Was he right? Leonard Cockayne, the field biologist, and advances in New Zealand plant ecology

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Leonard Cockayne (1855–1934) was not the first person to do ecological work in New Zealand, but he was probably the first major ecologist. In this paper I review some major themes from his work, and evaluate how well his ideas have stood up in light of the subsequent 100 years of advances in ecology. This is not to unfairly criticise him in hindsight for things that he could not have known about, but is rather to test the extent to which his early informal insights into the working of the local biota have been backed up, or challenged, by later discoveries.

Cockayne wrote three important books, which I use as the basis of this summary: *New Zealand plants and their story* (2nd Edition, 1919); *The vegetation of New Zealand* (2nd Edition, 1928), and *The trees of New Zealand* (with EP Turner, 2nd Edition, 1939). The title of the second shows the scope of Cockayne's ambition, and that book was not matched until the publication of Peter Wardle's identically named, but much larger book, *Vegetation of New Zealand* (1991). Cockayne's books show three major themes. First, the description of the species and their distributions (including work on hybrids, for which he later praised himself in the third person: "L. Cockayne broke new ground for New Zealand botany with a paper classifying the wild hybrids.." (Cockayne 1929). His second theme was the study and description of plant communities. Thirdly, he made many observations on what was then called "autecology" (now called population ecology), including human impacts, fire, the relative vigour of native plants, pollination, and dispersal. These autecological ideas are the major areas I will review here.

Impact of Māori on New Zealand vegetation

Cockayne thought Māori had had little impact on the vegetation seen by Cook in 1759. He said "although the neolithic population may have reached 200,000, its power to damage the vegetation was slight" even though "Maori appear to have made considerable use of fire for clearing forest etc." (Cockayne 1928, page 22). More recent information has shown that Cockayne's assessment greatly underestimated the changes that took place after Māori arrival in 1280 AD (dated by Wilmshurst et al. 2008). Recent work shows large and rapid impacts on vegetation, with sudden increases in charcoal, rises in fern spores and grass pollen, and decreases in tree pollen shortly after Maori arrival (e.g. Perry et al. 2012). These authors show how a small number of people could, perhaps inadvertently, convert large areas of the landscape from forest to open vegetation by the use of fire. The two key drivers are, firstly, that New Zealand had extremely low levels of natural fire before people arrived, with one of the lowest rates of lightning of anywhere on Earth (Ogden et al. 1998). Secondly, there is a “fire trap” in New Zealand vegetation, because early-successional species, such as kanuka (*Kunzea ericoides*) and akeake (*Dodonaea viscosa*), are more flammable than late-successional forest species, such as *Nothofagus* spp. and tawa (*Beilschmiedia tawa*) (Perry et al. 2012). In models that include a plausible targetting of fires in recently burned (and more easily ignited) areas, the landscape can suddenly reach a tipping point when about 20% of the landscape is recently burnt. Within 250 years a flip occurs to a new stable state where most of the landscape has been recently burnt (Figure 1). So the loss of large areas of forest was probably both unintentional and inevitable even with a low density of Māori (Perry et al. 2012).

Figure 1. The aftermath of a natural lightning fire in Hinewai Reserve in 2011. The flammable gorse on the ridges has all burned, while the less flammable native *Nothofagus* forest in the gullies has not. This sets back recovery to less flammable native forest. (Photo: Dave Kelly)

Vigour of the native flora

Unlike some earlier authors, Cockayne considered that native vegetation was very competitive under its natural disturbance regime. He noted that cleared native forest reverted quickly to forest again unless introduced herbivores prevented this, and said that "were such animals entirely removed from North Island, the whole of the present "permanent pastures" would in 100 years, or less, be well on the road once more to dense rain-forest! … Certainly, the effect of the grazing and browsing mammal cannot be overestimated" (Cockayne 1928, page 356). In this Cockayne took a different view from authors, including Darwin, who thought the New Zealand native flora was "weak" and slow-growing, and would inevitably be replaced by innately superior exotic plants (discussed in Webb et al. 1988, preface page xvii).

Cockayne has been vindicated by more recent work: the native flora is highly competitive under low levels of disturbance (from humans and their introduced exotic mammals), and is most commonly invaded by exotic plants under conditions of disturbance. For example, Linley Jesson (Jesson et al. 2000) looked at the distribution of weeds in Arthurs Pass National Park. She found that weeds were largely confined to sites around huts, along tracks, and in riverbeds where there was frequent human-induced or natural disturbance. Seeds of the weedy exotics *Anthoxanthum odoratum*, *Holcus lanatus*, *Cerastium fontanum* and *Hieracium pilosella* required disturbance to establish; transplants were somewhat less dependent on disturbance. She concluded that the native vegetation excludes most invaders, except in disturbed areas (Figure 2, page 28). This same principle has guided the ecological restoration of Hinewai Reserve on Banks Peninsula, where manager (and living legend) Hugh Wilson proposed that the major obstacle to the recovery of the native vegetation was not exotic plants. He said it was the mammalian herbivores (especially sheep, goats, and cattle) that kept cryptically removing native tree seedlings under the gorse (*Ulex europaeus*) canopy, coupled with human-induced fires in the highly pyrogenic gorse and kanuka early-successional stands (Wilson 1994). Although Wilson's ideas were initially controversial, Hinewai has clearly demonstrated that thorough removal of the last ungulate herbivores has allowed rapid replacement of gorse canopies by much less fire-prone native trees. More widely, globally it has been proposed that the removal of native herbivores and their replacement by exotic herbivores has facilitated the invasion of exotic plants in many different countries (Parker et al. 2006) in a kind of "invasional meltdown".

Pollination of the native flora

Another key question concerns which animal groups were most important for pollination of the New Zealand flora. Cockayne (1928) said that pollination had been little studied to date, although he mentions Cheeseman and Petrie who had earlier worked on pollination of *Knightia*, *Rhabdothamnus*, and *Vitex*. Cockayne cited Thompson's view that insects were not deficient in New Zealand.

Although we have few butterflies, there are plenty of Diptera, moths, and beetles. Cockayne did not mention native bees, although these are now known to be both widespread and often important for pollination (Newstrom and Robertson 2005; Robertson et al. 2005), as are some of the hoverflies (Campbell et al. 2010).

Figure 2. Douglas fir (*Pseudotsuga menziesii*) is one of the few exotic plants that can invade relatively undisturbed native forest, this sapling growing under a *Nothofagus solandri* var. *cliffortioides* canopy at Burnt Face, Arthurs Pass, 2015. (Photo: Dave Kelly)

In respect of bird pollination, Cockayne thought birds were important for pollination "in part or exclusively" for *Phormium*, *Knightia*, *Clianthus*, *Edwardsia* [=*Sophora*], *Metrosideros* (5 spp.), *Fuchsia* (2 spp.), *Vitex*, and *Rhabdothamnus*. That total of ~17 species is less than the ~30 species later listed by Godley (1979) and Clout & Hay (1989), but Cockayne was less dismissive of the role of birds than those later authors. In this view, Cockayne has also been vindicated by later work, reviewed by Kelly et al. (2010). It is now known that birds visit the flowers of far more native plant species than any of these earlier authors realized (85 species), and birds are often the most, or the only, effective pollinators (Figure 3). Widespread pollen limitation is present on the mainland, even for species where pollination is still functioning effectively on nearby offshore islands with less depleted bird populations (Anderson et al. 2011).

Figure 3. Bird pollination is relatively important in New Zealand, including in *Peraxilla tetrapetala*, which is dependent on bellbirds (here at Craigieburn in 2017) and tui for flower opening. (Photo: Dave Kelly)

Seed dispersal and biogeography

The next question is to consider the importance of bird seed dispersal to the New Zealand flora, and the wider biogeographic forces that determine the shape of the New Zealand biota. Cockayne had some views on dispersal, which with hindsight now seem odd, or at least inaccurate. He said "it is the community as a whole which moves and not its individuals, except in the community itself… Long-distance journeys for species, except by extremely short stages, appear impossible". In other words, he thought of plant communities as single entities, and discounted the importance of long-distance dispersal events by single species.

His view of communities as single entities which move *in toto* over long time scales has been shown to be inaccurate. The best example is in eastern North America where, post-glaciation, various species migrated north at different rates, so that the forest communities have been in a state of constant flux as new species arrive (Davis 1981, Davis and Shaw 2001).

To be fair, Cockayne's lack of appreciation of long-distance dispersal by single species was qualified by his recognition that gale force winds could carry even large seeds a long way. But he seemed unimpressed by the likely scale of dispersal of fleshy-fruited species on two grounds. Firstly, he said that many fleshy fruits had not been seen being eaten by birds, and secondly he pointed out that many of the fleshy-fruited tree species were not as widely distributed as might have been expected. Cockayne said "the trifling effect of bird-carriage" is shown by most fleshy-fruited tree species not occurring through both main islands.

However, his first point about not having observed fleshy fruit being eaten by birds is now recognised as a product of inadequate observation time, coupled with the observations being made in areas with a depleted avifauna. Where there are fewer bird species present, and fewer individuals of extant species (as is the case on the New Zealand mainland since the 1870s), the remaining birds may only feed on a subset of the plants that they would visit in areas with more intact bird communities. This point was well made for bird pollination by Castro and Robertson (1997) and Anderson et al. (2016). More recent tallies of bird visits to fruit have greatly increased the lists of which birds consume fruit of which plants (Kelly et al. 2010) (Figure 4). In any case, it would be implausible to assume that a fleshy reward around a fruit would have been selectively favoured on a plant species if there was not some vertebrate to disperse the seeds, albeit sometimes an unexpected one such as the flightless weka (Carpenter et al. 2018).

Figure 4. Observations over the years have improved the list of which birds feed on which fruits. Here a native silvereye feeds on fruit of patē (*Schefflera digitata*) at Hinewai. (Photo: Dave Kelly)

Secondly, Cockayne thought that if bird dispersal was effective, fleshy-fruited tree species should be widespread through both main islands. That may have been an unrealistic yardstick for measuring dispersal effectiveness. In fact more recent work has supported the idea that bird dispersal is important and effective. McGlone et al. (2010) showed that for tree species with wide ranges ($\geq$11 degrees of latitude) 77% are bird-dispersed, whereas for species with narrow ranges ($\leq$3 degrees) only 38% are bird-dispersed. So bird dispersal is clearly effective at spreading plants within New Zealand.

When it came to trans-oceanic dispersal, Cockayne also was more sceptical than current data now indicate, though he was certainly not alone in believing what was the perceived wisdom throughout the 19th and 20th centuries. It was not appreciated until quite recently how often plants moved and how far animals could migrate. Cockayne considered ancient land bridges the "burning question" in New Zealand biogeography, with the assumption that previous land must have been required as stepping stones for plant and animal dispersal to have any realistic prospect of success. He realised an important element of the New Zealand flora arrived from Southeast Asia in the Tertiary, but could not imagine how that could happen without land bridges. He knew that a number of shore birds migrate from Siberia to New Zealand and back, and thought this could perhaps account for seed movement between countries along this route. But even here he underestimated the abilities of the birds, following Hutton to say "the only possible explanation of oversea[s] migration seems to be that birds are following old land-lines… migration must have commenced when… no part of the course was an island so far off as to be invisible from those next to it. … [T]he land sank but force of habit kept up the migration".

Nowadays this seems an astonishing case of special pleading, but that is with the benefit of hindsight. We know that migratory birds have very remarkable powers of flight and of navigation. Godwits are perhaps the current migration champions, with satellite tagged birds revealing almost incredible (in the literal sense) flights. One particular female godwit (mundanely called E7) flew 11,685 km nonstop over 8 days from Alaska to New Zealand in September 2007. How a 350 g bird can fly for 8 days nonstop, and then find a small speck of land in the South Pacific, is truly hard to comprehend. On the outwards flight bird E7 "only" did a 10,265 km nonstop flight to the Yellow Sea (Battley et al. 2008).

However, we also know that trans-oceanic dispersal is common both for plants and animals (de Queiroz 2005). The discovery of continental drift in the 1960s replaced hypothesized land bridges (which went up and down in the same place) with land rafts (which went sideways), but even that contribution to dispersal turns out to have been smaller than expected. The classic Gondwanan genera were meant to have been on the original land mass and persisted on all the bits after they split up, such as *Nothofagus* which is found in South America, New Zealand, Australia and New Caledonia (and, from fossils, in Antarctica). But the molecular revolution has shown that, although New Zealand has had *Nothofagus* for a long time, the current species got here in two separate dispersal events about 30 million years ago, when the Tasman Sea was already as wide as it is today (Knapp et al. 2005). This led to a paradigm shift and we now know that on geological time scales, improbable long distance dispersal events are relatively frequent. Matt McGlone immortalised this in his summary that, rather than a Gondwanan ark, New Zealand was the “flypaper of the Pacific”, soaking up new migrants all the time (McGlone 2005).

On one biogeographic point, however, Cockayne was to prove correct. He considered evidence for whether New Zealand had been completely submerged for a time in the Oligocene, when the land area above sea level was certainly small. Cockayne, however, considered that New Zealand must have always retained at least some dry land: “It seems fairly certain that since early Mesozoic times New Zealand has never been completely submerged”, based on fossil evidence, but “I do not think that the land area during the Oligocene-Miocene times could have been very large” (Cockayne 1928, pages 422-424). In this conclusion he finds recent support, such as from Knapp et al. (2007) who agree that New Zealand was never completely submerged.

Conclusion

Considering that he was starting with very little information about the New Zealand biota and its ecology and biogeography, Cockayne did a remarkably good job working out the key processes. In some cases new information has disproved his views (such as knowing how well dispersed many species are), while in others he grasped the key points quite quickly (such as the importance of bird pollination). And above all else he was marvellously enthusiastic about the native flora and fauna, and was keen on its preservation (Figure 5, page 33). This is well summed up in a final quote from *The vegetation of New Zealand* (Cockayne 1928, page 426):

> *We, who now live in this wonderful country, and love its marvellous vegetation, have set aside sanctuary after sanctuary where the palaeotropic, Australian and palaeozelandic plants … 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?*

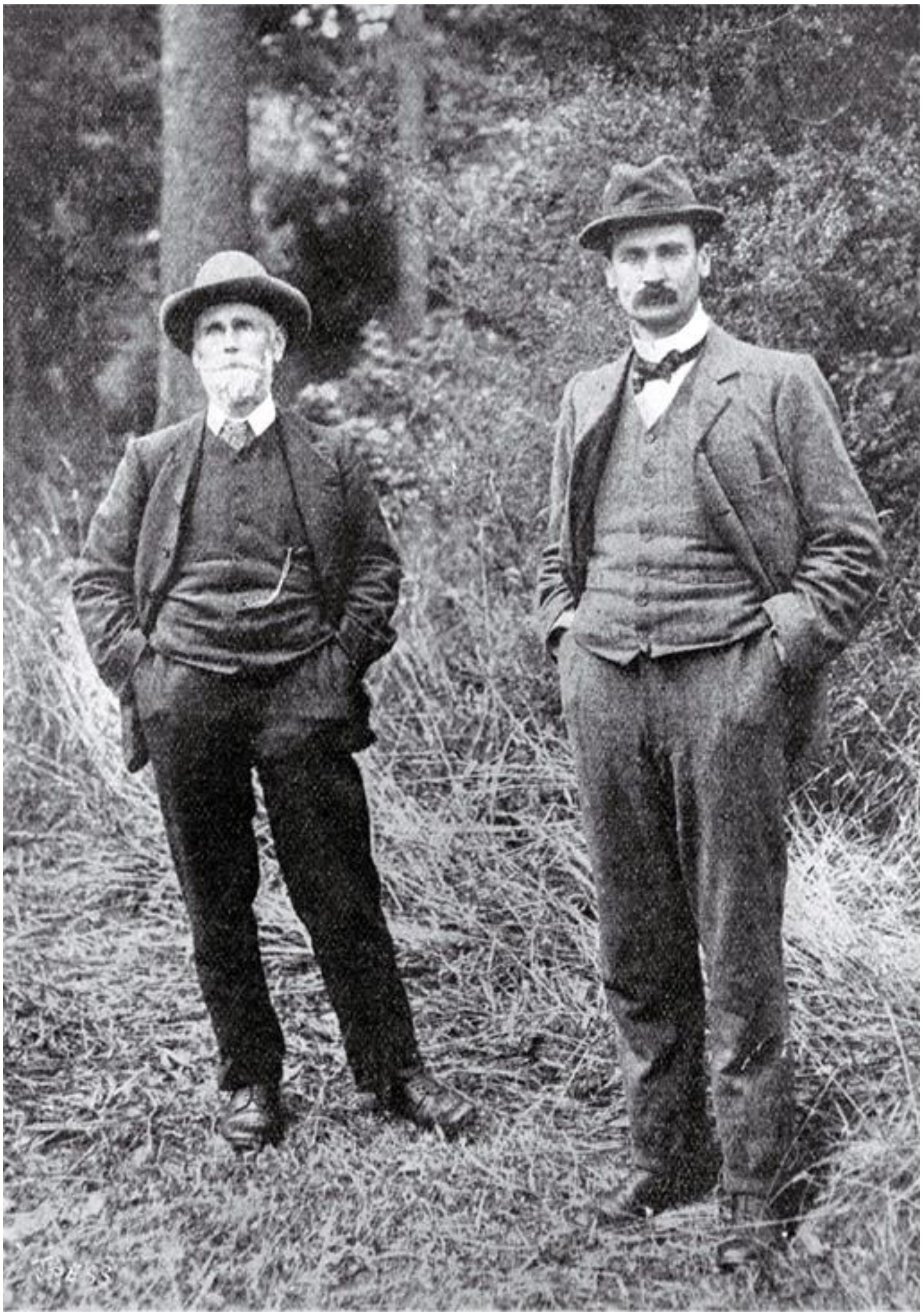

Figure 5. Dr Cockayne and Harry Ell (1904). Harry Ell and Leonard Cockayne worked together to ensure the conservation of natural areas and their species, notably in Christchurch at Deans (Riccarton) Bush, and in the Port Hills where "...the greater part of the plants are to be found in no other part of the world..." [Cockayne L 1914. A sketch of the botany of the Summit Road and its environs. In: The Summit Road, pp 23–30. Christchurch, Smith and Anthony]. (Photo: Christchurch City Libraries, File Reference CCL PhotoCD 6, IMG0058)

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