

# Leonard Cockayne: his contribution to ecological, biogeographic and evolutionary thought in New Zealand

Matt McGlone

Research Associate, Manaaki Whenua-Landcare Research

## Abstract

Leonard Cockayne was the leading plant scientist in New Zealand during the first 30 years of the 19th century. He had a profound effect on the development of plant ecology, systematics and biogeography in this country. Here I explore some of his ideas and their subsequent influence. His observations on the plant species and vegetation cover of New Zealand remain valuable, and his example of intensive field work and documentation and insistence on growing plants in order to understand them, were inspirational for the generation that followed. While many of his ecological and biogeographic insights are still valid, his ideas about evolution have been largely superseded. Nevertheless, some of the problems he highlighted, such as the causes of plant variability and the evolution of certain growth forms, remain hotly debated.

## Introduction

Leonard Cockayne's achievements are simply staggering: his copious publications, both scientific and popular; extensive botanical collections; gardens established; life-long support for conservation and successful advocacy for reserves; practical application of ecological knowledge to pressing environmental resource problems of the day; and mentoring of new generation of plant scientists (Moore 1967). The achievement is even more impressive when we consider the disadvantages he overcame. At the turn of the 19th century travel was slow and difficult, government science vestigial and the university system small and underfunded. Cockayne certainly felt his scientific isolation. As he wrote to Goebel, an eminent German botanist, in 1902:

*You will pardon me inflicting an account of these little matters [his experiments on *Discaria*] on you, but there are so few here that take any interest in these things. Our local botanists care only to argue whether a plant is a species or a variety and to bestow on the latter what they are pleased to designate in grandiloquent language 'specific rank' (Thomson 1979).*

Cockayne, although much celebrated and certainly invaluable to the powers that be as a source of sound scientific advice, never gained a permanent salaried position. The colonial government was not keen on supporting science unless it was directly related to improving agricultural productivity, forestry or the

extraction of mineral wealth and, although this led to some commissions for, for example, his work on grasslands and the forest estate, it was not a funding source he could rely on. His legacy must be assessed therefore against this background of a real struggle against the tyranny of distance, isolation from scientific peers, and shortage of funding. Despite the handicaps I have mentioned above, Cockayne took every opportunity to advance understanding of the New Zealand flora. He worked on many fronts, travelling incessantly throughout the country and to the offshore islands, making copious, meticulous notes, growing, documenting and photographing plants in gardens and, when possible, experimenting (Moore 1967). He firmly believed that New Zealand, because of its diverse environments, abundance of unmodified habitats, and unusual growth forms could offer deeper and more fundamental insights than could be obtained from what he saw as the profoundly modified lands of Europe.

Leonard Cockayne also had a profound and largely positive influence on his contemporaries and the next generation of botanists. When I joined Botany Division in the early 1970s some scientists were still working there who had known him, and most had been deeply influenced by him. Lucy Moore, for instance, had met with Cockayne and worked closely with one of his collaborators, Dr Harry Allan (Moore 1967) (Figure 1). Peter Wardle's grandfather had assisted Leonard Cockayne in the setting up of the historically significant Cockayne Plots in central Otago, and Cockayne was a major influence on the young Peter taking up ecology (McGlone and Lee 2011) – and certainly the inspiration for his own *Vegetation of New Zealand* (Wardle 1991).



**Figure 1.** Dr Harry Allan, Dr Lucy Moore, and visiting scientist Dr G F Papenfuss (California) in Auckland during the Pacific Science Congress, January 1949. Image reproduced with permission of the Alexander Turnbull Library, National Library of New Zealand (Reference PAColl-6883 1/2-136065).

But how have his ideas fared in the 85 years since his death? What does more recent research have to say about his achievement? Here I will first discuss his ideas about evolution and then his ecological and biogeographic observations.

## Evolution

Darwin's great book *On the origin of species* in 1859 established the reality of evolution for most scientists and the educated public in general, although the mechanisms were widely debated and no consensus achieved until the emergence of the modern evolutionary synthesis in the 1940s. Cockayne's ideas about evolution owed much to the ideas of the Dutch botanists Hugo de Vries, Johannes Lotsy (who visited him in 1925), and the English botanist George Henslow, who promoted alternatives to natural selection, such as evolution through large mutational steps or hybridisation. As well, he was influenced by his great friend and correspondent, the eminent German botanist Karl Ritter von Goebel who had a similar sceptical attitude to natural selection:

*[Goebel] was convinced that the variety of plant form was much greater than the variety of the conditions under which they grow, and saw in these various products many structures which could not be regarded as directly adaptive, but rather indifferent, being neither harmful nor useful. They can arise or disappear without being subject to selection, or they can group themselves and combine to produce members which may enable the plant to become adapted to quite other conditions than the primary ones, and the principle here implied was one of his chief guides in reflecting on the form relations of the plant. (Lloyd 1935)*

The stimulus for Cockayne's investigations was that persistent challenge: what is a species? He believed taxonomists working on the New Zealand flora neglected the ecological setting and inherent variation of the entities they examined as they were narrowly focused on delineating and naming species from collected specimens. Cockayne shared the opinion of (Lotsy 1916) that taxonomic species, termed 'linneons', were abstract concepts found nowhere in nature (Cockayne and Allan 1927). He therefore searched for evolutionary concepts that would make sense of the characteristic features of New Zealand plants and underpin an ecologically focused species concept. As he documented in his numerous publications, Cockayne found that New Zealand plants:

- were highly variable – he argued that 'normal' was a moot term;
- tended to have very different growth forms under differing external environmental influences – humidity, drought, wind, high light;
- often had marked juvenility (Figure 2, page 39), and heteroblastic forms; and
- often hybridized.



**Figure 2.** Examples of a taxonomic species: on the right and left adults of *Pittosporum rigidum*, not distinguished as varieties; in centre, juvenile form of plant on right (Cockayne 2011 plate 1 facing page 4). Image reproduced with permission of the Alexander Turnbull Library and acknowledgement of the Royal Society of New Zealand.

He urged taxonomists to consider the implications and to adjust their linneons to fit more closely to what he thought of as ‘true species’. In defining a true species he employed two concepts:

- Jordanon: a true-breeding group of individuals plainly distinct from any other such group.
- Epharmony: A change in form, or physiological behaviour, beneficial to an organism, evoked by the operation of some environmental stimulus (Cockayne 1928). Such a change was an ‘epharmonic’ adaptation, and distinguished from those variations not caused by any direct action of the environment.

In Cockayne’s view, a hybrid was not only the product of interbreeding between linneons, but the product of interbreeding between jordanons. While it may be thought that a jordanon might be the basis for a stable linneon classification,

Cockayne did not see it this way. While he recognised simple species – consisting of a single jordanon – he also allowed for complex species, which could be made up of a group of closely related jordanons, which would then be recognised as ecotypes, varieties or subspecies, and the hybrids between them. Most species in New Zealand he believed to be complex linneons. While he was aware that the jordanons that made up complex species would probably be recognised as true species by most overseas taxonomists, he seemed to have believed that the complex species solution was the best fit for the actual New Zealand situation.

We can readily transfer into present day terminology what Leonard Cockayne and Harry Allan were on about. Epharmones are, for the most part, regarded as the product of phenotypic variation. The jordanon is more or less what we now call a species. The complex New Zealand terrain and the recent and rapid growth of mountains over the last few million years has left a legacy of radiations of poorly differentiated species. Faced with the task of bringing order to this complex mess, Harry Allan adopted the Cockaynean habit of recognizing complex species and in Volume I of the Flora of New Zealand series described a number of complex species with their distinct end points connected by innumerable intermediates (Allan 1961). These have since been mostly disassociated into their respective jordanons (using Cockayne's terminology) and given status as linneons, or simple species. Indeed, recent taxonomic treatments have to some extent departed from the concept of complex species, the subspecies rank being far less used than previously, and varieties have fallen into disfavour (Burrows 2011, de Lange 2014, Heenan 2017). Only time will tell if these ever finer divisions of our flora into species will serve us better than previous system of varieties and subspecies. However, there are many even now who would side with Cockayne and prefer the convenience of a somewhat variable species to a large number of closely related species that are hard to separate in the field (or even in the laboratory at times) with any confidence.

On the other hand, Cockayne's concept of epharmonic variation is definitely at odds with current evolutionary theory:

*...I am of the opinion that in the hereditary epharmonic variations  
.... there is a much greater likelihood of them having been brought  
about by the direct action of the various ecological factors than by  
the continuous accumulative selection of fluctuating  
variations...(Cockayne 1911).*

That is, he believed in the inheritance of acquired characters. He made a large number of observations on epharmones which were the central element to how he envisaged evolution working. His observations showed that a number of divaricating shrubs (for instance, *Melicytus alpinus*) show this epharmonic switch from small leaved, tightly branched forms to laxer, larger leaved forms when shifting from exposed to sub-canopy positions. He wrote at length on the leafless juvenile form of *Rubus squarrosus* (which he included as part of a *R. cissioides* complex) which he saw as an exemplar of a xerophytic epharmonie,

induced under dry, windy conditions (Cockayne 1933). Under moister, more sheltered and shady conditions, the more leafy epharmones asserts itself, as he experimentally demonstrated. However, he also recognized that, as the xerophytic *R. squarrosus* epharmones does not fruit, it also could be seen as a juvenile form. Such juvenile forms, which he showed were abundant in the New Zealand flora (Cockayne 1901), he believed critical to the evolution of the numerous divaricating shrub species in this country. He argued that the epharmonic juvenile of a given tree species could, by flowering in that state, form by neoteny a new, shrub species.

Godley (1979), in his detailed paper on Cockayne and evolution, suggested that Cockayne got it the wrong way around, and that divaricating juveniles had formed as a result of hybridization between trees and closely related divaricating shrubs (giving as an example *Sophora prostrata* and *S. tetrapatera* hybridizing to form *S. microphylla*, which has a divaricating juvenile). I prefer Cockayne's hypothesis that divaricating shrubs have formed by neoteny of divaricating tree juveniles. *Streblus heterophyllus*, *Carpodetus serratus*, *Elaeocarpus hookerianus*, *Pennantia corymbosa* and *Prumnopitys taxifolia* all have well developed divaricate juveniles, but no closely related divaricating shrub with which they may have hybridized. *Fuscopora solandri* and *F. fusca* likewise have no corresponding divaricating shrub species but some populations of both have juveniles with attributes approaching divarication (Wardle 1984), and perhaps show an early or partially achieved stage in the evolution of juvenility. On the other hand, of the 18 or so genera that include divaricating shrubs (Wardle 1991), the only ones lacking tree species which could have generated the juvenile form are *Rhabdothamnus solandri* and *Teucrium parvifolium*, and even then they are only marginally divaricating.

It is clear that Cockayne appeared to have some problems with evolution by natural selection and was more in favour of large mutation jumps as suggested by De Vries (1901), or evolution by hybridisation. He particularly disliked the idea that minute or small variations in a true breeding species – his jordanon – might provide the answer to the evolution of species via the agency of natural selection. He raised numerous objections as he was convinced that small variations would be overwhelmed by chance events and variable environments, the small changes being an insufficient advantage to be of any import. What he seems to have suggested in place of natural selection is something that resembles Larmackism (see discussion in Godley 1979). Thus he writes about different environments inducing epharmonic changes and, over time, these becoming 'fixed'. Following the example of Diels (1897), he postulated a previous dry, cold steppe period in the recent past and suggested that many of the xerophytic elements and epharmones in the New Zealand flora had originated at that time, and had since become fixed or persisted as an inducible but hereditary epharmonic part of the species makeup (Speight et al. 1911).

While Johannes Lotsy and George Henslow have been largely forgotten, and the Hugo de Vries emphasis on saltationism rather than natural selection largely



discredited, the issues that they and Leonard Cockayne confronted remain. Some believe that non-adaptive evolutionary processes have been downplayed too much, and that they are major contributors to the diversity we see around us (Lynch 2007). Natural selection is, after all, just one of four fundamental evolutionary processes, the others being mutation, recombination, and genetic drift, and debate continues on the influences of the other processes. For example, The Unified Neutral Theory of Biodiversity and Biogeography proposes that within broad groups species are essentially neutral. That is, a particular species of tree does not on average have any significant ecological advantage over other trees and thus it is stochastic neutral processes that sort species across landscapes and govern their persistence (Hubbell 2001). Hybridisation, especially among polyploids which are abundant among plants, is seen as a major evolutionary factor (Abbott et al. 2013). Epigenetics, the environmental modification of gene expression that may be heritable without involving changes in DNA, is currently in vogue. It seems to me then that we have a long way to go before we can close the book on Leonard Cockayne's evolutionary ideas.

### **Ecology and plant biogeography**

As the first New Zealand ecologist Leonard Cockayne had a profound influence on the ecological research that followed. His work touched on nearly every aspect of the flora. In particular, in *The vegetation of New Zealand* (supported by many publications, intensive field work and report writing) he surveyed the entire vascular flora. He provided a physiognomic overview of the various plant forms relating them to climatic and historical processes; described the major vegetation types from the sub-Antarctic islands to the far north; erected botanical districts; described vegetational successional processes; outlined the influence of fire, humans, weeds and pests; and gave the first in depth analysis of the biogeography of New Zealand. Much of this he was first to discuss in any depth, and he added interesting and provocative insights to nearly every issue he examined.

As we have seen, divaricating shrub and tree juveniles and juvenile forms in general attracted Cockayne's interest (Cockayne 1901). Following (Diels 1897) he adopted the idea that many of the spiny and divaricating growth forms which are so abundant in this country owed their origin to a past steppe climate phase during the glacial age or earlier. While debate continues on this theme with many ideas still under consideration including the original hypothesis of origination during glacial periods (McGlone and Webb 1981), adaptation to dry forest environments (Wardle 1963a), and understorey light environments (Clearwater and Gould 1995, Day 1998), the majority opinion appears to be that divarication evolved as a response to avian browsing (Atkinson and Greenwood 1989, Bond et al. 2004), although recent work suggests that stressful climate regimes contribute as well (Lusk et al. 2016).

Cockayne was well in advance of his time in understanding how fluid and dynamic the vegetation cover is. He strongly believed that vegetation communities moved as a whole, and thus took a keen interest in successional processes and the myriad states vegetation formations adopt. This is demonstrated clearly in his major reports such as those on the sub-Antarctic islands (Cockayne 1909), the beeches (Cockayne 1926a), and grasslands (Cockayne 1926b). For instance, he formulated ideas about the ecology of the conifers that are, in nearly all essentials, still current (Lusk et al. 2015, McGlone et al. 2017). He noted that they could tolerate infertile soils and, in the case of *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Lepidothamnus* spp., *Manoao colensoi* and *Halocarpus* spp., poorly drained situations. He commented on their generally high demand for light and intolerance of shade in comparison with their broadleaved angiosperm competitors, and their relative tolerance of frost. Cockayne also pointed to the slower growth of the tall conifers, and their longevity relative to tall angiosperms, and thus their tendency to linger as aged individuals in communities largely given over to angiosperm trees. In this he anticipated the ‘tortoise and the hare’ theory concerning conifer-angiosperm competition made popular by William Bond (1989). However, he went further, linking contemporary conifer ecology with biogeographical and geological concepts. Drawing on macrofossil evidence, he argued that conifer and angiosperm species were locked in a longstanding evolutionary conflict. The historical tendency, as he saw it, was for conifers to retreat in the face of angiosperm competition and, although disturbance and poor soils could give them a temporary advantage from time to time, his opinion was that eventually they would become relic: “...a remnant merely of ancient conifer forests which have been in the process of gradual extinction by certain broad-leaved dicotyledonous trees – a process of extreme slowness.” (Cockayne and Turner 1928, p 21).

Cockayne’s observation that mature conifer stands have little regeneration was strongly supported and began a long-running debate which focused on why this should be so, some favouring climatic explanations (Nicholls 1956, Holloway 1964, Wardle 1963b, 1978) and other endogenous or disturbance-induced successional factors (Clayton-Greene 1977, Veblen and Stewart 1982, Ogden and Stewart 1995.). The consensus is now that successional processes and the long life span of the tall conifers is largely responsible for lack of regeneration in mature forest (Lusk and Smith 1998).

The Cockayne concept of the slow retreat over geological time of the conifers in the face of broadleaved competition played some role in the subsequent thinking of ecologists. Robbins (1962), after a descriptive survey of the conifer-angiosperm forests of the North Island, likewise claimed the angiosperm forest “represents a broadleaf forest climax which is surely replacing a more ancient podocarp forest climax, remnants of which still remain mingled with the broadleaf forest”. Similar sentiments were voiced by other forest ecologists (McKelvey 1963, p 127). The perhaps unintended concept that New Zealand



conifers were uncompetitive and, being doomed to slowly reduce in numbers were thus not worth preserving, gained wide currency for a while – especially among those with an interest in milling them.

While these ideas have thankfully long since been countered, nevertheless, the broader concept that the conifers and other older broadleaved genera represent an unchanging ancient rainforest element from a Gondwana before the 80-85 Ma separation of the ancestral Zealandia continental fragment, has persisted. The popular conservation literature often refers to the conifer-rich lowland forests of New Zealand as ‘dinosaur forest’ (Bellamy 1990, McGlone 2005), and a recent publication on the fossil history of the southern hemisphere rainforests referred to their characteristic taxa as ‘southern wet forest survivors’ (Kooyman et al. 2014), thus emphasizing their antiquity and embattled persistence. This presumption of ‘primitiveness’ guides the tenor of much ecological discussion about southern conifers, which becomes focussed on how they have managed to survive in an ‘advanced’ angiosperm dominated world, and Cockayne was one of the first to articulate this idea.

Some of Cockayne’s biogeographical concepts have persisted. He identified the important floristic break at 38° south latitude for instance, and his botanical districts concepts survived as a basis for later iterations. He envisaged the New Zealand forests as having a composite origin and divided them into ‘subantarctic’ (largely Nothofagaceae) and ‘subtropical’ rainforest communities. He believed the first to be the more primitive and consisting of palaeozealandic and subantarctic elements, while the second was of an equally ancient palaeotropic stock (Cockayne 1928, p 417). While we no longer use these terms, the concept that the New Zealand flora consists of some lineages derived from an ancient Gondwanic element that evolved while the New Zealand region was at high latitudes during the Cretaceous and may subsequently have arrived via Antarctica, and an ancient tropical element shared with Queensland and southeast Asia is still very much alive (Winkworth et al. 2015, Givnish et al. 2016, He et al. 2016). However, Cockayne struggled to explain the origin of the mountain flora and the recent Australian element as he knew from recent research that during the Oligocene New Zealand was low-lying and that tall mountains and glaciations had come much later. Therefore, although the movement of continents was well out of favour at the time he wrote, he recognised the need for some means for plants to cross oceans and noted that “..the zoological evidence .... is so strongly in favour of a former ‘land bridge’ ....that the author, though reluctantly, declares himself in favour of great land extension” (Cockayne 1967, p 242). Replace ‘former land bridge’ with ‘plate tectonics’ or ‘island chains’ and he can be seen as sharing the views of many present day researchers. However, with regard to most alpine and mountain plant lineages, their recent development and close relationship with species in distant regions makes it highly likely that nearly all are a product of transoceanic dispersal (McGlone et al. 2018).

Cockayne was, before the term was invented, a conservationist and materially assisted in the identification and setting aside of reserves at a time of the rampant destruction of the natural vegetation cover. In this he went against the prevailing wisdom that New Zealand's natural resources were essentially inexhaustible. Harry Allan, who knew him well, wrote:

*On every possible occasion, whether on Royal Commissions, at public meetings or in scientific circles, he would throw all his powers into advocating the preservation of New Zealand's vegetation and flora.*  
(Allan 1935)

One only has to read the final words of *The vegetation of New Zealand* (Cockayne 1928, p 426) to realise how heartfelt his concern was:

*We, who now live in this wonderful country, and love its marvellous vegetation, have set aside sanctuary after sanctuary where the palaeotropical, Australian and palaeozelandic plants, the survivors of that bitter strife with Nature, that commenced millions of years ago, can still pursue their destinies if unmolested by their human enemies and the horde of foreign plants and animals he has let loose.*

*Will our descendants prize this unique heritage from the dim past and preserve these sanctuaries intact?*

### **Concluding remarks**

When we consider the obstacles Leonard Cockayne faced – no degree, from a provincial centre in England, an ex-school teacher, independently but somewhat precariously funded by a small inheritance, and working in these remote and sparsely populated islands – we can only wonder at how much he achieved. His example had an outsize impact. Researchers in the DSIR and the Forest Service, who were those most influenced by Cockayne, took his dictum “go to the plants themselves” to heart, initiating a half century of intensive field work and experimental garden investigations: Harry Allan, Colin Burrows, Henry Connor, Elizabeth Edgar, and Lucy Moore followed the Cockaynean precept of growing plants and observing them closely in the field before undertaking taxonomic revisions; John Nichols, Tony Druce, and Norm Elder took to heart the example of Cockayne's indefatigable fieldwork and meticulous documentation; Jack Holloway, John Wardle, and Peter Wardle his propensity for large, synoptic overviews and provocative hypotheses.

Cockayne is no longer a direct influence on our science. I suspect that neither are his many papers and reports, or his books, *The vegetation of New Zealand* and his popular *New Zealand plants and their story*, still read to any extent. This loss of Cockayne to history is a shame: even after 100 or more years his prose is as readable as ever and a source of ecological insights. As Brian Molloy recently said: “He didn't get a lot wrong!”

All New Zealand plant ecologists and biosystematists are to some extent heirs of Cockayne. He inspired the generation of researchers who followed him, impressing on them the necessity of moving outside the laboratory and the herbarium and looking at plants in the field and grown in the experimental garden. In his copious publications, documenting every aspect of the flora, he provided the best road map possible for the future.

## Acknowledgements

I thank Peter Bellingham for his insightful comments on the draft, and John Clemens for editing and sourcing the illustrations.

## References

- Abbott R, Albach D, Ansell S, Arntzen JW, Baird SJ, Bierne N, Boughman J, Brelsford A, Buerkle CA, Buggs R 2013. Hybridization and speciation. *Journal of Evolutionary Biology* 26: 229–246.
- Allan HH 1935. Leonard Cockayne (1855-1934). *Proceedings of the Linnean Society of London Session 1934-1935*: 167–171.
- Allan HH 1961. *Flora of New Zealand*. Volume 1. Wellington: Government Printer.
- Atkinson IAE, Greenwood RM 1989. Relationships between moas and plants. *New Zealand Journal of Ecology* 12: 67–96.
- Bellamy D 1990. *Moa's Ark: the voyage of New Zealand*. London: Penguin.
- Bond W 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society* 36: 227–249.
- Bond WJ, Lee WG, Craine JM 2004. Plant structural defences against browsing birds: a legacy of New Zealand's extinct moas. *Oikos* 104: 500–508.
- Burrows CJ 2011. Genus *Pimelea* (Thymelaeaceae) in New Zealand. 4. The taxonomic treatment of ten endemic abaxially hairy-leaved species. *New Zealand Journal of Botany* 49: 41–106.
- Clayton-Greene KA 1977. Structure and origin of *Libocedrus bidwillii* stands in Waikato district, *New Zealand*. *New Zealand Journal of Botany* 15: 19–28.
- Clearwater MJ, Gould KS 1995. Leaf orientation and light interception by juvenile *Pseudopanax crassifolius* (Cunn.) C. Koch in a partially shaded forest environment. *Oecologia* 104: 363–371.
- Cockayne L 1901. An inquiry into the seedling forms of New Zealand phanerogams and their development. *Transactions and Proceedings of the New Zealand Institute* 33: 265–298.

- Cockayne L 1909. The ecological botany of the subantarctic islands of New Zealand. In: Chilton C (Ed.), *The Subantarctic Islands of New Zealand*, pp 182-235. Philosophical Institute of Canterbury, Christchurch.
- Cockayne L 1911. Observations concerning evolution, derived from ecological studies in New Zealand. *Transactions and Proceedings of the New Zealand Institute* 44: 1–50.
- Cockayne L 1926a. *Monograph on the New Zealand beech forests*. WAG Skinner, Government Printer.
- Cockayne L 1926b. *Tussock grassland investigation in New Zealand. Aims and methods in the study of vegetation*. Crown agents for the colonies. London: 349–361.
- Cockayne L 1928. *The vegetation of New Zealand*. Leipzig: Engelmann.
- Cockayne L 1933. A case of epharmony in a New Zealand *Rubus*. *American Journal of Botany* 20: 545–551.
- Cockayne L 1967. *New Zealand plants and their story*. Wellington: Government Printer.
- Cockayne L, Allan HH 1927. The bearing of ecological studies in New Zealand on botanical taxonomic conceptions and procedure. *Journal of Ecology* 15: 234–277.
- Cockayne L, Turner E 1928. *The trees of New Zealand*. Wellington: Government Printer State Forest Publication.
- Day JS 1998. Light conditions and the evolution of heteroblasty (and the divaricate form) in New Zealand. *New Zealand Journal of Ecology* 22: 43–54.
- de Lange PJ 2014. A revision of the New Zealand *Kunzea ericoides* (Myrtaceae) complex. *PhytoKeys*: 1.
- Diels L 1897. Vegetations-Biologie von Neu-Seeland. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 22: 202–300.
- Givnish TJ, Zuluaga A, Marques I, Lam VKY, Gomez MS, Iles WJD, Ames M, Spalink D, Moeller JR, Briggs BG, Lyon SP, Stevenson DW, Zomlefer W, Graham SW 2016. Phylogenomics and historical biogeography of the monocot order Liliales: out of Australia and through Antarctica. *Cladistics* 32: 581–605.
- Godley EJ 1979. Leonard Cockayne and evolution. *New Zealand Journal of Botany* 17: 197–215.
- He TH, Lamont BB, Fogliani B 2016. Pre-Gondwanan-breakup origin of *Beauprea* (Proteaceae) explains its historical presence in New Caledonia and New Zealand. *Science Advances* 2.
- Heenan PB 2017. A taxonomic revision of *Cardamine* L. (Brassicaceae) in New Zealand. *Phytotaxa* 330: 1–154.

- Holloway J 1964. The Forests of the South Island: The Status of the Climatic Change Hypothesis. *New Zealand Geographer* 20: 1–9.
- Hubbell SP 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton and Oxford: Princeton University Press.
- Lloyd FE. 1935. Karl Ritter von Goebel. *Plant Physiology* 10: 203–208.
- Lotsy JP 1916. *Evolution by means of hybridisation*. The Hague: Martinus Nijhoff.
- Lusk CH, Jorgensen MA, Bellingham PJ 2015. A conifer-angiosperm divergence in the growth vs. shade tolerance trade-off underlies the dynamics of a New Zealand warm-temperate rain forest. *Journal of Ecology* 103: 479–488.
- Lusk CH, McGlone MS, Overton JM 2016. Climate predicts the proportion of divaricate plant species in New Zealand arborescent assemblages. *Journal of Biogeography* 43: 1881–1892.
- Lusk CH, Smith B 1998. Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology* 79: 795–806.
- Lynch M, 2007. The frailty of adaptive hypotheses for the origins of organismal complexity. *Proceedings of the National Academy of Sciences of the United States of America* 104: 8597–8604.
- McGlone M, Lee B 2011. Peter Wardle MSc (Otago), PhD (Cantaur.), FRSNZ, ONZOM 14 February 1931-6 December 2008. *New Zealand Journal of Ecology* 35: 119–126.
- McGlone MS 2005. Goodbye Gondwana. *Journal of Biogeography* 32: 739–740.
- McGlone MS, Heenan P, Millar T, Cieraad E 2018. The biogeography, origin and characteristics of the vascular plant flora and vegetation of the New Zealand Mountains. In: Hoorn C, Perrigo A, Antonelli A (Eds), *Mountains, climate and biodiversity*, pp 375-389. Wiley Blackwell.
- McGlone MS, Richardson SJ, Burge OR, Perry GLW, Wilmshurst JM 2017. Palynology and the ecology of the New Zealand conifers. *Frontiers in Earth Science* 5.
- McGlone MS, Webb CJ 1981. Selective forces influencing the evolution of divaricating plants. *New Zealand Journal of Ecology* 4: 20–28.
- McKelvey PJ 1963. *The synecology of the West Taupo indigenous forest*. Wellington: New Zealand Forest Service.
- Moore LB 1967. The Cockayne Memorial Lecture, 1965: Leonard Cockayne, botanist. *Transactions of the Royal Society of New Zealand: General* 2: 1–18.
- Nicholls J 1956. The historical ecology of the indigenous forest of the Taranaki upland. *New Zealand Journal of Forestry* 7: 17–34.

- Ogden J, Stewart GH 1995. Community dynamics of the New Zealand conifers. In: Enright NJ, Hill RS (Eds), *Ecology of the southern conifers*, pp 81-119. Melbourne: Melbourne University Press.
- Robbins RG 1962. The podocarp-broadleaf forests of New Zealand. *Transactions of the Royal Society of New Zealand, Botany 1*: 33–75.
- Speight R, Cockayne L, Laing RM 1911. The Mount Arrowsmith district: a study in physiography and plant ecology. *Transactions and Proceedings of the New Zealand Institute 43*: 315–378.
- Thomson AD 1979. Annotated summaries of letters to colleagues by the New Zealand botanist Leonard Cockayne –1. *New Zealand Journal of Botany 17*: 389–416.
- Veblen TT, Stewart GH 1982. On the conifer regeneration gap in New Zealand - the dynamics of *Libocedrus bidwillii* stands on South Island. *Journal of Ecology 70*: 413–436.
- Wardle JA 1984. *The New Zealand beeches: ecology, utilization and management*. Wellington: New Zealand Forest Service.
- Wardle P 1963a. Evolution and distribution of the New Zealand flora, as affected by Quaternary climates. *New Zealand Journal of Botany 1*: 3–17.
- Wardle P 1963b. The Regeneration gap of New Zealand gymnosperms. *New Zealand Journal of Botany 1*: 301–315.
- Wardle P 1978. Regeneration status of some New Zealand conifers, with particular reference to *Libocedrus bidwillii* in Westland National Park. *New Zealand Journal of Botany 16*: 471–477.
- Wardle P 1991. *Vegetation of New Zealand*. Cambridge: Cambridge University Press.
- Winkworth RC, Hennion F, Prinzing A, Wagstaff SJ 2015. Explaining the disjunct distributions of austral plants: the roles of Antarctic and direct dispersal routes. *Journal of Biogeography 42*: 1197–1209.