Extinctions and radiations in the New Zealand scale insect fauna

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Abstract: An overview of the historical biogeography of New Zealand from Miocene to present leads to the conclusion that climate changes and depletion of host plants have been major influences on the scale insect fauna of New Zealand. Recently discovered fossils associated with a Miocene lake, including a well-preserved diaspidid dated 20 million years old, provide more detail about climate and forest composition than had the previous pollen record. A second new scale insect fossil, dated 34,000 years, is on a leaf of *Nothofagus menziesii* (Nothofagaceae) with the pouch gall of an extant species, *Madarococcus cunicularius* Hoy (Eriococcidae). Gaps and radiations are present in the major scale insect families today. Examples of modern scale insect faunal patterns are discussed.

Key words: fossils, Coccidae, Diaspididae, Eriococcidae, Pseudococcidae, Aleyrodidae, mountain building, glaciation.

Introduction

New Zealand was traditionally thought to be a 'Noah's Ark', an isolated piece of Gondwana carrying its original load of flora and fauna since breaking away from the Australian continent 80 million years ago (mya). However, this notion of antiquity has been increasingly questioned by geologists and botanists as data of the fossil record and information about plant lineages accumulates (Gibbs, 2006; Pole, 1993). Earlier botanical studies focussed on the pollen record from diverse sites and ages (Mildenhall, 1989; Pocknall, 1989; Pole & Douglas, 1998). Now the extensive deposits of well-preserved plant macrofossils at the site of a large Miocene freshwater lake system provide much greater detail of the changes in forest composition over about 10 million years (Pole, 1993; Pole *et al.*, 2003). The great freshwater Lake Manuherikia extended over Central Otago in the South Island of New Zealand, and at its maximum covered an area of over 5,600 km^2 (Gibbs, 2006; Mildenhall, 1989; Pole *et al.*, 2003). The stratigraphic record here demonstrates that plant diversity in New Zealand was relatively high 15 to 20 mya, (Gibbs, 2006; Pole, 1993; Pole & Douglas, 1998; Pole *et al.*, 2003) but subsequent volatile geological ages brought extinctions and depletions in the floral taxa (Lee *et al.*, 2001). This depletion of available host plants could explain why the modern scale insect fauna has become generally depauperate. Gaps and radiations are present in the major scale insect families today, as illustrated on *Nothofagus*, for example, by a radiation of species in Eriococcidae but an almost complete absence of Diaspididae. New Zealand has been isolated for a very long time compared with continental landmasses such as North America. In New Zealand, if a taxon was lost during a period of climatic extreme (such as glaciation), then it would be unable to readily re-establish from populations at the edge of the glaciation, as in North America (Gibbs, 2006).

Historical biogeography

In the early Miocene, New Zealand was a low-lying, subtropical to warm-temperate archipelago (Gibbs, 2006). Rainfall was probably generally high at Lake Manuherikia in the south, although in late Miocene there were dry periods when the flora included eucalypts and fire was experienced (Pole, 1993). Fossils of well-preserved leaves have been described (Pole, 1993) and the plant assemblage was like no other existing today (Gibbs, 2006). Some elements such as *Araucaria*, Proteaceae and eucalypts may be found in New Caledonia and

Australia today but had nearly all vanished from New Zealand prior to European colonisation. Others such as *Dacrycarpus*, *Nothofagus* and *Metrosideros* persisted through to modern New Zealand.

The land rose again in the later Miocene and Pliocene due to the inception of a new tectonic plate boundary under the New Zealand landmass, associated with volcanism and mountain building (Gibbs, 2006). The formation of the Alpine fault on the active plate boundary resulted in uplifting of the Southern Alps, by shearing pressure as the Australian and Pacific Plates collided and slid in opposing directions (Gibbs, 2006). The South Island of New Zealand began to take the elongate shape it is today. The plant assemblages changed dramatically in response to cooling climate and at least 15 families and 36 genera of subtropical elements were lost (Lee *et al*., 2001). The following Pleistocene ice ages further promoted extinction of warm climate species. However, new niches created by raised topography and varied climate allowed radiations of cool tolerant plants and associated invertebrate herbivores (Gibbs, 2006; Lee *et al*., 2001).

Glacial cycling over the past 5 million years has destroyed the fossil record of the Pliocene and Pleistocene except that of the last cycle, creating a gap in the record between the Miocene macrofossils and recent Holocene subfossils deposited in the last few thousand years to present.

Materials and methods

Data on the composition of the extant scale insect fauna of New Zealand was compiled from the New Zealand Arthropod Collection (NZAC). Species richness was tabled for the nine coccoid families that have native species represented in New Zealand, together with native species of Aleyrodidae. The scale-like whitefly family in New Zealand demonstrates a depletion corresponding to that in some of the coccoid families. Host plant genera selected as examples for scale insect pattern diversity were *Kunzea* with *Leptospermum, Hedycarya*, *Hoheria*, *Metrosideros*, and *Nothofagus*. The armoured scale insects *Eulepidosaphes pyriformis* (Maskell), *Leucaspis* spp. and *Pseudaulacaspis phymatodidis* (Maskell) are given as examples of either host or species radiations.

Results and discussion

Fossil extinction

A recent exciting discovery in the Lake Manuherikia deposits was a leaf of an extinct species in Elaeocarpaceae with aspidiotine diaspidid scale covers, of a species also apparently extinct in New Zealand (Harris *et al*., 2007). The scale covers are so well preserved they appear almost lifelike, but there were no scale bodies beneath them (A. Harris, pers. comm.) It is interesting that aspidiotine armoured scales now have almost completely disappeared from the native New Zealand fauna, with just one rare species (*Aspidiodes corokiae* (Maskell)) known, whereas diaspidine scales are predominent. Australia undoubtedly has more representatives in the aspidiotine tribe, but the Australian diaspidid fauna has not been well researched. The importance of the Miocene diaspidid fossil is its uniqueness and the solid evidence it provides that scale insects in that group were present in New Zealand 20-25 mya.

Fossil of extant species

A new discovery is a 34,000 years old fossil leaf of *Nothofagus menziesii* from Howard Valley in the Nelson Lakes area. This leaf is deformed by a pouch gall that clearly matches the host-specific gall of the extant species *Madarococcus cunicularius* Hoy (Eriococcidae). The date marks the beginning of three major ice advances and the temperature was 2–3 degrees cooler than present day (M. Marra, pers.comm.).

Composition of modern native scale insect fauna

The most successful scale insect families in New Zealand for native species richness are Eriococcidae, Diaspididae and Pseudococcidae, followed by Coccidae (Table 1). The number of undescribed Diaspididae included is approximate and consists almost entirely of *Leucaspis* spp. Endemism is highest in Phencoleachidae because the single genus is endemic. Generic endemism is next highest in Eriococcidae (66%) and Coccidae (65%), and less in Pseudoccidae (32%) and Diaspididae (22%).

Table 1. Diversity of native scale insects and whiteflies by family in New Zealand.

Family	Number species described	Number species undescribed	Endemic genera NZ	Total genera in	% generic endemism
Aleyrodidae	9	1		8	0
Asterolecaniidae	1	2		1	0
Cerococcidae	2			1	0
Coccidae	45		11	17	65
Diaspididae	33	33	6	27	22
Eriococcidae	94	3	12	18	66
Margarodidae	10		2	4	50
Ortheziidae	3			1	0
Phenacoleachiidae	2		1	1	100
Pseudococcidae	65	1	9	28	32

Although Aleyrodidae and Margarodidae appear to rank together (Table 1) with ten species each, their success is unequal. Native whiteflies are not common whereas the abundance of some margarodids can be spectacular, in particular the sooty beech scales (*Ultracoelostoma* spp.) in the southern beech forests and *Coelostomidia wairoensis* (Maskell) in the North Island on *Kunzea*. There are no endemic genera in Aleyrodidae, Asterolecaniidae, Cerococcidae or Ortheziidae, and one each of the three ortheziid species is shared with New Caledonia and Australia respectively.

The uneven number of species in the coccoid families is perhaps a consequence of Pliocene depletions. Those more successful families have members that responded well to cooling climate and were able to thrive on temperate host plant species.

Examples of host plants and their scale insect faunas

(1) *Hedycarya*

Hedycarya provides an example of the selective species richness hosted by a small broadleaf tree in lowland forest. The scale insect fauna here is predominantly Coccidae (11 species) followed by Diaspididae (6 species); Eriococcidae and Pseudococcidae are less numerous with 3 species each. No other coccoid families are recorded on it (Table 2).

(2) *Hoheria*

Hoheria species have an endemic coccoid fauna of generic diversity but with few species. These are predominantly Eriococcidae with eight species in six genera. The single soft scale species recorded, *Epelidochiton piperis* (Maskell), is more common on other host plants.

Table 2. Diversity of native scale insect species by family on *Hedycarya* in New Zealand.

Family	Coccidae	Diaspididae	Eriococcidae	Pseudococcidae
Nº of species	11	6	3	3

(3) *Metrosideros*

The genus *Metrosideros* can be divided into two groups, one of tree species (*M. excelsa*, *M. robusta*, *M. umbellata*) and the other of climbers or lianes (Table 3). Each group hosts its own mutually exclusive suite of scale insect species as well as some other generalist species. The tree group hosts all four *Lecanochiton* species (Coccidae); *Eriococcus pohutukawa* Hoy, *E. rata* Hoy and the under-bark-dwelling *Capulinia orbiculata* Hoy (Eriococcidae); and *Anoplaspis metrosideri* (Maskell) (Diaspididae).

In the liane group, *M. perforata* is distinct in that it hosts a specific gall-inducer, *Eriococcus abditus* Hoy. The diaspidid *Anoplaspis maskelli* Morrison is specific to the liane group of *Metrosideros* spp. The other *Metrosideros* lianes support non-host specific scale insects.

Table 3. Number of mutually exclusive scale insect species by family, on the two groups of *Metrosideros* species in New Zealand.

Family	Coccidae	Diaspididae	Eriococcidae	Margarodidae	Pseudococcidae
Tree group	4	1	3	2	4
Liane group	1	1	2	1	3

(4) *Nothofagus*

Nothofagus has been present in New Zealand since before the Miocene and has proved to be highly adaptable to change, successfully colonising difficult mountain terrain. Problems from nutrient deficient soils are mitigated by their symbiotic mychorrhizal fungi. The genus supports an arboreal scale insect fauna with representatives of six sternorrhynchan families. The endemic radiation of eriococcid species has been found to be monophyletic and part of a *Nothofagus* clade also present in Australia and South America (Hardy *et al*, submitted). Pseudococcid species richness is high also, including a radiation in the host specific genus *Sarococcus*. With five species in two genera (*Coelostomidia* and *Ultracoelostoma*), margarodids are very important in southern beech forest because their honeydew production underpins the food chain. The species in Aleyrodidae, Cerococcidae, and Coccidae are all host specific (Table 4).

Table 4. Diversity of native scale insect and whitefly species by family on *Nothofagus* species in New Zealand.

Family	Aleyrodidae	Cerococcidae	Coccidae	Eriococcidae	Margarodidae	Pseudococcidae
Nº of species	2	1	2	22	5	12

Radiation among armoured scales (Diaspididae)

(1) *Eulepidosaphes pyriformis* (Maskell): wide host range

Eulepidosaphes pyriformis is close to *Lepidosaphes* (B. Normark, pers.comm.) which may indicate that it is a recent arrival in New Zealand, perhaps within the last 5 million years. Reflecting the phenomenon of host expansion by new exotic introductions, its host range is large and expanding, covering gymnosperms, monocots and dicots. Currently it is recorded on 53 plant species in 29 genera, all of which are natives. There are two closely related species, *Scrupulaspis intermedia* (Maskell) on *Kunzea* and one undescribed species on grasses.

(2) *Leucaspis*: species radiation

The pupillarial tribe leucaspidini in New Zealand comprises *Labidaspis myersi* (Green) plus 17 described *Leucaspis* species. A further 31 undescribed *Leucaspis* species are under study at present, although this number may be adjusted slightly when tested against DNA analysis.

(3) *Pseudaulacaspis phymatodidis* or fern scale

Ferns are well understood as ancient plants present since Cretaceous (Gibbs, 2006), yet surprisingly they host few scale insect taxa in New Zealand. The one predominant is the diaspidid fern scale, recorded on tree ferns, ground ferns and epiphytic ferns to a total of 34 species in 17 genera. Perhaps fern scale is another example of diaspidid dispersal to New Zealand within the last 5 million years.

Changes brought by human colonisation

Polynesian colonisers began the wave of destruction on New Zealand's biota when they brought fire, dogs and rats. European colonists first modified the New Zealand landscape in the mid 1800s, bringing major change to the vegetative composition by clearing the native forest for farmland. Australian and European plants were introduced, with mammals, rats, mustelids, and the marsupial possum. In pre-human New Zealand, birds were dominant in the absence of mammals and they probably exerted greater pressure on scale insect populations than today because about 50% depletion of terrestrial native bird species and similar loss of abundance has occurred since the advent of mammalian predators. The diet of some endangered extant native birds includes scale insects such as the large coccid *Ctenochiton*, and *Eriococcus* spp. on *Leptospermum* and *Kunzea* (Leathwick *et al*., 1983; Hay *et al*., 1985; Greene, 1998). Scale insects must benefit from reduced predation by the present scarcity of native birds. Alternatively, decimation of forest trees such as *Metrosideros*, by the Australian brushtail possum (*Trichosurus vulpecula*), seriously impacts on the scale insects in those habitats.

Kunzea and Leptospermum: long distance dispersal of Australian immigrant scales.

Three adventive felt scales have self-introduced on *Kunzea* and *Leptospermum* over about the past 100 years. First records for them are: *Eriococcus campbelli* Hoy, 1982; *E. leptospermi* Maskell, 1890; *E, orariensis* Hoy about 1940. J.M. Hoy (1961) measured long-range wind dispersal of *E. orariensis* in New Zealand, and suggested that was a possible mechanism for the insect's introduction from Australia. Although the strong west to east wind flow is a well-known transport mechanism for Australian insects crossing the Tasman to New Zealand, particularly Lepidoptera, it is implausible that tiny scale insects could survive such a journey, be lucky enough to land on a suitable host plant on arrival, and become established. Yet their chances greatly improved when forests were cleared by European colonists and their Australasian host plants proliferated. *Leptospermum scoparium* in turn colonised the new farmland so successfully that it became a scrub weed and *E. orariensis* was used as a biocontrol agent against it for a time. The Australian diaspidid *Chionaspis angusta* Green was first recorded in 1890 and could have arrived on imported garden plants, although it is also found in native forest.

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