The Flora of New Zealand: work in progress

New Zealand Plant Species Radiation Group[1]

The New Zealand flora is a model for understanding the world's plant evolutionary and ecological processes. Developing our understanding requires interdisciplinary research. This means undertaking studies in palynology, morphological, ecological, physiological and genetic variation, and requires the collaboration of biologists, mathematicians, physicists, computer scientists, climatologists and geologists. The New Zealand Plant Species Radiation Group is an interdisciplinary group of New Zealand scientists working in association with overseas collaborators to study the phenomenon of species radiation. Examples of research being undertaken by the group in New Zealand include modelling climate change, palynology and the study of ancient DNA from caves and soils, the mathematical description of species radiations, the sequencing of template genomes for model plants, critical examination of adaptive radiation and the molecular dating of species diversification. The following article is an adaptation of material to be found on the website of the New Zealand Plant Species Radiation Group http://awcmee.massey.ac.nz/~NZ_Plant_Species_Radiation_Group. Updates of progress will be posted through the New Zealand Systematics Association's web page http://www.math.canterbury.ac.nz/bio/SYSTANZ.

Introduction

Comprehending plant biodiversity requires understanding plant species radiation - a global phenomenon in which genetically similar, but morphologically and ecologically diverse species can arise and go extinct over short periods of geological time. These radiations provide an unparalleled opportunity for studying how evolution works. Towards this end, studies of the macro- and micro-fossil record [1-3], the genetics of plant development [4, 5], molecular ecology and systematics [6-15] converge in helping to explain how explosive radiations have occurred in certain places and times in the past. New Zealand is one of those places, where radiation is happening now, and where there is currently great potential to study it. Here, history of the flora is intimately linked with local geological and global climate change [1, 16-22], and while some elements of the New Zealand biota are likely to be truly ancient, recent findings indicate that plant speciation is far more rapid and dynamic than generally appreciated. Although the New Zealand landmass is ancient, its flora is not a Gondwanan relic.

The importance of New Zealand for understanding plant biodiversity

Volcanic islands have long been useful for scientists to develop evolutionary theory. Geologically young and tractable for study, archipelagos such as the Hawaiian Islands, have provided important models for understanding plant biodiversity [2, 6-9, 12, 14, 15, 23-26]. However, a shortcoming of volcanic islands as model systems for studying evolution is that they are short-lived. They also have virtually no fossil records, and many classes of plant, such as conifers, are absent.

The New Zealand archipelago represents a more complex model system. It is home to approximately 2,200 native vascular plants, a flora twice the size of Hawaii. New Zealand has an oceanic island character that parallels other island systems, such as Hawaii, Juan Fernandez, Canary and the Galapagos Islands. However, New Zealand is not an island. It is a continental remnant and thus more relevant to the world as a whole. In contrast to volcanic islands, New Zealand has an excellent plant fossil record extending back to Gondwana. It is habitat-rich with latitudinal and climatic zones ranging from tropical to alpine and sub-antarctic. Unlike studying the phenomenon of radiation on volcanic islands (which typically means tracking the pattern of dispersion between islands), studying the phenomenon in New Zealand also means evaluating the impact of novel habitats (e.g. alpine, dry land, high rainfall and scree) on plant evolution. This includes studying plant groups that have radiated extensively (e.g. *Ranunculus, Epilobium, Hebe, Celmisia, Dracophyllum, Asplenium* and *Blechnum*) as well as those that have survived for long periods of

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Scree slopes, to which a few specialist plants are restricted

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geological time without radiating (e.g. *Agathis, Knightia, Pseudowintera* and *Dacrydium*).

Originating from an ancient continental land fragment that became geographically isolated in the South Western Pacific more than 65 million years ago (mya), New Zealand was first settled by Polynesians perhaps less than 1,000 years ago [27, 28]. A consequence of this is that some habitats, particularly alpine, are little affected by human activities. Thus, the study of these habitats promises considerable insight into ecological and evolutionary processes important in alpine radiation. Further, many lowland habitats in New Zealand have been significantly impacted by human settlement, and the long term effects of these ecological disturbances can more easily be studied in New Zealand than in larger, more complex and less isolated continental landscapes. Thus the human-disturbed biotic systems of New Zealand are in some ways as interesting for study as the more pristine habitats.

Recently, the unique geology and floristic diversity of New Zealand has caught the attention of film makers with its magic captured in film epics such as *Walking with Dinosaurs* (produced by the BBC) and Tolkien's *Lord of the Rings* (produced by New Line Cinema). However, the potential of New Zealand for understanding plant evolution has been appreciated for much longer [29], as indicated by comments by the noted biologist Gareth Nelson from the American Natural History Museum:

"With regard to general problems of biogeography, the biota of New Zealand has been, perhaps, the most important of any in the world. It has figured prominently in all discussions of austral biogeography, and all notable authorities have felt obliged to explain its history: explain New Zealand and the world falls into place around it."

An evolving perspective of the New Zealand flora

In recent years, molecular descriptions of the New Zealand flora have changed our understanding of

Some plant lineages in New Zealand are indeed very old, possibly ancient Gondwanan relics. Agathis (kauri) is our best example of this [31]. In contrast, other plants are clearly more recent immigrants to New Zealand

its plant biodiversity and origins. New Zealand has traditionally been thought of as a "Moa's Ark", home to relic species undergoing slow changes over long periods of time. However, we now realise that this view is far too simplistic, and a more dynamic, almost tumultuous view of New Zealand's biodiversity is emerging [30]. Some plant lineages in New Zealand are indeed very old, possibly ancient Gondwanan relics. *Agathis* (kauri) is our best example of this [31]. In contrast, other plants are clearly more recent immigrants to New Zealand. This is a finding that supports the notion of the New Zealand flora being dynamic. The finding also surprises many, because it had long been considered that research would show that much of the New Zealand biota had evolved *in situ* from ancient lineages always present in New Zealand.

Despite our currently poor understanding of the mechanisms involved, the founders of many plant groups arrived in New Zealand by transoceanic dispersal [30]. Fossil records suggest trans-Tasman Sea dispersals from Australia to New Zealand throughout the Tertiary period. Over this time many plant groups first appear in the fossil record in Australia and then subsequently in New Zealand. Presumably seeds were dispersed passively or actively eastward with prevailing circumpolar winds and sea currents [32, 33].

Molecular data, like the fossil evidence, record many events of dispersal during the Tertiary, with the late Tertiary being a particularly important period for origins of the modern flora of New Zealand. DNA studies suggest that genera such as the alpine *Ranunculus* (buttercups)

established in New Zealand with the onset of Pliocene mountain building (by 5 mya), and soon after began to radiate extensively into many distinctive habitats [12]. During radiation and range expansion within New Zealand, species were dispersed from New Zealand to other Southern Hemisphere lands. This pattern of late Tertiary arrival, radiation and dispersion from New Zealand has been repeatedly inferred in the study of numerous endemic plant groups [30, 34, 35].

Until the findings of recent molecular investigations were known, the geological age of species-rich groups in New Zealand had been uncertain. However, evidence from fossil studies [1, 3, 17, 36-38] and studies of genetic diversity [30] are consistent in suggesting that species radiations are geologically young in New Zealand. Many seem to have occurred sometime during the late Tertiary to late Quaternary period (within the last 5 million years), a time of dramatic geological and climatic change in New Zealand [17, 39, 40].

A tectonic and climatic framework for plant evolution in New Zealand

An important aspect of ongoing biodiversity research in New Zealand is to develop a better understanding of the tectonic and climatic change that has accompanied species radiation. Already, much is known, but more needs to be learned before we can properly assess the significance to the modern flora of the major geological, geographic and climatic changes since New Zealand separated from Gondwana.

The alpine *Ranunculus buchananii*

The promise of detailed knowledge on the course and timing of plant evolution, and in particular, species radiations, provided by improved molecular phylogenies raises the possibility of a comprehensive approach to the interaction of climate and landscape change on one hand, and evolutionary change on the other. New Zealand is particularly suited for this sort of study because of its limited land area, isolation, well described flora, and excellent geological record. Although there have been a number of previous syntheses [37, 41-43], as well as numerous detailed studies on the New Zealand biota, biological and geological information was until recently insufficient for all but the most general of conclusions to be drawn.

Geological background

New Zealand is an extraordinarily dynamic landmass. Unlike the major continental landmasses, it owes its very existence largely to its position athwart a major plate boundary. For millions of years after the nascent Tasman Sea forced it apart from Antarctica and Australia, the New Zealand landmass slowly subsided until it nearly vanished (reduced to 20% of its current size) in the Oligocene. Uplift in the later Tertiary, associated with the creation of the transcurrent Alpine Fault system, increased the land area and created the first substantial mountains. Tectonic uplift continued to increase in tempo, peaking at around 2 mya with the formation of the high Southern Alps. Many areas of the country are still subject to rapid uplift and frequent earthquakes.

The generalised uplift that began roughly 10 mya along the Alpine Fault fundamentally changed the nature of the New Zealand landscape. First of all, it created a series of new adaptive zones in the form of permanently ice-covered terrain, and alpine and subalpine habitats. Second, it promoted the formation of rock-falls, screes, alluvium-choked river valleys, and plains constructed of coarse debris. Third, the taller mountains created a high rainfall, mild, westerly zone and a more

continental, drier and more variable eastern zone. The uplift markedly increased the rate at which soils and regolith were turned over, except in the relatively stable northern third of the North Island and eastern Otago-Southland.

In paleogeographic terms, New Zealand has undergone very marked changes, ranging from being a scatter of low-lying islands in the early Oligocene to one massive mountainous mainland island with some small off shore islands during the Pleistocene glaciations. The glacial-interglacial cycles accompanied by fluctuations of sea level by 150m, tectonism, dune building and offshore volcanism in the north, have resulted in repetitive formation and recoalescence of varying combinations of mainland islands, and size changes of the terrestrial landmass by 50%.

Climate background

Although isolated in mid-latitude oceans, New Zealand has also had a tumultuous climate history. During the late Cretaceous and early Tertiary, the area that was to become New Zealand lay close to the Antarctic Circle, and thus had long dark winters and brief summers. Despite the near polar climate, the oceans were ice-free and relatively warm. In the course of the Tertiary, New Zealand moved towards the Equator and into warmer oceans, experiencing at times sub-tropical climates. The circumpolar ocean, with its strong, persistent westerly airflow and ocean currents, was established in the mid-Tertiary. Along with the intensification of global cooling in the late Tertiary, which culminated in the early Pleistocene, this created the present highly variable but oceanic climate regime.

Epilobium brevipes from Mount Lyford

It appears now that fundamental changes in the Earth's geography sparked off reciprocal alterations of the Earth's climate. The massing of land around the North Pole appears to have provided the basis for the giant but unstable ice sheets of the northern hemisphere, while the thermal isolation of Antarctica at the South Pole gave rise to the hypercold but much more stable Antarctic ice sheets. More recently the narrowing of the seaways north of Australia promoted the formation of the West Pacific warm pool, the heat engine and source of most of the atmospheric water vapour for the globe.

Milankovitch cycles and global climate change

As long as the Earth has existed it has been subject to the pull of other massive planets which cause it to tilt and wobble around its axis, and its orbit to oscillate between more and less elliptical paths. These orbital changes (known as Milankovitch Cycles) affect the amount of solar radiation falling at any particular latitude, but not to any extent total global radiation. The southern and northern hemispheres are essentially out of phase. It has long been known that fluctuations in solar radiation received at high northern hemisphere latitudes affect the waxing and waning of the northern hemisphere ice sheets. Glaciations, the regular ebb and flow of ice sheets at the poles and the marked increase and decrease of global temperatures, are in phase with the changing solar radiation at high northern latitudes. One result of this connection is that New Zealand (and all southern latitudes) has a solar radiation budget effectively out of phase with global cooling and warming. Thus, during the coldest glacials, New Zealand experiences high summer insolation (as much as 10% or more above that of the present) and low winter radiation. The reverse occurs during warm interglacial peaks. It is also now well established that carbon dioxide levels have fluctuated roughly in synchrony with glacial-interglacial cycles, lowest levels coinciding with glacial cold and highest with interglacial warmth, although there

can be prolonged periods where they are out of phase.

Basic information on the nature of climate change during the last 2.5 million years is being collected in a number of ways. One promising avenue is the calculation of the direct effects of solar radiation for which recent results have demonstrated a striking correlation between differentiated global ice volume and mean summer solar radiation [40]. Edvardsson in collaboration with our group has recently begun calculating radiation curves for New Zealand latitudes. An early finding from this work is that direct summer solar radiation in mid- to high southern latitudes appears to explain subtle differences in temperature records from northern and southern polar sites. This is the first direct indication that mid- to high latitude summer insolation has markedly affected the degree of global cooling or warming experienced in the south. Edvardsson's calculations provide information independent from empirical measures to help understand the evolution of New Zealand habitats in the late Tertiary and Quaternary, and as such they are helping provide us with a climatic framework to investigate the biological consequences of climate change.

Climate and habitat

Whilst New Zealand has diverse habitats, a consequence of tectonics, altitudinal and latitudinal gradients, it also has floristic peculiarities in the range and extent of specific habitats. Its extreme geographic isolation from compatible floras elsewhere, which might otherwise provide a source of novelty, has meant that plants must either respond to habitat selection or face extinction [1, 43, 44]. Although there are ecologically diverse species groups in New Zealand, there are also whole adaptive suites not well developed or missing in the flora including cold-hardy trees, fast-growing seral and riverine trees and shrubs, non-caespitose (non-clumping) grasses, annuals, nitrogen-fixing trees [45], and plants with specialised pollinators [46].

It is clear that climate change has had significant effects on the ecology of New Zealand plants in the past.

For instance, despite its oceanic setting, New Zealand has experienced fluctuations in vegetation cover as extreme as those of any continental landmass, and it has been suggested that this is because the flora is unable to retain adaptations for either extreme of the glacial-interglacial cycle [43, 47]. It may also be having effects in the present day, for example, as suggested by the observation that nitrogen-fixing woody weeds and cold-adapted conifers are beginning to dominate certain previously indigenous habitats.

One question of considerable international interest concerning the impact of climate change on plant evolution is the refugial debate [48].

Plant refugia have been postulated for New Zealand, and there has been a lively debate about how to define them, where they may have existed, and their influence on current plant distributions [17, 37, 43, 49]. Major areas of high genetic and specific diversity have been defined [44], but it is not at all clear that these geographic regions have had the same function for all species within them. In making inference about the existence of refugia, one problem concerns the interpretation of the age of plant distributions. Another problem is a lack of understanding of the relationships amongst more widespread species with congeners from within the high diversity areas.

McGlone [37] suggested that the plant distributions within the refugia could be the result of ancient tectonic mountain building, marine inundation, and fault movement. But more recent fossil and molecular evidence has cast some doubt on whether most distributions are as old as postulated (prior to major glaciation ca. 2 mya). Recently it has been suggested that the older landscapes within the high diversity regions could have acted as "species traps" for recently evolved but poorly dispersing species [43]. On the other hand, there is some evidence for "nunataks", ice-free regions within glacial terrain for plant species distributions (P.B. Heenan pers. comm.). There is also the neglected question of interglacial "refugia" for full glacial plant specialists, possibly represented by scattered populations of cold tolerant species in the north. New Zealand

The distinctive fronds of the fern *Blechnum novae-zelandiae*

provides, therefore, a setting with its major geological changes and diverse topography, to create a more sophisticated model to address pointed questions at the concept of "refugia".

Despite considerable international interest to understand the relationship between plant diversity and changing local and global environments, current understanding is limited. One exciting development concerns a recent report in *Science* (April, 2003) of ancient DNA being extracted from soils in the Northern Hemisphere and in New Zealand [50]. If confirmed, and some technical difficulties can be overcome, study of such DNA would "free ancient DNA researchers from the shackles of needing fossils to be able to look into the past" [51]. We are currently developing molecular approaches [52] to test and identify, to the species/genus level, plant remains present in cave soil and peat bogs from New Zealand. This work has the potential to allow direct monitoring of changes in forest plant communities with Pleistocene climate change.

Many other projects are underway as part of the New Zealand Plant Species Radiation Group initiative, details of which can be found at the URL address provided.

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