Forests and Native Wildlife

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Abstract

This chapter describes the composition of the modern forests; the discovery of the Pureora Buried Forest and the significant information about ancient environments and extinct invertebrates it preserved; and the past and present wildlife of the native forest community, especially the rare native species now protected within Pureora Forest Park.

Keywords

Pureora Buried Forest · Dating the Taupo eruption · McKelvey’s volcanic succession hypothesis · North Island podocarp forest · Vegetation dynamics and patterns · Recolonization of volcanic surfaces · Mountain mires · New Zealand native wildlife · Extinct avifauna · Kiwi · Kokako · Tuatara · Mystacina · Dactylanthus · Tymnoiptus

Early European Descriptions

Eye-witness descriptions of any scene are always framed by the previous knowledge of the author and the interests of the intended audience. Maori developed an intimate understanding of the forest and its food resources, a product of many generations of settled dependency by the people of the land, the tangata whenua (Chap. 3).

Modern forest ecologists view and interpret the forest environment quite differently, even when they are referring to the same places as did Maori. Both views are or were quite different from the reactions of the early European explorers, whose accounts give us the nearest picture now available of what the land and the
forests looked like after they had recovered from the Taupo eruption, and how people used them during the classic period of Maori culture.

The early European visitors who first ventured into the forest in the mid nineteenth century found an environment totally different from anything they had ever seen before. Naturally, they searched for comparisons with familiar scenes that would make sense to the readers of their detailed reports. Some of their wide-eyed descriptions are intensely moving, especially when we remember that they were describing these forests before the arrival of ship rats, possums and deer.

Not all available accounts refer specifically to forests closely similar to those found in Pureora, and their terminology has often been updated since, but the general picture of magnificent ranks of immense trees and ferns reappears in many different accounts.

There is a solemn grandeur in these primeval forests, with their strange and luxuriant vegetation. Most of the trees are of the pine tribe, and grow to an enormous height. …Beneath and among these and the other lords of the forest, are seen the less aspiring plants; the beautiful tree fern, reaching sometimes to the height of thirty feet….. the venerable ratu [rata] tree [is] often forty feet in circumference, and splendid with its dazzling scarlet blossoms; while graceful creepers, with their various coloured flowers, spread from tree to tree, and form an almost impenetrable barrier [53: 6–7].

There is no country in the world so rich in ferns as New Zealand—the variety and elegance of their forms from the most minute species, to the giant tribe, is astonishing—some attain a height of forty feet, whilst others of exquisite beauty are extremely small. Two examples of the tree-ferns are figured in the accompanying scene [Plate VI: Fig. 2.1]—the *Cyathea medullaris*, and the *Cyathea dealbata*; the pulp of the former, at certain seasons of the year, is used as food by the natives, and when boiled, resembles apple sauce.

During night, the forests frequently present a most beautiful appearance—the decaying and fallen trees, and the whole surface of the ground, covered with decomposed vegetable matter, sparkles with phosphorescence in every direction. So exuberant is vegetable life in these damp and gloomy forests, that it is difficult to find a single space, even on the trunks of the largest trees, not covered with plants; the warm and silent dells, eternally shaded from the sunbeams, by their lofty canopy of foliage, and fed with the ceaseless moisture that drops from every spray, are filled with palms, ferns, and countless parasites—all luxuriant to excess…… A vast portion of New Zealand, is covered with forest-clad mountains, yielding some of the finest timber, and the most ornamental and elegant woods in the world [1: 22–23].

I cannot call to mind any tropical forests which excel those of New Zealand in beauty, for here there is magnificent timber, without the jungle of undergrowth which obstructs the view in more torrid climes. Brilliant parasites and creepers hang from the uppermost boughs of the loftiest trees, straight as cathedral bell-ropes, or, winding from stem to stem with fantastic curves, interlace distant trees, in the very extravagance of their luxuriant beauty. The lofty Totara, and the Rimu with its delicate and gently weeping foliage, and the shade-loving tree fern, the most graceful of all forest trees. Wild flowers are few and rare, but the ferns are more numerous and varied than in any other country [41: 117].

In parts of the landscape affected by Maori fires, thick forest gave way to open country.
This large area [the Tihoi Plains] comprising nearly 1000 square miles, was the country described upon the maps as covered with dense bush; and where we had expected to travel through primeval forests we found magnificent open plains, clothed with a rich vegetation of native grasses, and composed of some of the best soil we had met with during our journey. As we rode over these plains, the scenery was magnificent, as much by reason of the vast scope of country that stretched before us as by the variety of mountain scenery that surrounded the plains in every direction [28: 319–320].

These descriptions are especially valuable because contemporary scientific descriptions can see only the natural vegetation cover that has survived to the present. Contemporary forests often look very different from the descriptions left by the early explorers 150 years ago. Fortunately, the Rangitoto and Hauhungaroa Ranges still support extensive and diverse tracts of native-dominant vegetation, including some of the few substantial remnants of North Island dense podocarp forests (native southern conifers) remaining anywhere.

The Forests Today

The forests in what is now Pureora Forest Park (PFP) were explored by the Polynesian ancestors of the Maori soon after their arrival in the central North Island some 700 years ago. From then until now, the forests have been appreciated from widely differing perspectives—for their provision of food and shelter, for their spiritual significance, for their timber, and more recently for their conservation value. They also contain some of New Zealand’s most intensively studied forest ecosystems.

In 1963, Peter McKelvey [39] produced the earliest definitive account of the broad forest pattern, based on extensive plot data collected during the 1946-55 National Forest survey (Chap. 6). This work provided the basis for much of the subsequent utilisation of the native timber contained in these forests, first through clear felling, and then through early attempts at sustainable silviculture.

In the early 1980s, once logging had ceased, two ecological areas at Pureora (Waipapa and Pureora Mountain) were used by Forest Research Institute (FRI) plant ecologists as test sites within which to develop and demonstrate the use of ‘modern’ methods for the description of vegetation patterns. The first of these studies was carried out on Pureora Mountain, using semi-quantitative plots to describe both the forests [33] and the extensive wetland located near Bog Inn (Fig. 14.9) [7]. This work was later extended to cover the forests, shrublands and wetlands of the Waipapa Ecological Area [32]. These descriptions, along with the numerical analysis of forest/climate relationships by John Leathwick and Neil Mitchell [34], emphasise the complex interplay between climate, topography and disturbance that drives the broad vegetation patterns in PFP. Information from all of these sources has been used to compile the following account. For a general description of forest types, see Box 2.1.

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**Box 2.1 Revised forest classifications describing the principal forest types in Pureora Forest Park. From Nicholls [47]**

The large tree species present in PFP are broadly divided into two major groups: conifers (gymnosperms) and broadleaved trees (angiosperms). The traditional forestry terms for these two groups are softwoods and hardwoods respectively, but this can be misleading because the actual hardness of the wood varies widely within and between these categories. A third group, the southern beeches, is almost entirely absent from PFP but dominant on most of Ruapehu, on the axial ranges of the North Island, and across much of the South Island.

The family Podocarpaceae includes rimu, miro, matai, totara, Hall’s totara, kahikatea, tanekaha, toatoa, mountain toatoa and bog pine. They are classed as southern conifers, but are quite unlike the conifers of the Northern Hemisphere; to avoid confusion with those, we retain the collective term “podocarps”. Broadleaved trees belong to many different families, and those typical...
of PFP include tawa, rewarewa, hinuau and pukatea, black maire, pokaka, broadleaf, tawheowheo and kamahi. Unlike the native broadleaved trees of the Northern Hemisphere, all these species are evergreen. Scientific names are listed as an Appendix.

Broad scale forest mapping (scale 1:63,360) was produced by Peter McKelvey [39] to accompany his 1963 report. More detailed vegetation maps (1:10,000) were produced for the Pureora Mountain [33] and Waipapa Ecological Areas [32] after intensive field surveys by FRI staff working to develop methods for describing vegetation pattern in scientific reserves.

John Nicholls’ scheme of forest types [47] is somewhat oversimplified, but was widely used for decades and is still mentioned in literature relating to Pureora, so a quick summary may be useful here.

**Class L, Podocarp forest (Southern Conifers)**

Class L is restricted to tall forest where podocarps are abundant, and to dense conifer pole stands that are successional to tall forest. The tallest of these magnificent trees grow up to 65 m, their branches draped with epiphytes and lianes. The drooping, shaggy bronze foliage of rimu is instantly recognisable; darker crowns of matai, miro and totara accompany them. Their flawless straight columnar trunks, 1–2 m across at waist height, soar up to the closed canopy above. The forest floor is covered with ferns, lichens and liverworts, and fallen logs are rapidly draped with mosses and saplings. Broadleaved trees are commonly present but confined to the understoreys. Appreciable areas of this class grow only in the central districts of the North Island.

**Class M, Rimu-Matai-Broadleaved forest**

In this class, the giant southern conifers, matai and rimu, are still impressive in number and size, but no longer so dominating. They appear as scattered emergents above a lower canopy of smaller broadleaved trees and ground plants. On the lower slopes, tawa dominates the many species of the subcanopy, and is replaced at higher elevations by kamahi. The class differs from other conifer-broadleaf classes in the presence of matai, totara, and kahikatea.

**Class D, Rimu-Tawa forest**

Podocarps tend to be very occasional in this class, although rimu, the commonest, is usually a large tree. The broadleaf northern rata is the only other large tree, no commoner than rimu generally and becoming sparse in some areas. Rata can (or could, before the arrival of the introduced Australian brushtail possums: Chap. 12) grow up to magnificent trees 30 m tall, but start as epiphytes perched on the branches of other established trees. The rata sends down roots on all sides, which eventually fuse and enclose the host tree; by the time it dies, the rata can stand alone. The beautiful scarlet flowers of the rata are a vital source of nectar for native honey-eating birds, and a favourite food of possums (Fig. 12.2). Other broadleaved trees are always abundant, with tawa predominating almost throughout.

**Class F, Rimu-General Broadleaved forest**

Forests of this class grow in a few, widely separate localities immediately above the altitudinal limits of taraire and tawa. Montane forests generally are different, not only because of their species composition, but also because they suffered the least damage from historic Maori fires [50]. Podocarps may be occasional to frequent; rimu is the commonest, but miro and Hall’s totara are more numerous than is usual at lower altitudes. Broadleaved species are usually abundant, but in places many have died out in the last 10 to 20 years, especially rata and kamahi.
Class G, Lowland Steepland and Highland Podocarp-Broadleaved forest

This class contains many different mixtures of podocarps and broadleaved species, and any of these may be occasional to locally abundant. Forests of this type grow mainly where beeches are absent on the high country and above the altitudinal limit of rimu. There it is usually low forest, with stunted podocarps and malformed and shrub broadleaved species often prominent in the canopy. Also included are podocarp-broadleaved forests below the altitudinal limit of rimu on broken steep country or exposed ridges; that is to say, on sites where kauri or beeches are normally present. Where rimu grows it is usually small, and outnumbered by miro, Hall’s totara, or tanekaha. Tawa usually persists on these sites, but several characteristic lowland broadleaved species do not.

The hill-country forests are generally the most predictable, with a strong and generally consistent relationship between forest composition and elevation. Most of the mature forests at low to middle elevations consist of scattered large podocarps, mostly rimu and matai, emergent over a canopy of broadleaved trees. Tawa, pukatea, kamahi and northern rata generally dominate the canopy at low elevations, along with occasional rewarewa, although rata has declined in abundance since the invasion of PFP by possums (Chap. 12). Tawa-dominant forests, often with pure stands of rewarewa along the margins, are most widespread in the north of PFP (from the northern parts of the Waipapa EA north, including in the Okahukura and Mangatutu catchments), and west of the Hauhungaroa Range in the southern part of PFP.

With progression to higher elevations, first pukatea and then tawa drop out, and dominance shifts to hinau and various low-stature tree species. Tawheowheo and kamahi gradually become dominant at high elevation, e.g., on upper slopes of Pureora and along the Hauhungaroa Range. Similarly, rimu, matai, kahikatea and miro are gradually replaced by Hall’s totara and mountain toatoa. Tawheowheo forms locally pure stands in these upper elevation forests, particularly on sites with extreme soils, including around the margins of mires or on steep ignimbite escarpments, where it is often accompanied by scattered toatoa e.g., above the headwaters of the Ongarue River in the Pureora Mountain EA (Fig. 11.6). Along the tops (e.g., towards the summit of Pureora), the canopy gradually reduces in height and the scrubby vegetation is dominated by broadleaf, haumakaroa, stinkwood and mountain fivefinger. There are several notable local exceptions to this general pattern. One high-elevation site just south of the hut at the southern end of the Hauhungaroa Range (Fig. 14.9) supports a distinctive community of silver pine growing in company with a range of mire plants. Isolated stands of silver beech survive in steep ignimbrite gorges on the southern and eastern flanks of the Hauhungaroa Range. Seeds from such remnants in the headwaters of the Mangatu Stream have dispersed by water transport to establish several riparian stands of young silver beech downstream, including where the Waihaha track crosses this stream about 2 km west of SH 32. An unusually dense stand of northern rata surviving on the western slopes of the Hauhungaroa Range, adjacent to the Piropiro Flats, has been protected as the Rata-nu-nui Ecological Area.

The forest pattern becomes much more complex on flat sites, reflecting the interactions between topography and the drainage of cold air and water. Measurements of frost intensity in the Waipapa EA found very steep temperature gradients over short distances, particularly where cold air drains downslope during frosts. Water drainage often follows similar patterns, so that some sites experience both water-logged soils and periodic extreme cold air. Such conditions favour podocarps rather than the broadleaved trees that dominate hill-country forests at the same elevation—the famed dense podocarp forests of Pureora. In both the Waipapa and Waihaha Ecological Areas, cold air drainage is locally severe enough to produce inverted treelines. Then, broadleaved trees such as tawa, rewarewa and hinau are
excluded from cold basin sites, even though they happily occupy the surrounding slopes. One of the most accessible examples can be observed along the Waipapa Stream downstream of the Pureora Forest Park Lodge, where forests growing on well-drained alluvial deposits of Taupo Pumice on the valley floor are dominated by the most cold-tolerant podocarps and broadleaved trees. Matai, kahikatea and black maire form a dense high canopy over an impenetrable understorey of frost-tolerant divaricate shrubs and lianas.

On the extensive plateau country of the Waipapa EA, well drained sites support abundant tall podocarps, including rimu, kahikatea, miro, totara (Fig. 2.2) and matai, emerging above diverse broadleaved canopies of tawa, hinau, kamahi and pokaka. The understoreys are diverse with abundant mahoe, fuchsia, pate, raukawa, wheki, mountain horopito, and climbers such as supplejack, lawyer and climbing ratas. On more poorly drained sites, rimu and kahikatea are generally dominant over a stunted canopy of tawheowheo and/or tawa, and locally abundant tanekaha (celery pine).

Disturbance by fire has, at times, profoundly affected the vegetation pattern of PFP, particularly around the eastern margins. Peter McKelvey [39] provided an excellent summary of its long-standing effects. In the North Block, fire history is clearly reflected in the dense stands of rewarewa along the park margins, e.g., along the southern part of Ranginui Road, and in the extensive area of secondary vegetation in the centre of the Waipapa EA. There, the complex patterns of vegetation succession after fire are intimately linked to topography and its controlling effect on frost intensity. Silver tussock and monoao dominate the coldest basin sites, while various mixtures of divaricate shrubs, kohuhu and lancewood dominate the intervening low ridges. On steeper sites, post-fire successions are often dominated initially by bracken, then by a gradual transition to broadleaved shrubs such as fivefinger, plus rangiora on the least frost-affected sites.

In the southern part of PFP, similarly complex patterns of forest succession after recurring fires are visible in the Waimanoa EA, with complications added by the complex topography. Some of the dissected rhyolitic landforms, including prominent knolls with skeletal and presumably drought-prone soils, support dense stands of tanekaha and/or toatoa. Further south, extensive secondary shrublands in the Waihaha EA can be readily observed along the track from

Fig. 2.2 A fine specimen of a totara in Pureora, 1956, before it was felled. It stood 127 feet (38.7 m) tall, with 47 feet (13.3 m) to the first limb. Photographer unknown, copyright assumed SCION 4536
SH 32 to the Waihaha Hut. Here the vegetation pattern is broadly similar to that of the Waipapa, although on a grander and frostier scale. It includes dense stands of young conifers along the margin of the mature forest, with tanekaha particularly prominent. The mature forests on the basin floors closer to the Hauhungaroa Range support impressive stands of frost-tolerant podocarps, dominated by matai and totara on the flats, with few broadleaved trees.

Basin sites that have been infilled to varying degrees by water-transported Taupo pumice have developed into wetlands, which are numerous throughout the park from about the Waipapa EA south. The extensive mires in the Waipapa EA are dominated by square sedge and tangle fern, plus upright cutty grass, which has a very limited distribution elsewhere in the North Island.

The Mires

Mires are natural peat-forming wetlands, and seven of them lie within the Pureora Ecological District and PFP (Fig. 2.3). All the mires of PFP sit on a metre-thick layer of Taupo ignimbrite covering the blasted-flat remains of the former forest, some of them at unusually high elevations [6].

The most common plants in the mires are sedges and ferns, mainly square sedge, straw sedge and tangle fern. Two mires in the Waipapa Ecological Area have charred logs of bog pine on the peat surface, showing that a former shrub mire was burnt at some time in the recent past.

The Pureora mires are especially important places for palaeo-botanists, because they preserve the remains of long-vanished vegetation in the form of plant macrofossils and pollen deposited among dateable layers of debris and mud. Surveys of the living plants compared with analyses of what lies underneath them can offer vital information with which to reconstruct the history of the forest before the Taupo eruption, and the recovery and probable future trends in the vegetation of the park [6]. Hence, the historical records retrieved from the Pureora buried forest are of regional and international significance.

The Buried Forest

Krakatoa is justly famous as an example of how life returned to an island totally sterilised, at least temporarily, by the drastic consequences of an enormous volcanic eruption. Pureora is a mainland version of the same kind of cataclysmic
event, except that, unlike Krakatoa, the area
devastated by the Taupo eruption (Chap. 1)
retains clear evidence of what life was like there
beforehand, and was not isolated from potential
sources of recolonisation.

That fact makes Pureora one of the most
exciting places in the world for ecologists and
foresters to study the history of forests and their
inhabitants—and the responses of natural habitats
and biota to cataclysmic destruction. Ancient and
modern plant assemblages can be compared, in
order to illustrate some of the differences between
the present and the pre-human, pre-rat past.

The extremely violent surge of the Taupo
ignimbrite across the landscape in AD 232 \(\pm 10\)
generated an air-blast shockwave that flattened
the forest over the surrounding 20,000 km\(^2\), and
the pyroclastic flow that followed engulfed and
incinerated most of the fallen trees (Box 1.1). At
Pureora, some plant materials were turned to
charcoal at temperatures of up to 364 °C; but
most of the fallen vegetation was only slightly or
not at all charred, perhaps protected by the wet
leaf litter, or the cooling of the flow \([24, 37]\).
Intact litter layers and prone trees all lay as they
fell, facing away from the vent, with their bark
intact and undamaged. All the remains have been
beautifully preserved since AD 232 under the
sterile blanket of Taupo ignimbrite, right down to
leaves, seeds, fruits and invertebrates \([4]\). How
did this happen?

Where the normal drainage channels were
blocked by volcanic deposits, the water table rose
to the surface. Layers of peat then gradually
developed on the boggy ground above the
ignimbrite. The whole assemblage from the top
down became permanently waterlogged, and the
buried trees and their associated fruits and leaves
remained saturated, immune to decay in the
anaerobic conditions, and so were preserved
intact.

Several such post-eruption wetlands lie on the
western flanks of the Hauhungaroas, northwest
of Lake Taupo (Fig. 2.4). One of them covers
about 37 ha of open ground, only 2.5 km from
the Department of Conservation (DOC)’s

Pureora Base. In 1983 a bulldozer driver was
sent to dig drainage ditches through it. His digger
repeatedly snagged on buried logs, which caused
him a lot of irritation and prevented him from
finishing his work on time. He complained to his
boss, John Gaukrodger, who called on Rob Guest
(NZFS District Forester based at Te Kuiti) to go
with him to have a look. They recognised what
they saw, and Guest called for advice from the
experts at the Forest Research Institute in
Rotorua.

They discovered that the logs causing all the
trouble were the remains of the pre-eruption
forest, flattened and buried under a metre-thick
bed of pumice. Geologists identified the overly-
ing material as comprising layers of soft Taupo
ignimbrite \([22, 24]\). Subsequent excavations at
Pureora, and at a second site at Benneydale about
20 km away, caused great excitement among
scientists (Fig. 2.5) and comment from the
Fig. 2.5 A coordinated field trip to the Pureora Buried Forest site by geoscientists, botanists, ecologists and others on 14 February 1984. The presence of a TV crew recording the scene (right, with camera behind microphone) illustrates the high national interest stirred up by the discovery. 

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Fig. 2.6 The discovery of the Buried Forest in 1983 caused much excitement, not least among bushmen who had recently been told there was no more standing timber available for logging. Cartoon by Eric Heath, published in The Dominion, 1 February 1984

interested public (Fig. 2.6). The site became an important destination for field trips for students and members of natural history clubs. To guard against too much trampling, all the ditches except one were re-flooded in 1985 to preserve the forest remains.

Detailed descriptions of preserved plant macrofossils (leaves, stems, fruits and seeds) have been used to interpret the pre-eruption vegetation at three sites along a 20 km transect, from Pureora westward to Benneydale. All the stands were on flat or undulating terrain and were dominated by podocarps, mostly rimu and tanekaha [9]. The mean width of the growth rings of 18 trees from the buried forest was 0.71 mm, suggesting that they grew only slowly. Broadleaved trees were generally more abundant at the Benneydale site, which is at lower elevation and has a milder climate. So the three samples of buried forest illustrate a gradual change in forest composition, from Pureora where horopito was prominent, to Benneydale, where rewarewa and northern rata were important canopy components.
Dating the Taupo Eruption

The exact date of the eruption has been debated for years, but recent research has pinned the date down to AD 232 ± 10 (1718 ± 10 calendar years before present, ‘present’ taken as AD 1950). This date was derived by matching 25 high-precision 14C dates from decadal samples of tanekaha logs from the Pureora buried forest against high-precision, first-millennium AD subfossil kauri calibration data [22].

Roman and Chinese literature recording red skies and poor summers in about AD 186, and a Greenland ice-core date of AD 181 ± 2 recording a layer of sulphate generated by an eruption, were for a long time assumed to have been correlated with this event. More recent research by Alan Hogg et al. [22] shows that the true date was in fact about 50 years later and, furthermore, that those historic Northern Hemisphere records have no connection to the Taupo eruption.

Taupo erupted in the late summer or early autumn of the year, because the buried forests at Pureora and Benneydale have preserved seasonal fruit and seeds (Fig. 2.7), and there is no late-wood (formed late in the growing season) on the outermost rings of the flattened trees [8, 49]. Even more interesting, the assemblage of preserved insect remains lying under the pyroclastic flow deposits, excavated near what is now Link Road, suggested to Bev Clarkson et al. [8: 433] that the final phase of the lengthy eruption sequence (Fig. 1.4: the phase that produced the ignimbrite) was late in the day.

Some of the most interesting information derived from the excavation of the buried forest sites was the picture they painted, not only of the process of forest recovery, but also of differences in composition between the pre-Taupo and living forests. Were these differences related to geographical conditions, or was there a historical element as well? The answer has important implications for understanding the contemporary ecology of the forests.

Pollen diagrams from surrounding areas show that after the Taupo eruption, the earliest colonising vegetation dominated by bracken had stabilised the surface within five years [55]. It gave way to a shrubland with bog pine, then mountain toatara, followed later by totara and matai; tall forest had returned within about 200 years.

At Pureora, the contemporary forests are dominated by matai and rimu, which contrasts strongly with the pre-eruption forests, which grew on old, infertile soils favouring the dominance of rimu and tanekaha, including several species that prefer a climate warmer than now [7]. Furthermore, tawa, kamahi and mahoe, which are all common dominants in the contemporary forests surrounding the site, were not recorded in any buried forest.

At Benneydale, the dynamic nature of these forests was demonstrated again by a pollen diagram constructed from samples representing the roughly 6000 years between the even older Mamaku tephra and the Taupo ignimbrite [10]. Pollen from the basal zone of the peat core...
(c. 8000 years old) indicates forest quite different in composition from that immediately preceding the Taupo eruption. Hence, the forest at Benneydale around 8000 years ago had included a markedly different mix of species from that destroyed by the Taupo eruption in AD 232.

**The Volcanic Succession Debate**

One of the most contentious debates related to the forests of Pureora concerns the nature of dense podocarp forests and the place that they occupy in a linear succession initiated by the most recent Taupo eruption.

This debate was sparked by McKelvey’s suggestion, in his seminal 1963 monograph, that the dense podocarps closest to Lake Taupo were the youngest forests, and represented a pioneering stage in the eastward colonisation of the sterile pumice surface by tree species spreading from the less damaged forests further west (Fig. 2.8). In addition, he argued that, with time, further succession would lead to a gradual replacement of the podocarps in these stands by less commercially valuable broadleaved tree species. In making this suggestion he was influenced by then-prevailing theoretical ideas of linear succession [48], in which an orderly and predictable change in the dominant species leads inevitably towards a ‘climax’ forest dominated hypothesis are no longer accepted. Kanuka is short-lived, even where not suppressed by podocarps. *From Morton et al. [42: 59], courtesy David Bateman Ltd*
by species different to those dominant at earlier successional stages. McKelvey’s concept is summarised in a lavishly illustrated description of the rather similar pattern at Whirinaki State Forest, by Morton et al. [42].

McKelvey’s hypothesis was hugely influential, not only because it claimed largely to explain the existing pattern of the forests. It also supported then prevailing views about the necessity of logging native forests. It offered a broad understanding of the mosaic of wildlife habitats of very high conservation value in PFP, and provided a background for early research on management of native wildlife in PFP [27]. Over time, this influence has been challenged strongly by different researchers producing new information to re-analyse his key assumptions, as follows.

First, while McKelvey assumed that the largest podocarp trees are the oldest, subsequent studies in dense podocarp forests showed that stem diameters are only weakly correlated with tree age [20]. The largest known tree in PFP, the Pouakani totara, is possibly about 1500 years old [5], but most other giant trees are much younger. Unfortunately, most podocarps that reach such a size are hollow at the base, so their age can be estimated only from the section of sound wood that can be sampled.

Second, McKelvey assumed that the existing dense podocarp forests are the first generation of trees to have colonised the original Taupo ignimbrite pumice surface, but more recent evidence demonstrates the rapid recolonisation of the fresh tephra surfaces by forest within 200 years of the Taupo eruption [55]. Hence, at least some sites occupied by dense podocarp stands must have supported two or more generations of trees since the Taupo eruption. McKelvey later agreed that the dense podocarp stage includes several generations of long-lived trees, so could not be a single colonising first crop [40]. Moreover, disruptive events such as fires and wind-throw, which open canopy gaps and reset the succession (Fig. 2.8), have made the existing pattern more a mosaic than a simple linear sequence [15].

Third, McKelvey assumed that the present distributional limits of many podocarp species have been set by the slow processes of recovery after the Taupo eruption. But a numerical study of the distributions of major forest tree species, using forest plot data collected during the National Forest Survey (Chap. 6, Fig. 13.17) linked to climate estimates for individual plots, found strong evidence that these limits are more likely to be set by climate and topography than by history [34].

Fourth, McKelvey assumed that dense podocarp forest is not self-sustaining, but is replaced in time by forest dominated by broadleaved species. This idea proved to be a useful argument for advocates of the logging industry. Canopy collapse or hollow stumps observed in large, long-lived trees implied to some forest managers that the podocarp component of the forest was “overmature” and dying, and therefore must be harvested quickly before it fell down.

Up until the early 1980s, this fear of wasting a valuable resource was used to strengthen the case for logging of old-growth forests both at Pureora and at Whirinaki, 100 km away on the edge of Te Urewera National Park. Indeed, the official management plan for Whirinaki asserted that the giant podocarps were senescent and were not replacing themselves. The plan illustrates the then attitude of NZFS, which saw itself as conducting a salvage operation: “The long term objective of forest management in Whirinaki is to anticipate natural decrement by judicious selection logging” [46: 34].

This justification for continued logging was severely criticised by forest ecologists at the time [42], and later studies of regeneration and stand dynamics of podocarp/broadleaved forests showed that these forests can sustain themselves over multiple generations, at least where tawa is rare or absent [36]. The Buried Forest data support this conclusion [8].

And there is another complication, especially on the eastern slopes of PFP nearest to Lake Taupo. This area was a major centre of Maori settlement (Chap. 3), and forest clearance by fire
had a long history there [50]. The repeated post-fire successions that followed have probably
produced vegetation patterns that mimic the processes of forest recovery set off by the Taupo
eruption (Fig. 2.8).

Overall then, McKelvey’s post-volcanic succession hypothesis now seems too simplistic to
account for the heterogeneity—in terms of physiography, soils, and climate—of the physical
environment and the corresponding diverse patterns of forest disturbance and recovery. Espe-
cially, it underestimated the effects of the long-term maturation (podzolisation) of soils
under the humid climatic conditions of west Taupo. Recent re-measurement of permanent
plots in PFP showed little evidence that tawa, the supposed final dominant in the succession,
increases in plots where it was not already prominent, supporting Leathwick and Mitchell’s
[34] conclusion that most forests in the region have now returned to limits largely determined
by climate. McKelvey [40] later agreed that there is no evidence to assume that the west Taupo
podocarp forests are senescent or failing to replace themselves.

Interactions Within the Forest Community

The community interactions within a mature forest are nowhere better demonstrated than in
the mutual dependence of forest trees and the birds that help to disperse their seeds. NZFS
scientist Tony Beveridge [30] documented these effects in podocarp forest near Pureora over a
period of 7 years (1958–64). The timing of his work was very significant, because possums
were only just arriving in the region and had not yet added to the ongoing disruption of these
ancient relationships already being imposed by rats and introduced birds [3]. The study included
observations of birds feeding in the crowns of fruiting podocarps, and seed traps set to collect
data on the abundance of seeds, their condition and fate.

Podocarp seeds are produced every year, but in huge abundance some years and very few in
other years. The seeds often detach from the receptacles in the tree crowns before they fall to
the ground. Seeds of green miro fruits are broken open by kaka, and totara seeds by kakariki. Rimu
seed is favoured by many seed-eating birds, rodents and insects; chaffinches and other finches
feed in tree crowns (Fig. 2.9).

New Zealand pigeons travel long distances on seasonal migrations, and concentrate on trees
offering an abundance of food—a fact well known to the Maori (Chap. 3). Their dropping of ingested
seed from perches in large broadleaved trees and podocarps has important consequences for the
regeneration of mixed podocarp/broadleaved forests. Pigeons have always been the main dispersers
of miro, matai and tawa seed, assisted by kokako and moa in earlier times, and still by tui, bellbirds
and silvereyes, sometimes in local concentrations [11]. Now, feral pigs may help by grubbing up
fallen tawa berries and miro fruits, and depositing the seeds elsewhere along with large amounts of
fertiliser.

Killing native birds to get samples for gut analyses is not encouraged, so for one study, the
New Zealand Wildlife Service (NZWS) made the most of 144 pigeons confiscated from poachers
in central North Island forests. In summer, the succulent berries of species such as fuchsia,
wineberry and mahoe were common foods, and tawa berries in late summer [38]. Most hunters
targeted the pigeons only between May and August when the birds were feeding on miro
berries, so, predictably, the guts of birds collected during the autumn were crammed with
miro fruits. At Whirinaki, a year-long study confirmed that pigeons have a strong preference
for miro and tawa fruits, but they also need access to a range of fruits, foliage and flowers
through the seasons [14].

During the autumn of 1978, PFP produced the best rimu seed crop for 10 years [45]. Most of the
sound seed fell, with fleshy ripe receptacles attached, during periods of strong winds in
mid-April and early May, but during calm
periods, finches feeding on the seed contents dropped the ripe receptacles detached from the seed and split seed coats. Whiteheads, silvereyes, bellbirds and tuis dispersed many smaller seeds, ship rats fed on the seeds that had fallen into the counting trays, and possums ate the receptacles, some with seed attached.

In 1978 there was seed enough for all. From counts of the numbers of seeds fallen to the ground under large trees (>5000 sound fallen seeds per m²), Beveridge estimated that a single mature tree in PFP could produce a crop of 2 million seeds. In other years (monitored 1958–64) the rats and other introduced seed predators might well reduce the number of seeds available to birds [3].

**Forest Regeneration**

Southern Hemisphere conifers (podocarps) are very long-lived. That means that their population dynamics operate over longer time scales than those of broadleaved angiosperm trees [48]. It also means that they are better adapted to low-frequency, large-scale disturbances than to more stable environments [16].

The age distributions of existing old stands suggest that, after a disturbance such as a canopy gap or a fire, the first cohorts of podocarps establish in a predictable sequence, variable with local microclimate but generally starting with the least shade tolerant: first totara, then matai, then...
rimu, and finally miro. The reverse sequence tends to follow progressive collapse of an existing canopy [36], except that light-demanding totara does not re-establish, and broadleaved species become increasingly important over time.

Regeneration rates are the key to sustainable management of any kind of resource, so in 1960 and 1976, forest ecologists assessed the regeneration rates of podocarps in second-growth forest in the Waipapa Ecological Area. They marked a 200 m line transect of successive permanently-marked 2 × 2 m plots [2] along a transect extending outwards from the high forest margin through zones of shrub broadleaves, manuka and monoao to open frost flats. Podocarp regeneration was fastest in a narrow belt of large kamahi between tall podocarp/tawa forest and scrub associations. Seedlings grew in patches of broad-leaved shrubs, but not on frost flats.

The regenerating podocarp forest did not spread out uniformly from the high forest margin, but as a mosaic of developing podocarps in patchy broadleaved shrubs on higher ground, only slowly invading frosty depressions. Manuka, fivefinger and lancewood provided shelter for small podocarp seedlings, many of which did not survive unless they reached heights of 2–3 m.

Rimu, totara, matai, kahikatea and tanekaha were all abundant as seedlings, but not miro. Well-established podocarp seedlings added height by only 6–12 cm/year from 1960 to 1976, as new growth can be damaged by frost and cold wind. The figures indicated a substantial increase in densities of established podocarp seedlings in the period observed [2].

On a larger scale, assessments over 7600 ha of secondary vegetation in the Waihaha Block of Tihoi State Forest have provided regeneration data by canopy type. They showed dense pole stands developing around the forest margins, mainly of tanekaha, on 5 % of the area, and a high overall abundance of podocarp regeneration, especially in the general broadleaved shrub cover type (45 % of total area), sufficient to replace trees over the next century. Rimu and totara (mainly Hall’s totara) will be significant elements in the future forests of these sites. Significantly, John Herbert [19] added, the forest supports the main prerequisites for podocarp regeneration, which are viable bird populations for seed dispersal, suitable nurse species and adequate seed production.

Native Wildlife

Extinct Vertebrate Species

In the limestone landscape of the southern Waikato, barely 50 km northwest of Pureora Village, the Waitomo Caves preserve a matchless record of the pre-human fauna of the central North Island. Sinkholes and underground caverns have trapped examples of many now-extinct species that were once important food sources, at least for a while, for the earliest Polynesian settlers (Chap. 3).

The remains of these long-vanished species may also be found in places near the west Taupo forests where the earliest human settlers once lived. For example, fragments of tuatara and North Island takahe have been excavated from the lower levels of two archaeological sites on the shores of Lake Taupo (Fig. 2.10: [23]).

Fig. 2.10 A rock shelter at Waihora Bay, near Taupo. Fragments of tuatara and takahe, once important as food for Maori but now locally extinct, have been recovered from the older archaeological levels. Modified by Max Oulton from Hosking and Leahy [23].
By the time of Dieffenbach’s visit in 1839, the tuatara was already long gone from the mainland, but he had heard of it, and eventually obtained a live specimen from offshore:

I had been apprized of the existence of a large lizard, which the natives called Tuatera, or Narara, with a general name, and of which they were much afraid. But although looking for it at the places where it was said to be found, and offering great rewards for a specimen, it was only a few days before my departure from New Zealand that I obtained one, which had been caught at a small rocky islet called Karewa, which is about two miles from the coast, in the Bay of Plenty, and which had been given by the Rev. W. Stack, in Tauranga, to Dr. Johnson, the colonial surgeon. From all that I could gather about this Tuatera, it appears that it was formerly common in the islands; lived in holes, often in sandhills near the sea-shore; and the natives killed it for food. Owing to this latter cause, and no doubt also to the introduction of pigs, it is now very scarce; and many even of the older residents of the islands have never seen it. The specimen from which the description is taken I had alive, and kept for some time in captivity: it was extremely sluggish, and could be handled without any attempt at resistance or biting [12: 205].

According to traditions recorded in the Minute Books of the Native Land Court, the takahē (moho) were once hunted in the Pureora hills as far as Titiraupenga. The North Island species of takahē is extinct, though the South Island species survives under Department of Conservation (DOC) protection in Fiordland [18].

Likewise, the kakapo, a large flightless ground parrot, was once widespread throughout the North Island, and its bones are well represented in the limestone caves of the Waitomo area [57]. It was still present in the central North Island in the early 1800s [18], but is very vulnerable to human hunters and dogs. It is long gone from the North Island mainland, and remains one of New Zealand’s most severely threatened species, surviving only on predator-free offshore islands or in captivity. Many other species once common in forests similar to PFP until less than 800 years ago have also disappeared (Figs. 2.11 and 2.12).

Hochstetter [21: 179] was fascinated by stories about the moa, and he concluded from a review of the localities where moa bones had been discovered that those birds were once distributed throughout the North Island. He tried hard to gather a good collection of specimens, but he was too late.

Upon North Island I had scoured every district, that had been noted for the occurrence of Moa bones, I had ransacked all the so-called Moa caves, but all in vain. The Moa enthusiasts, that had been there before me, had carried off the last fragment of a Moa bone, and the Maoris on having discovered, that they could make some money by it, had gathered whatever there was still to be found, and sold it to European amateurs at enormous prices. The only relic I at least found out, was in the possession of a chief in the Tuhua district, who produced from the dust and rubbish of his raupo-hut an old bone, which he had hidden for a long time, and with which he parted only after lengthy negotiations. It was the pelvis of a small species [21: 184].

In a later chapter he described this incident slightly differently:

My stay at Katiaho enabled me also to buy from a Maori for the price of one pound Sterling the pelvis of a small Moa which had been found near Teruakuaho a few miles above Katiaho on the Ongaruhe, under a cliff of the Herepu mountain. This was the first Moa relic, that fell into my hands, and I was not little gratified at the lucky circumstance [21: 354].

Living Species of Land Vertebrates

The total list of native land fauna now living in PFP (Box 2.2) includes many endangered, nationally threatened, regionally threatened and rare species (Fig. 2.13). It has been claimed that PFP has the greatest concentration of rare and endangered species of any area in New Zealand [43, 56], hence the great urgency and significance of protecting it.
Box 2.2 List of living species of native land vertebrates present in PFP

Scientific names are listed as an Appendix.

Endangered, threatened and rare endemic species
North Island kokako, North Island brown kiwi, blue duck, New Zealand falcon, North Island kaka, yellow-crowned kakariki, rifleman, North Island fernbird, North Island robin, long-tailed cuckoo, lesser short-tailed and long-tailed bats, and Hochstetter’s frog.

Non-threatened to common native and self-introduced species

*Self-introduced since European settlement.

Fig. 2.11 An imaginary scene in a central North Island forest about 20,000 years ago. Left to right, above red-crowned kakariki, morepork, kereru (native pigeon), **piopio (New Zealand thrush), *North Island saddleback, *North Island kokako, grey warbler, short-tailed bat, harrier hawk, kaka. Left to right, below brown kiwi, **bush wren, *Hochstetter’s frog, *kakapo, *snipe, *tuatara, *blue duck, **giant moa, weka, forest gecko, **laughing owl, **small moa, **stout-legged wren, *little spotted kiwi, **owlet-nightjar. Species marked with one asterisk are now rare or threatened, and survive only under DOC protection or on offshore islands; those with two asterisks are totally extinct. Modified by Ellen Clarkson from a painting by Pauline Morse.
Introduced species

California quail, eastern rosella, skylark, Australian magpie, yellowhammer, goldfinch, greenfinch, chaffinch, redpoll, song thrush, blackbird, house sparrow, dunnock, starling, Indian myna.

Data from Imboden [27], updated from Leigh and Clegg [35], R. Hay and T. Thurley (pers comms).

Hochstetter [21: 179] reported that “the natives speak of sorts of Kiwi, which they distinguish as Kiwi-nui (large Kiwi) and Kiwi-iti (small Kiwi). The Kiwi-nui is said to be found in the Tuhua district, West of Lake Taupo, and in my opinion Apteryx Mantelli.” In his time the kiwi was still abundant in mountain country, although “nearly exterminated by men, dogs, and wild cats” in the inhabited areas. Not long afterwards, Kerry-Nicholls agreed that kiwi were still common in the west Taupo forests [28: 364].

Now, brown kiwi still survive in parts of the central North Island, especially under DOC’s active protection in Tongariro Forest Kiwi Sanctuary (Fig. 0.1 in Preface, and 12.10). Their prospects for survival in the Hauhungaroas, and in other areas outside sanctuaries with kiwi-focussed pest management, are not good [51].
Bushman and forest rangers working in the Pureora bush in the 1940s (Chap. 8) remarked on the numbers of kaka, kakariki and pigeons they saw (“Flocks of 50–100 kaka screaming overhead”, remembered Ivan Frost; “we used to hear them all the time”, added Buster Seager) [54]. By the 1950s, these autumn flocks were down to 20 or 30 birds, but could still be observed in the tops of fruiting miro at Pikiariki, cracking open the green unripened fruit to extract the contents of the hard seed coats [3].

Kakariki (yellow-crowned parakeets), often heard flying over high forest, were common in late summer, feeding on the seed of tanekaha that flanked dense podocarp forest, or in the forest edge around Pureora village (Fig. 9.1). On Pureora Mountain, Tony Beveridge found caches of Hall’s totara seed with the fleshy receptacles removed but no seed eaten. Only parakeets extract the contents of totara seed after cracking the seed coats.

The North Island kokako (Fig. 2.13), like many other predator-sensitive endemic species, had been common and widespread throughout the lowland forests of the North Island before the arrival of Europeans and their rats, and in 1944 were still reported as “fairly plentiful in SF 93—say one to every 100 acres” [44]. The unlogged parts of Pouakani SF 93 (Fig. 7.3) were later taken into Pureora SF 96 (Fig. 10.1).

By 1978 there were very few remnant kokako populations left, all apparently declining (Fig. 13.13), and forest staff working all day in the bush

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Fig. 2.13 Endemic species still resident in Pureora Forest Park: karearea (falcon), whio (blue duck), brown kiwi, North Island kokako. Crown Copyright, Department of Conservation Te Papa Atawhai. Photographers: falcon, B.J. Harcourt (1974); whio, T. Smith (2005); kiwi, R. Colbourne (1980s); kokako, unknown
never saw a kokako. But this beautiful and nationally endangered bird became disproportionately important to the story of the protest action (Chap. 9) and the subsequent creation of PFP (Chap. 11).

One very important and nationally threatened resident of Pureora is the endemic lesser short-tailed bat. The population of bats surviving there is one of the few remnants of a once abundant species found throughout New Zealand [29]. It belongs to a distinctive lineage that originated in Australia, some of whose members flew across the Tasman millions of years ago, when New Zealand was free of all four-footed mammals. At that time, feeding on the ground was a safe and energy-saving strategy, and the new arrivals adapted well to those conditions, in time evolving into the short-tailed bat and its larger cousin the greater short-tailed bat (now extinct). They became the principal pollinators of the endemic *Dactylanthus taylorii*, a flowering root parasite (Fig. 2.14), which produces quantities of nectar on the ground. Both the bats and plants are now severely threatened by rats and possums.

**Invertebrates**

Many of the invertebrates of PFP’s terrestrial and freshwater habitats are unknown, although those that are known are very diverse [25, 26]. Entomologists often complain that forest ecologists know almost nothing of the insect component of the ecosystem on which so much else hinges [25]. In PFP, this is a serious loss: the insects of the central North Island are especially significant, because they offer a window into the very different world of the pre-human past.

The central North Island forests support many insect groups unique to New Zealand. Some of the insects of PFP belong to lineages that could have lived in ancient Zealandia since the Pleistocene or long before, only distantly related to other groups that have disappeared everywhere else in the world, and new species are frequently found [13]. For example, we have hard evidence, from dateable subfossil deposits, of several large, flightless invertebrates that are now extinct. The most important and revealing of such deposits come from two quite different sources.
First, the buried forest material contained remains of many insects preserved in ideal anaerobic conditions, representing the layer of litter and humus that was on the forest floor and on the surface of acid (pH 3.5–4.9) bogs at the time of the Taupo eruption [17]. Chris Green identified a total of 210 insect species, mainly beetles (Coleoptera)—and 68 species of these were weevils. Other groups represented were mites, bugs, cockroaches, ants and flies.

All except two of the insect species identified in the buried forest material are present in the central North Island today. The two exceptions are both giant, flightless weevils, one a species of *Anagotus*, and the other, *Tymbopiptus valeas*, both now presumed extinct. *T. valeas* belongs to the tribe Phrynixini, represented in Chile by three living genera which have no relatives elsewhere in the Neotropic but many in the Australian Region. That dates the ancestry of the group back to at least the late Cretaceous [31: 21–25].

Second, fragments of insects have been recovered from a limestone shaft at Waitomo (Fig. 0.1 in preface), alongside bones of takahē, kiwi, weka and kakapo in a layer dated to around 200 years after the Taupo eruption [57]. Both *Anagotus* sp. and *Tymbopiptus valeas* were among them. They were both flightless ground-feeding insects, “considerably larger” than any living New Zealand Phrynixini. They survived the eruption in c. AD 232, but not the arrival of Pacific rats after around AD 1280.

*T. valeas* has only ever been found as a subfossil (Fig. 2.15), and the closest living relatives of the vanished *Anagotus* weevils are now restricted to rodent-free islands offshore, or to high country of >1000 m elevation. Still, Kuschel was an optimist: he coined the name of *T. valeas* from the Greek *tymbos*, a tomb, and *pipto*, to fall, plus *valeas*, a Latin farewell bidding that does not give up hope of an eventual return [31].

The implication of this story, that the arrival of rats was catastrophic for the largest of the endemic flightless invertebrates, is illustrated by contemporary experiments comparing the abundance of insects on islands with and without rat control. The species most often eaten by rats, the large Auckland tree weta (a flightless endemic insect related to the crickets), increased in numbers threefold in areas where rats were held to fewer than four per hectare for three consecutive
years [52]. As soon as the rats came back, the weta declined again.

The living insect fauna of PFP is, predictably, very rich [25]. It would be impossible to sample all species equally, so one study concentrated just on the beetles of the Waipapa Ecological Area. Malaise traps, made of fine netting which guides insects passively to collecting jars, are suitable for catching low flying species. Three of these traps were set and cleared at weekly intervals over spring, summer and autumn (September 1983 to March 1984), in shrubland and in the adjacent mature podocarp forest. The results demonstrated many differences in the beetle faunas by habitat, especially in the diverse vegetation protected in Waipapa EA.

Nearly 5000 beetles of 400 species from 50 families were captured and analysed by a classification procedure which grouped the beetles by habitat. About 125 species were restricted to each of the two habitats, and 150 were shared. The shrubland samples were dominated by beetles that feed on live plants, and those from the forest were dominated by beetles that break down debris [25].

References


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