or flowers, and rarely on animals, which is the normal diet of other genera in this family of crickets (Anostostomatide) in New Zealand and elsewhere. The only significantly poisonous animal in New Zealand is the katipo spider (*Latrodectus katipo*), which, judging by its close relation to the infamous Australian red-back (*Latrodectus hasselti*), must have arrived on New Zealand beaches in recent geological time.

Gigantism

Gigantism has in the past been identified as a distinctive feature of the biota, but most of the animal groups usually identified as being represented by giant forms in New Zealand (e.g., earthworms, centipedes, land snails, flatworms, millipedes, slugs, stick insects, weta, longhorn beetle, a weevil, a moa, and an eagle) also have species as large or, in most cases, larger in other parts of the world. A weta (cricket) is credited in New Zealand as being the heaviest insect recorded anywhere; female *Deinacrida heteracantha* in the wild average about 32 g (a much higher, anomalous weight of 71 g is famously recorded from a captive egg-engorged female). On the whole, animal groups with large species in New Zealand also contain many (usually the majority) smaller taxa. This is true even for the famous moa; although *Dinornis giganteas* was very big (240 kg), a bigger ratite (*Aepyornis maximus*) is known to have existed in Madagascar, and other moa were considerably smaller (*Megalapteryx didinus* ~25 kg). There are a number of "megaherbs" with large, glossy leaves and large, colorful floral displays associated with the moist environments of some offshore islands, including Chatham Island forget-me-not (*Myosotidium hortensia*) and Campbell Island daisy (*Pleurophyllum speciosum*). The extinct New Zealand eagle (*Harpagornis moorei*) and the giraffe weevil (*Lasiorhynchus barbicornis,* which owes half of its length to a long, thin snout) are the largest of their respective kinds, but there is little evidence for a dominant evolutionary pattern across the biota.

Flightlessness

About a third of New Zealand land birds at the point of human contact were flightless; many are now extinct. All modern ratites are flightless, and New Zealand had diverse fauna of moa (11) and kiwi (5). Similarly, six species of penguin (Spheniscidae) breed in New Zealand. Other flightless species were members of volant groups. Rails have the greatest propensity to evolve flightless forms, as observed on many other islands, and 11 species (70%) are known from the New Zealand archipelago. *Porphyrio*, *Gallirallus, Gallinula,* and *Fullica* are each represented by one or more flightless species on New Zealand main or offshore islands; each is a product of a separate colonization by a flying ancestor. Other flightless taxa include a parrot (*Strigops*), the strange rail-like predator (*Aptornis*), ducks (*Anas*), geese (*Cnemiornis*), and wrens (*Xenicus*). Much, and in some cases everything, that is known of these birds has been gleaned from their Holocene bones preserved in sand dunes, swamps, and caves.

Floral Peculiarities

The New Zealand flora consists of some 2300 native species, of which 85% are endemic. A relatively large proportion of the angiosperms have separate sexes or some degree of sexual dimorphism (23% of genera). There is a predominance of white flowers and unspecialized pollination systems among the largely evergreen trees and shrubs of New Zealand. Many (e.g., *Nothofagus, Dacrydium, Chionocloa*) display a high variance in fruiting from one year to the next (masting), and this has a significant impact on breeding of endemic birds (in particular kakapo, *Strigops*) and introduced mammals (mice, *Mus*). There is a high frequency of small-leaved, tangle-branched shrubs (divaricating habit), a form that has evolved independently in 20 plant families (e.g., *Coprosma, Myrsine, Melicytus, Pseudopanax, Pittosporum, Olearia*). There are about 60 species with tiny leaves and interlacing branchlets, and about 14% of these represent juvenile stages of plants that later grow into adult leafy trees of normal habit and foliage (e.g., matai, *Prumnopitys taxifolia;* putaputaweta, *Corpodetus serratus*). Two competing hypotheses explain the unusual abundance of this plant growth form: moa browsing and climate. From subfossil remains we know that moa did indeed eat these divaricating plants. However, the probable recent origin and distribution of the divaricating species, added to the fact that they have not been replaced in the >200 years since moa went extinct, suggests that climate is the more likely selective force. Skinks and geckos appear to be important seed dispersers for many of these small/divaricating shrubs.

Honeydew is a sugar-rich secretion produced by sap-sucking insects. In New Zealand, beech trees (*Nothofagus*) are frequently infested with scale insects (*Ultracoelostoma*) that secrete honeydew through a long, hairlike, waxy tube that extends from the bark of host trees and is an important resource for native birds (e.g., kaka, tui, bellbird). Exotic bees and wasps (especially *Vespula*) compete for honeydew, and in some forests they take almost all of it, depriving local birds.

Group Diversity and Radiations

Many invertebrate groups have high diversity and endemism that are the product of species radiations, including some carabid beetles (e.g., *Mecodema*), alpine cicadas (*Maoricicada, Kikihia*), weta (Fig. 2), and land snails large (predatory taxa of Rhytidae including *Powelliphanta*) and small (including Punctidae and Charopidae). The latter show high levels of sympatric species diversity in some parts of New Zealand.

Species diversity within bird groups is less prominent; there are relatively few endemic species of birds in New Zealand (176 endemics of 245 species at human contact) but high representation of taxonomic diversity (20 of 27 orders). Among the more speciose are kiwi (5) and moa (11), and the *Cyanoramphus* parakeets represent a young radiation of some 10 species in the New Zealand archipelago. Seabirds are well represented, and even today albatross (*Diomedea epomophora*), gannet (*Sula bassana*), and two penguins (*Megadyptes antipodes, Eudyptula minor*) nest on the mainland, although many others are now restricted to offshore islands.

Notably speciose plant groups include *Coprosoma*, *Hebe, Ranunculus* (buttercup), *Celmisia* (daisy), and *Asplenium* (fern); the products of relatively young radiations.

HUMANS IN AOTEAROA

Human Contact

As with most oceanic islands, the arrival of humans in New Zealand had a major impact on the composition and structure of the flora and fauna. The first people (Maori) to colonize the New Zealand archipelago (Aotearoa), came from central Polynesia and made first contact with these islands 1000 to 600 years ago. They introduced, during a succession of exchanges, a number of commensal animals, including the Pacific rat (kiore, *Rattus exulans*) and dogs (the extinct kuri) and some plants for cultivation (e.g., kumara, *Ipomoea batatas*). Early Maori hunted birds that provided a ready and abundant resource of food and materials (e.g., feathers woven into cloaks known as *korowai*). Moa were probably hunted to near extinction within about 100 years of colonization, and it is likely that low fecundity and slow growth resulted in their subsequent extinction. Other large ground birds (the flightless goose *Cnemiornis,* the adzebill *Aptornis*) were also soon extinct, and other forest birds (the weka rail *Gallirallus* and the keruru pigeon *Hemiphaga*) were harvested using specialized techniques including snares and traps. Sea mammals including seals and sea lions were taken in great numbers at their coastal rookeries, and seabirds (titi petrels, *Puffinus*) were gathered at their nesting grounds that were often far inland. Maori also used fire to clear land as tribal structure developed.

The first confirmed contact with New Zealand by a European was made by Abel Tasman in 1642. James Cook and Jean François Marie de Surville reached the islands more than 100 years later in 1769, and subsequently whalers, traders, and missionaries began arriving. Colonization by European people did not start in earnest until 1840 but resulted in accelerated modification of the landscape and biology of New Zealand. In particular, land was cleared of trees as timber was harvested, and pasture farming developed. Today, about 22% of the prehuman vegetation/habitat remains in a relatively pristine condition.

Introduced wild or feral animals included mice, cats, pigs, rats (ship and Norway), deer, goats, hares, and rabbits, and early European settlers continued to add familiar species from "home" after settlement. Many "garden" birds (e.g., song thrush, sparrow, blackbird, several finches, pheasant) and hedgehogs were also introduced under the auspices of regional Acclimatization Societies. A total of 33 bird species and 34 terrestrial mammal species have established in New Zealand. Trout, salmon, and 18 other freshwater fish have been introduced, to the detriment of native freshwater fish and invertebrates. In an early (1882) misguided attempt at biocontrol, mustelids (stoats, weasels) were introduced to limit the burgeoning rabbit population. It soon became apparent that, as predicted by a few scientists of the time, the predators did not restrict their attentions to rabbits, and today mustelids remain major predators of native birds, lizards, and invertebrates. Despite early attempts in the late nineteenth century to protect notable endemic species, the impacts of introduced predators and natural history collecting continued to be felt. For instance, a species of wren (*Xenicus insularis*) was extinguished from Stephen's Island in the Cook Strait in 1895 through the attention of cats brought to the island by the lighthouse keepers. In the 1890s a pair of huia (*Heteralocha acutirostris*), captured for translocation to a reserve island, were in fact sold illegally to a collector in the expectation that more could be found and conserved, but this never happened and the species was lost. The brush-tailed possum (*Trichosurus vulpecula*) was introduced from Australia in 1837 with the aim of supplying the fur trade; this possum is now a major pest in New

Zealand. Eating leaves, flowers, and fruits of native trees, it competes with native birds, and it also directly preys on eggs and nestlings. Some 76 native bird species have thus become extinct since the arrival of people in New Zealand, including 41% of the 176 endemic species. A large number of plant species have also been introduced (about 1630 alien plant species have established), and many of these are now invasive weeds. For vascular plants, land mammals, land birds, and freshwater fish, over 40% of the species now found in New Zealand are exotics. Habitat modification also appears to have opened the way for a number of self-introductions; first records for birds include the silvereye *Zosterops* in 1832, the welcome swallow *Hirundo tahitica* in the 1950s, the spur-wing plover *Vanellus miles* in 1932, and the cattle egret *Bubulcus ibis* in 1963. Exotic insects include the monarch butterfly *Danaus plexippus,* which arrived in the 1880s. Although perhaps facilitated by human activities, this process very much continues a prior persistent feature of sporadic colonization (see the section on "Assembly of the Biota").

Conservation

Despite the ravages of habitat modification and exotic taxa, a number of distinctive bird species have been kept from extinction by the efforts of New Zealand conservationists, who have pioneered management techniques now applied worldwide. Prominent successes include the black robin (*Petroica traversi*), resurrected from just five birds (two females, three males) in 1980 using a combination of translocations, cross-fostering, and supplementary feeding. The intensely managed night-parrot, kakapo (*Strigops habroptilus*), which, despite an extreme male bias and intermittent breeding, has experienced a gradual improvement in its meager population, which today stands at 90.

Among the most valuable resources available to New Zealand conservation are the offshore islands, from which introduced predators are removed to provide vital reserves for protected species. Several endangered taxa owe their survival thus far to remnant populations on offshore islands (e.g., Hamilton's frog, *Leiopelma hamiltoni,* on Stephens Island; hihi, *Notiomystis cincta,* Little Barrier Island; saddleback or tieke, *Philesturnus carunculatus,* on Hen Island and Big South Cape Island). New Zealanders also pioneered mammal eradication techniques to clear islands of introduced pest species; the largest island to have been successfully cleared of rats is Campbell Island (114 km^2). A dozen species of exotic mammal have been eradicated from other islands in the region including mice, possums, cattle, pigs, goats, rabbits, and cats. The use of sophisticated fencing techniques and predator control programs have also allowed the development of "mainland islands" that protect dwindling biodiversity and provide a valuable point of contact between people and the natural environment. Conservation efforts are now supplemented by stringent biosecurity measures that strictly limit the importation of further exotic species to New Zealand.

CONCLUSION

New Zealand as a land mass has a long and complex biological history. Proximity to a large continent (Australia) and composition of continental crust have complicated inferences about the origins of the biota. The biota has assembled over many millions of years, but relatively few (conceivably none) of the lineages that must have been present when Zealandia broke from Gondwana survive today. Episodes of extinction and colonization have acted upon the biological assemblage, but, as with most islands, the key influence on New Zealand's biological character has been speciation.

SEE ALSO THE FOLLOWING ARTICLES

Bird Radiations / Flightlessness / Gigantism / Madagascar / New Caledonia, Biology / New Zealand, Geology / Vicariance

FURTHER READING

Campbell, H., and G. Hutching. 2007. *In search of ancient New Zealand.* Hong Kong: Penguin Books.

Gibbs, G. 2006. *Ghosts of Gondwana: the history of life in New Zealand.* Nelson, New Zealand: Craig Potton Publishing.

Goldberg, J., S.A. Trewick, and A.M. Paterson. 2008. Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. *Philosophical Transactions of the Royal Society* B 363: 3319–3334.

McGlone, M. 1985. Plant biogeography and the late Cenozoic history of New Zealand. *New Zealand Journal of Botany* 23: 723–749.

Pole, M.S. 2001. Can long-distance dispersal be inferred from the New Zealand plant fossil record? *Australian Journal of Botany* 49: 357–366.

Trewick, S.A., A.M. Paterson, and H.J. Campbell. 2007. Hello New Zealand. *Journal of Biogeography* 34: 1–6.

Wardle, P. 1963. Evolution and distribution of the New Zealand flora, as affected by Quaternary climates. *New Zealand Journal of Botany* 1: 3–17.

NEW ZEALAND, GEOLOGY

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In geological terms, New Zealand may be regarded as an emergent portion of a sunken continent. This is unusual globally; the Kerguelen Plateau may be the only other