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### New Zealand's native forests: driven by natural disturbances, now influenced by invasive plants and animals

Peter J. Bellingham

Plant ecologist, Landcare Research, Lincoln

New Zealand is an exciting place to be an ecologist. It is the last large piece of land to be settled by people, and it still has vestiges of ecosystems that developed without the direct or indirect influences of people. Conversely, there are few landscapes on earth that people have so utterly transformed as some in New Zealand. For example, the Canterbury Plains are almost entirely dominated by introduced plants and animals, the remaining native species only a trace. These extremes occur in a small land area, influenced by extraordinary gradients of rainfall and geological differences. Therefore, New Zealand is a good place to ask questions about how humans influence the natural world, and how resilient is its biodiversity to the pressures of the modern world.

#### **New Zealand's forests are disturbed frequently**

New Zealand's physical landscape and the forces that influence it have produced a flora and fauna that is resilient to disturbances, large and small. In the **Taupō region, the Hātepe eruption of about AD 180** and the much bigger Oruanui eruption of 26,500 years ago are some of the largest eruptions ever. **The Hātepe eruption annihilated forests across** thousands of square kilometres, yet tall rain forests were back across the landscape within 200 years (Wilmshurst & McGlone 1996). Although formed by a tiny eruption in comparison, Rangitoto, which is only about 600 years old (Nichol 1992), shows that forests, which now cover most of it, can colonise inhospitable hard surfaces of 'a'ā lava that retain little moisture (Wilcox 2007). Mountain building and **earthquakes result from New Zealand's straddling the** boundary of the Pacific and Australian plates. Major movements of the Alpine fault periodically denude forested slopes throughout the western South Island, and the debris generated buries forests meters deep on the floodplains, while the outwash produces new dunes and reshapes river courses (Wells et al. 2001, Wells & Goff 2007, Howarth et al. 2012). Major movements of the Alpine fault occurred in c. 1460, c. 1615, and 1717, all of magnitudes >7 (Wells & Goff 2007), yet rain forests cover most of the landscape now (Wardle 1977). Earthquakes also denude forested mountainous regions of the North Island (e.g., Robbins 1958).

Glacial advances and retreats are major influences **on New Zealand's flora and** fauna. The warm interglacial period we are fortunate to live in has

been the less prevalent condition during the last 2.6 million years, a time that has been punctuated by repeated glacial advances. These events changed **New Zealand's landscapes drastically**. The mountainous landscapes were covered under hundreds of metres of ice, which shaped many of the deglaciated landscapes we see now, such as the fjords of the southwestern South Island. Less obvious to us now was the drop in sea level, which meant that **New Zealand's land area was** substantially bigger, and the North and South Islands were connected. Many of our offshore islands were continuous with the mainland, including those of the Marlborough Sounds and Hauraki Gulf, as recently as 20,000 years ago (McGlone 1997). **When Māori** arrived in New Zealand, they encountered a largely forested landscape, but 20,000 years ago continuous forest was restricted to north of Raglan and Tauranga. South of this were patches of forest among scrub and grassland. Bare ground and grassland was also widespread, especially in the east (McGlone et al. 2001). Advancing glaciers eliminated some plant species in regions where there were no refuges for them, such as in central Westland. This is **probably why some plants' distributions** are discontinuous between Otago and north-west Nelson (McGlone et al. 2001). Successive glacial advances in Westland eliminated beech (Nothofagaceae) from part of its former range, and other trees such as maire (*Nestegis* sp.; Moar & McKellar 2001). When the glaciers last retreated, from about 11,500 years ago, most of the landscape became forested within 2000 years. Although reforestation was quite rapid, it was variable among species; for example, beech has not yet recolonised parts of its former range, such as in central Westland (Wardle 1988).

**New Zealand's oceanic climate also brings** disturbances, most often related to the strong westerly cycle that brings large storms and high rainfall. Storms denude forested hillsides and cause major floods (e.g., Griffiths & McSaveney 1983), and cause destructive föhn winds on the eastern side of dividing ranges (Jane 1986). Extratropical cyclones **are a powerful influence on New Zealand's forests,** with the accompanying rainfall causing landslides (Marden & Rowan 1993), and uprooting and snapping of trees, sometimes at large scales. Cyclones affect forests in northern New Zealand most often (Martin & Ogden 2006), but they can



**Fig. 1.** Mountain beech forest after the 1994 earthquake, Basin Creek, Avoca Valley, Craigieburn Forest Park. Photo: PJB, 1997.

affect forests of the South Island as well, as shown by the destructive effects of Cyclone Ita, in April 2014. Periodic droughts, especially those during strong influences of the El Niño Southern Oscillation (Grant 1984), and prolonged frosts (Bannister 2003) **can kill trees. New Zealand's forests are resilient to all such events.**

The forests in the Craigieburn Range, inland Canterbury, provide insight to their capacity to withstand different kinds of disturbance. Between 1970 and 2015, the forests have been subject to the sometimes interacting effects of wind and snow storms, attacks by a native bark beetle (*Platypus* sp.) and associated fungal diseases (Wardle & Allen 1983), and a magnitude 6.4 earthquake in 1994 (Fig. 1) which denuded up to a quarter of some catchments (Allen et al. 1999). Mountain beech (*Fuscopora cliffortioides*) is the only canopy tree over 9000 ha, from valley floors to treelines, with very few other woody plants in the understoreys. The forests are highly resilient; mountain beech has recolonised all denuded or disturbed stands (Coomes & Allen 2007). Almost no other woody plants have colonised. These remarkably species-poor forests are

resilient, despite a widely held view that they should not be (e.g., May 2001).

### **New Zealand's ecosystems are recently invaded**

The introduction of plants and animals has happened **very recently in New Zealand. Māori society** depended on the crops and mammals that they brought from eastern Polynesia in c. 1280, and since the first Europeans arrived, a much greater number of plants and animals have been introduced in the last 250 years. Human survival in New Zealand, and our modern economy, depends largely on introduced **plants and animals. New Zealand's cultures exemplify those that depend on transplanted 'portmanteau biota'** (Crosby 2004). Most New Zealanders are aware that some of the plants and animals (as well as fungi, viruses, and other organisms) introduced to the country have been very harmful to native biodiversity. The introduction of predatory mammals, such as rats and stoats, has been catastrophic, causing an unprecedented wave of extinction among native large invertebrates, birds and reptiles that is probably not yet over. Introduced social wasps (*Vespula* spp.) have had similarly catastrophic effects in some ecosystems on the abundance and diversity of native invertebrates. Predatory mammals and **social wasps both occupy 'functional gaps' in the native biota of New Zealand; worldwide, introduced organisms have their strongest adverse effects on the native species if they fill such gaps** (Simberloff 1995).

The effects of other introduced species are less clear (Allen & Lee 2006). Introduced mammalian herbivores can have profoundly adverse effects in some ecosystems, but their effects are hard to detect in others. The number of introduced plant species in New Zealand now exceeds the number of native plant species, yet it is challenging to predict which introduced plant species will have adverse effects on native ecosystems and in what circumstances.

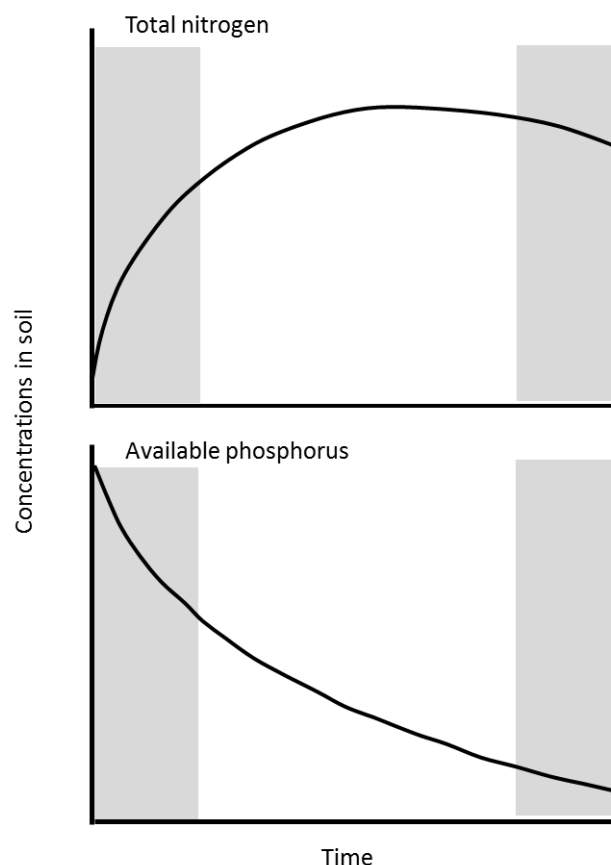
### **A framework for understanding how New Zealand's forests respond to disturbance**

**New Zealand's modern agriculture often depends on** input of nutrients, whether as added nitrogen, in the form of urea, or phosphorus, applied as superphosphate. This should alert us that, over much of the country, these elements, which are critical for plant growth and reproduction, are in short supply. While there are other critical factors for plant growth, such as temperature and moisture, an understanding of the role of two key elements – phosphorus and nitrogen – in the New Zealand landscape is more likely to help us understand why some areas seem more prone to the effects of introduced plants and animals than others. These elements derive mostly from different sources. Weathering of bedrock provides the main source of phosphorus in most ecosystems, although there are some exceptions; for

example, seabirds transport marine sources of phosphorus (derived from their prey) back to their nesting sites, such as on some islands near Auckland (Fukami et al. 2006). In contrast, most nitrogen derives ultimately from the atmosphere. The amounts and forms of phosphorus and nitrogen available to plants changes substantially after disturbance.

A key study in New Zealand has advanced our understanding of phosphorus in ecosystems and how it changes after disturbance. Professor Thomas Walker and colleagues studied soils that had developed after the retreat of the Franz Josef Glacier in Westland (Walker & Syers 1976). Each retreat of the Glacier leaves newly exposed till and bedrock on which soils develop, and these soils range in age from brand new to c. 120,000 years old (Fig. 2). In newly exposed glacial till phosphorus is in a mineral form from which it is weathered into solution that most plants can take up readily through their roots. As soils age, not only does the total amount of phosphorus decline, but the proportion easily taken up by plants declines. Over time, most phosphorus is in organic forms not easily available to plants. Plants that can obtain phosphorus in organic forms often do so by means of mycorrhizal fungi associated with their roots. At Franz Josef, by the time soils are 120,000 years old, the total amount of phosphorus is very low and nearly all of it is in different organic forms that are all difficult for plants to take up and use (Turner et al. 2007). Only disturbances that expose till and bedrock rejuvenate the process.

Whereas phosphorus is never more readily accessible and abundant for plants than soon after disturbances that expose bedrock, the total amount of nitrogen available to plants is never lower (Fig. 2). Overcoming the short supply of nitrogen is crucial for soil and ecosystem development. Lichens that colonise bare surfaces can provide some nitrogen. Some of the plants that colonise these bare sites have symbiotic relationships with microbes that can fix atmospheric nitrogen and make it available for plant growth. New Zealand has several native plants, most of them small trees or shrubs, with nitrogen-fixing symbiotic microbes. They include legumes such as native brooms (*Carmichaelia* spp.) and kowhai (*Sophora* spp.), tutu (*Coriaria arborea*) and its relatives, and matagouri (*Discaria toumatou*). Fixing nitrogen has a high demand on phosphorus, so ready access to it from mineral sources in newly exposed shattered bedrock ensures rapid growth of these plants. If plants with nitrogen-fixers colonise a newly disturbed site, then other plants that lack symbionts colonise around them, benefiting from nitrogen made available from decaying litter and roots. Forest canopies can develop within a few decades on freshly disturbed sites (Fig. 3). Over time, as forests develop, nitrogen inputs to the ecosystem from the atmosphere continue by rainfall, and from recycling



**Fig. 2.** Schematic representation of changes in concentrations of two key mineral nutrients needed for plant growth as ecosystems age after disturbances that expose geological parent material. Grey bands at left represent a period during which soil phosphorus, from weather parent material, is most available to plants, but nitrogen is least available, and depends on plants that can fix atmospheric nitrogen. Grey bands at right represent a point where phosphorus is highly limiting to plant growth. The time axis is variable, according to climate and parent material. After glacial retreat exposes parent material at Franz Josef, central Westland, phosphorus available to plants is in very low supply after 120,000 years (Turner et al. 2007). Figures are adapted from Walker and Syers (1976) and Peltzer et al. (2010).

of nitrogen from litter (including humus in tree crowns), decaying roots, and mineralisation by microbes in the soils, once there is sufficient organic matter. After the earliest stages, the total amount of nitrogen remains rather constant over time (Fig. 2), although the amount available to plants can decline in very nutrient-poor systems because it can become bound in litter and humus in organic forms (Peltzer et al. 2010).

There are three broad periods after disturbance that expose bedrock. In the shaded zones at left in Figure 2 are young developing ecosystems, high in available phosphorus, but low in nitrogen, which can be provided if plants with nitrogen-fixing symbionts colonise. In the centre of Figure 2 is a period that represents mature ecosystems (such as tall old-growth forests) that develop long after disturbance;





**Fig. 3.** Rain forests on soils exposed c. 30 years ago, after the retreat of the Franz Josef Glacier. Photo: PJB, 2013.

as these ecosystems develop, they become increasingly limited by phosphorus. In the shaded zones at right in Figure 2 is a period very long after initial disturbance, where plant growth becomes limited by very low levels of available phosphorus and where nitrogen can become limiting to plant growth as well.

After disturbance, the youngest and the oldest stages of soil development (the shaded zones of Fig. 2) support trees that have strongly contrasting traits. Their leaf traits are a good example (Table 1, Mason et al. 2012, Laughlin et al. 2015). On young soils (left-hand zones of Fig. 2), leaves are cheap to construct and therefore cost little to discard, as long as the problem of nitrogen availability is solved. The abundance of soil minerals including phosphorus and easy access to them, along with plenty of light, favour trees with rapid growth and early maturity. **New Zealand's ten fully deciduous** trees and others that are semi-deciduous, are most abundant on young, recently disturbed soils (McGlone et al. 2004), and this is indicative of cheap leaf construction costs. **Examples include** *kōtukutuku* (*Fuchsia excorticata*, deciduous) and *makomako* (wineberry, *Aristotelia serrata*, semi-deciduous). Thin leaves without defence chemicals fall as litter that decomposes rapidly and is readily incorporated into the soil, where their nutrients become available to other plants.

On severely nutrient-limited soils that develop long after disturbance (right-hand zones of Fig. 2), forests are short, with sparse crowns (Fig. 4). Leaves are very costly to construct because nutrients are in such short supply, and are small to very small and retained as long as possible. They are thick and tough and well defended against herbivores, especially insects, because the plants divert resources into producing defence chemicals such as polyphenols. These defences against herbivores result in leaf litter that is very slow to decompose (Wardle et al. 2005), and the living trees resorb most nitrogen and phosphorus from the leaves before



**Fig. 4.** Rain forests on soils exposed c. 120,000 years ago, after retreat of the Franz Josef Glacier. Photo: PJB, 2013.

shedding them (Richardson et al. 2005). Even though the litter that falls is very low in nutrients and slow to decompose, obtaining nutrients that recycle slowly from the litter is critical for these trees, and this is often achieved by symbiotic mycorrhizal fungi associated with their roots.

Some trees that colonise newly disturbed sites have tough, well-defended leaves. **Kānuka** (*Kunzea* spp.), which colonises landslides and floodplains, is **one example** and **pōhutukawa** (*Metrosideros excelsa*), which colonises cliffs and young volcanoes, is another. Other trees with tough, well-defended leaves occur across the full spectrum of soil age and nutrient availability depicted in Figure 2. Southern **rātā** (*Metrosideros umbellata*) colonises freshly exposed bedrock at Franz Josef and is still a component of forests on very nutrient-poor soils that were last disturbed 120,000 years ago. Mountain beech colonises exposed new screes that arise after earthquakes, and forms the canopy on long-undisturbed soils. However, while some trees with thick, tough, well-defended leaves can colonise young ecosystems, trees with thin, poorly defended leaves only become dominant on young nutrient-rich soils and they never occur on extremely nutrient-poor soils.

### Where invasive plants and animals affect New Zealand forests

Since 2002, the Department of Conservation and the Ministry for the Environment have conducted an **objective national assessment of New Zealand's forests** – the first in more than 50 years. Teams have visited sample locations that are placed on an 8 km × 8 km grid across New Zealand. This assessment was initially to determine how much carbon was stored in our forests and how it changed with time, prompted by commitments under the Kyoto Protocol.

The data allow us to evaluate whether man-made carbon emissions are being offset by sequestration of carbon in natural forests. The sampling has been augmented to include assessments of plant

composition, bird communities, and abundances of some introduced mammals (e.g., brushtail possums, deer and goats).

The assessment shows that young, disturbed forests are most susceptible to invasion by introduced plants and animals. The ratio of number of introduced to native plant species is greatest in recently disturbed sites. Introduced trees and shrubs are most frequent in these sites; very few colonise the understoreys of old-growth forests (Wilson & Lee 2012). The trends are consistent with the propensity for many introduced plants to invade disturbed sites **worldwide (D’Antonio et al. 1999). Some herbaceous** plants can invade the understoreys of tall old-growth forests, amongst which wall lettuce (*Mycelis muralis*) is the most widespread (Wiser & Allen 2006).

Young, disturbed forests are also favoured by introduced mammalian herbivores such as brushtail possums, deer, goats, and chamois. This is because many of the native plants that colonise disturbed sites, with thin, poorly defended nutrient-rich leaves, are highly palatable to these mammals (Forsyth et al. 2005), and some of the introduced plants that colonise these sites, such as legume herbs like clovers (*Trifolium* spp.) are also eaten by these mammals (e.g., Gilmore 1965). Some native trees with thick, well-defended leaves with low nutrient contents are also consumed (e.g., **southern rātā** by possums; Monks & Efford 2006), but those with thin, poorly defended nutrient-rich leaves are especially vulnerable. For example, possums have browsed native trees that colonise recently disturbed sites, **such as kōtukutuku and tutu, so much** that they have become extinct in some catchments (Brockie 1992, Pekelharing et al. 1998). Deer and goats exert their strongest effects on the composition of young forests, such as those that develop after storm damage (Mason et al. 2010). In young forests developing on sand dunes at Woodhill, west

Auckland, trees and shrubs with poorly defended nutrient-rich leaves have been all but eliminated by abundant fallow deer (*Dama dama*) from beneath **kānuka** (*Kunzea amathicola*) canopies. Only a few small fenced areas give any hint of the diverse forest that would develop if the deer were absent (Smale et al. 1995). We are beginning to understand the consequences of losing nutrient-rich native plants from ecosystems. For example, on floodplains and landslides in central Westland, a native broom, *Carmichaelia odorata*, is the main component of the winter diet of chamois (Yockney & Hickling 2000). This small tree has bacteria that fix nitrogen in nodules on its roots. When it is eliminated from floodplains and landslides, the rate at which forests develop on them is much slower, and soils and other plants are much lower in nutrient content (St. John et al. 2012). On other floodplains, hares have all but eliminated other native brooms (*Carmichaelia juncea* and *C. vexillata*; Grüner & Norton 2006), and goats likewise (*C. carmichaeliae*; Williams 1989); the consequence could be that forest development in these sites is hindered, but this requires investigation.

The national assessment of forests shows that the number of introduced bird species is greatest in disturbed sites and declines into old-growth forests (Bellingham et al. 2014), which is consistent with studies at local scales (Kikkawa 1964). Some introduced birds such as starlings (*Sturnus vulgaris*) are common at forest margins and scarcely occur in old-growth forests (Bellingham et al. 2014), and are important dispersers of introduced plants, such as inkweed (*Phytolacca octandra*, Ferguson & Drake 1999). Introduced birds are critical to the successful invasion of disturbed sites by some introduced plants, for example, successful invasion of hawthorn (*Crataegus monogyna*) in deforested inland Canterbury depends on dispersal of its seeds by blackbirds (*Turdus merula*, Williams et al. 2010).

**Table 1:** Characteristics of leaves and litter of trees on newly exposed surfaces soon after disturbances such as landslides or floods, and on surfaces long after disturbances.

	Ecosystems developing on newly exposed surfaces	Ecosystems on long-undisturbed surfaces
Leaf size	Variable but often large	Small
Leaf thickness and toughness	Often thin and not tough	Thick, tough
Defence chemicals in leaves	Uncommon	Common
Leaf lifespan	Short (< 3 years), with some deciduous species	Long (often > 5 years)
Litter decomposition rate	Rapid	Very slow
Example species from the New Zealand tree flora	<i>Fuchsia excorticata</i> <i>Carmichaelia odorata</i> <i>Aristotelia serrata</i> <i>Schefflera digitata</i>	<i>Dracophyllum longifolium</i> <i>Phyllocladus alpinus</i> <i>Lepidothamnus intermedius</i> <i>Leptecophylla juniperina</i>

Introduced plants that invade on young soils soon after disturbance have the same shortage-of-nitrogen dilemma faced by native plants (left-hand zone of Fig. 2). Many of the introduced plants that colonise these soils have symbiotic microbes that fix atmospheric nitrogen, including legumes such as clovers, gorse (*Ulex europaeus*), and Scotch broom (*Cytisus scoparius*), and others such as alder (*Alnus glutinosa*). Other plants that invade disturbed sites do not fix nitrogen, but can gain access to soil mineral resources by means of mycorrhizal fungi; examples include willows (*Salix* spp.), pines (*Pinus* spp.) and perhaps buddleja (*Buddleja davidii*) and this can allow their rapid growth.

Some introduced plants readily invade areas that were deforested for agriculture. As soils have degraded or eroded, or where farming became unprofitable, gorse and pines are now widespread (Fig. 5). In many areas, the response to this has been to try to retard their invasions, usually with herbicides. Many of these attempts have proven futile and now some managers are explicitly incorporating introduced plants in efforts to return areas to native forests (e.g., Wilson 1994). Introduced plants can influence the type of forest that develops. For example, pines cause major changes in soil nutrient cycling by increasing the dominance of bacteria in soil, the concentrations of nitrate and plant-available phosphorus in soils; all of this is likely to be caused by the mycorrhizal fungi **associated with the pines' roots (Dickie et al. 2014)**. Some of the immediate beneficiaries of the changes in soils caused by the pines are introduced grasses, such as browntop (*Agrostis capillaris*), which grow rapidly in soils altered by the pines, even if the pines are removed. In contrast, the forests that develop under introduced legumes such as gorse and Scotch broom have soils that are rich in nitrogen. This favours growth of some native tree species, like māhoe (*Melicytus ramiflorus*) that can ultimately overtop and replace the introduced legumes, but it may not favour others. For example, in catchments with similar histories of deforestation and abandoned farming near Nelson and Wellington, native conifers **colonised under canopies of kānuka**, where it established first into former farmland, but seldom under canopies of gorse where it established first (Sullivan et al. 2007). The reasons for these differences are unknown.

The role of introduced woody plants and how they can influence the rate at which future forests develop, and their composition, is increasingly appreciated, but less attention is paid to the effect that the many introduced herbs and grasses can have. For native trees that are dependent on disturbance for the development of new populations, rapid growth of introduced herbs and grasses can suppress germination and growth of seedlings. For example, the deciduous tree *Olearia hectorii* would

normally germinate on rich alluvial soils after floods but, because pasture grasses often cover those sites, it regenerates rarely (Rogers 1996). Introduced herbs and grasses can also provide shelter for herbivores, such as introduced slugs, that consume newly established native plants (Sessions & Kelly 2002). In a study after a major flood in the Kowhai River valley, near Kaikoura, many species of introduced grasses and herbs colonised the bare floodplain, as well as native herbs and woody plants (Fig. 6). If the introduced herbs and grasses were **removed, then native plants such as tutu and kānuka** colonised readily, but when they were present, the colonisation by native plants was much reduced (Fukami et al. 2013). Many of the introduced herbs **and grasses occupy 'functional gaps'** in the native flora. Many of those on the floodplain are annuals (these are very rare in the native flora) and many of the herbs have nitrogen-fixing microbes associated with their roots (very few native herbs do). They grow rapidly and die after a season, and have leaves rich in nitrogen that are also very thin, so that their litter and remains are incorporated rapidly in the young soils of the floodplain. As a result, they cause much quicker development of soils, and different kinds of soil microbes prevail under them (Peltzer et al. 2009).



**Fig. 5.** Lodgepole pine invading deforested landscapes, currently comprised of native and non-native grasses, near Twizel. Photo: PJB, 1998.



**Fig. 6.** Tutu, buddleja and *Trifolium arvense*, four years after floods created denuded surfaces in the Kowhai River valley, NW of Kaikoura. Photo: Chris Morse, 2008.



**Why might there be ‘functional gaps’ in the native flora?** Why do we have so few annuals, nitrogen-fixing herbs, or trees such as willows that grow on disturbed sites in New Zealand? There is no consensus among ecologists about this. Some find these absences surprising (Dansereau 1964), but others consider that we have an optimum flora for our circumstances (Wilson & Lee 2012), and that the dominance of introduced plants is a transient state best explained by their not being controlled by the herbivores and diseases that prevent their invasiveness in many of their native ranges.

It is useful to consider these problems in terms of the origins of New Zealand’s flora. **Most of the flora** is surprisingly recent in its origins. Most of our flora dispersed across the Tasman Sea from Australia or Southeast Asia; as Matt McGlone (2005) put it, **we are not so much a “Time Capsule of the South Seas” in terms of our flora but rather the “Fly-paper of the Pacific”.** We can also consider Australia’s flora, from which most of ours is derived, within a framework of how soils develop after disturbance (Fig. 2).

Australia has some young soils rich in phosphorus and low in nitrogen (left-hand shaded zones of Fig. 2), but they are few (Walker et al. 1981). Most of Australia is an ancient, weathered and generally very tectonically stable landscape, where soil nutrients are highly limiting (Walker et al. 2001), i.e., like the right-hand shaded zone of Figure 2. Considered in these terms, Australia offered very few opportunities for the evolution of the equivalents of willows, poplars, buddlejas, or other rapid-growing trees of nutrient-rich floodplains. Australia offered few opportunities for the evolution of herbs (nitrogen-fixing or otherwise) and grasses that could colonise landslides, such as those caused by earthquakes. **If New Zealand’s origins as a land mass had been an equivalent distance from the east of China, which is fertile and tectonically active, rather than Australia, the traits of plants in New Zealand might have been very different!** Instead, the Australian influences in **New Zealand’s flora confer many attributes in plants** that tend towards conservative use of soil nutrients, building long-lived leaves that are well defended, even when plants colonise resource-rich sites. We see this in plants such as heaths (for example, species of *Dracophyllum*) that can invade disturbed sites, yet have long-lived, tough, well defended leaves.

### **New disturbances**

**Australia’s influence on New Zealand’s modern flora** has probably resulted in a generally conservative approach to how plants allocate resources and use available nutrients. Some of the disturbances that shaped the evolution of ancestral plants in Australia, such as droughts and storms, occur in New Zealand, although drought stress in New Zealand is usually trivial in comparison. However, one frequent and

sometimes severe disturbance that is a major evolutionary driver in Australia – fire – has been unimportant in New Zealand. Lightning strikes are a very rare source of ignition in most New Zealand forests, and fires caused by other means (such as volcanoes) were too infrequent to act as evolutionary drivers.

In Australia, evolutionary responses to fire are well developed, such as resprouting (Clarke et al. 2013) and mechanisms to store seed in tree crowns until just after fire, so that the seeds can be released into ash beds where nutrients are briefly plentiful, and where competition from other plants is least. Some Australian plants have evolved to be flammable, either to promote fire so that it passes quickly, or to scorch their competitors. A few New Zealand native trees exhibit some of these traits. Matagouri is very flammable and resprouts after fire and, in some parts **of the country, mānuka (*Leptospermum scoparium*)** has seed capsules that split after fire to release seeds (Perry et al. 2014). Both of these have close relatives in Australia, and especially in the case of many Australian *Leptospermum* species, the adaptations to fire are much more strongly expressed there. Fire is fatal for most New Zealand trees.

The rare occurrence of fire and its minor role in the **evolution of New Zealand’s forests changed irrevocably when people arrived about 730 years ago. When Māori set fires in the rain shadow regions** of the North and South Islands, the effects on the native forests were catastrophic. Within 100 years of arrival, almost all of the forests of the eastern South Island were eliminated by fire, and were replaced by native shrubs and grasses that were flammable and could survive repeated fires (Perry et al. 2012). Almost no trace now remains of once widespread **forests dominated by mataī (*Prumnopitys taxifolia*)** in the lowlands and by mountain toatoa (*Phyllocladus alpinus*) and bog pine (*Halocarpus bidwillii*) that were **present before the arrival of Māori, and the seed sources are so reduced that there is almost no prospect of their return.**

The landscapes that people burned and rendered flammable became even more so after European colonisation. Europeans burned the flammable shrublands and grasslands of the eastern North and South Islands even more frequently and they added new mammalian herbivores – sheep, cattle, rabbits – as well as pasture grasses and herbs that further altered their composition. They also introduced fire, far more **than Māori had, into the higher rainfall regions.** While setting fires in the rain forests was difficult, in dry years and with enough attempts at ignition, they burned. One example is the litter-supported fire that killed the roots of old-growth kauri (*Agathis australis*) forests, so that the large trees died standing (Orwin 2004).

Since European settlement, disturbances caused by fire have another important ingredient: introduced highly flammable plants that evolved in fire-prone regions, and which benefit from fire. Some are Australian, such as prickly hakea (*Hakea sericea*). Others are from western North America, such as lodgepole pine (*Pinus contorta*), radiata pine (*P. radiata*), and Douglas-fir (*Pseudotsuga menziesii*), or from fire-prone parts of Europe, such as gorse and Scotch broom. Some, like lodgepole pine, are quickly colonising deforested regions and are forming new forests that will be persistent if they burn periodically (Fig. 5). Native gumlands are maintained by periodic fire, but the invasion of gumlands by combustible gorse and prickly hakea will probably increase the fire frequency and severity and could result in the latter becoming dominant.

Most of the introduced flammable species colonise recently disturbed sites, such as landslides, or invade abandoned agricultural zones. The net result is an incremental increase in the area of fire-supporting forests that New Zealand never had before. Fire is a new disturbance that is here to stay, and will generally favour introduced plant species over native ones. Especially in the drier regions of New Zealand, which are forecast to become hotter and drier with current climate change and therefore more likely to burn, the incremental shift towards more fire-prone forests is likely to chip away at the extent of remaining native forests, which have hitherto been resilient to so many other natural disturbances.

## Conclusion

**The long period of isolation in which New Zealand's forests evolved is over.** The large cargo of introduced plants and animals, along with diseases, will shape how its forests respond to disturbances in future. Introduced plants and animals will colonise disturbed sites where future forests will develop, whether large or small in area and no matter how remote. We can manage some aspects of this, for example, by suppressing fires or reducing populations of some mammals. Currently, the emphasis is on suppressing predatory mammals in forests, which is likely to **benefit birds (Russell et al. 2015), including kererū (*Hemiphaga novaeseelandiae*)** without which the seeds of some native trees do not colonise forests that develop in disturbed sites (Bellingham et al. 2010).

A few decades ago, the emphasis was on suppressing herbivorous mammals in forests, especially deer (McKelvey 1995), whereas now deer (along with chamois and Himalayan tahr) are now regarded as a hunting resource to be maintained in New Zealand (Game Animal Council Act 2013); I have emphasised how they can influence forests that develop in disturbed sites and that this influence can **endure. My point is that people's perceptions of the**



**Fig. 7.** *Fuchsia excorticata* regenerating, protected from possums, on a recent landslide, upper Kokatahi River valley, SE from Hokitika. Photo: Caroline Thomson, 2014.

most important **things to manage in New Zealand's** forests change and may not endure. Similarly there has been a shift in emphasis from securing and managing remote sites, such as campaigns to protect Paparoa National Park in the 1980s, towards protecting forests that have been disturbed by logging and fires close to where people live, such as **fenced sanctuaries at Tāwharanui, Maungatautari, and Karori in the 2000s.** However we choose to manage our forests in future, we need to be mindful of the disturbances that are certain to affect them. For example, how will an inevitable earthquake affect the management of Karori Sanctuary in Wellington, or an inevitable cyclone affect the management of **Tāwharanui (cf. Scofield et al. 2011)?**

We could view disturbances as a nuisance or, at worst, catastrophes that undo our hard work. A more positive approach is to regard them as opportunities to focus our efforts where they will yield maximum benefit. Long-undisturbed forests, especially those in very nutrient-poor sites, will benefit little or slightly from most human interventions, other than suppressing predatory mammals to benefit birds. In recently disturbed sites, we can expect maximum benefit from our interventions. Attention paid to removing introduced plants, suppressing introduced mammals, and promoting native birds that disperse seeds will enhance the opportunities for growth and dominance of the native trees that colonise these sites.

Maintaining populations of trees threatened by introduced plants or animals, such as **kōtukutuku or *Olearia hectorii*,** will allow them to colonise other disturbed sites (Fig. 7). Young forests that develop in recently disturbed sites lack the grandeur of old-growth stands, but their health and maintenance has



enduring consequences that will shape the composition of future old-growth forests. Attention paid to ensuring the development and protection of diverse young forests, comprised of the full range of native plants that could colonise, may help to ensure that our future forests are as resilient to disturbances as they have been in the past.

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