

REVIEW ARTICLE

Ecology and long-term history of fire in New Zealand

George L. W. Perry^{1,2*}, Janet M. Wilmshurst^{1,3} and Matt S. McGlone³¹School of Environment, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand²School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand³Landcare Research, PO Box 69040, Lincoln 7640, New Zealand*Author for correspondence (Email: george.perry@auckland.ac.nz)

Published online: 13 May 2014

Abstract: Fire is a complex physical and ecological process and one that has dramatically affected New Zealand's landscapes and ecosystems in the post-settlement era. Prior to human settlement in the late 13th century, the Holocene palaeoenvironmental record suggests that fire frequencies were low across most of New Zealand, with the notable exception of some wetland systems. Because few of New Zealand's indigenous plant species show any real adaptation to fire, the greatly increased fire activity that accompanied human settlement resulted in widespread, and in some cases permanent, shifts in the composition, structure and function of many terrestrial ecosystems. The combined effects of Maori and European fire have left long-lasting legacies in New Zealand's landscapes with the most obvious being the reduction of forest cover from 85–90% to 25% of the land area. Here we review the long-term ecological history of fire in New Zealand's terrestrial ecosystems and describe what is known about the fire ecology of New Zealand's plant species and communities, highlighting key uncertainties and areas where future research is required. While considerable emphasis has been placed on describing and understanding the 'initial burning period' that accompanied Maori arrival, much less ecological emphasis has been placed on the shifts in fire regime that occurred during the European period, despite the significant effects these had. Post-fire successional trajectories have been described for a number of wetland and forest communities in New Zealand, but in contemporary landscapes are complicated by the effects of exotic mammalian species that act as seed and seedling predators and herbivores, reduced pollination and dispersal services due to declines in the avifauna, and the presence of pyrophyllitic exotic plant species. Many invasive plant species (e.g. *Pinus* spp., *Acacia* spp., *Hakea* spp., *Ulex europaeus*) are favoured by fire and now co-occur with indigenous plant species in communities whose long-term composition and trajectory are unclear. On the other hand, some highly-valued ecosystems such as tussock grasslands may require recurrent fire for their long-term persistence. Combined, the direct and indirect effects of the introduction of anthropic fire to New Zealand may have shifted large areas into successional 'traps' from which, in the face of recurrent fire, escape is difficult. Developing appropriate management strategies in such a context requires a nuanced understanding of the place of fire in New Zealand's ecosystems.

Keywords: charcoal record; fire regime; human–fire interactions; invasive species; pyrogeography

Introduction

New Zealand has been held up as the archetypal isolated Oceanic ecosystem that suffered dramatic environmental change following the arrival of humans (Bowman & Haberle 2010). The post-settlement loss of forest and the accompanying collapse in its vertebrate fauna, and its functional implications, are well documented (McGlone & Wilmshurst 1999a; Kelly et al. 2010; Lee et al. 2010). The key agent in forest loss was the introduction of human-lit fire to woody ecosystems that were previously ignition-limited and highly susceptible to fire. Recent advances in our understanding of fire activity during New Zealand's early prehistory have emphasised that forest loss was rapid and intense, with flow-on effects to other ecosystem processes and services (McWethy et al. 2010; Perry et al. 2012a, b). Human actions have rescaled New Zealand's fire regime in both time and space; fire is now not only more frequent than in the past, but operates in landscapes that are fragmented, and so relatively smaller, making fires effectively larger. The effects of humans on the fire regime have been abrupt and obvious. They are so recent that they have occurred

in the absence of major climate shifts, making New Zealand an ideal setting in which to explore human–fire interactions (Bowman et al. 2011; McWethy et al. 2013).

In his survey of the forests of west Taupo, McKelvey (1963, p. 11) commented: '...much intensive research is needed before the relationship between fire and fire-induced vegetation is fully understood'. Fifty years later the impacts of fire on New Zealand's ecosystems, and their resilience, or otherwise, to this altered disturbance regime are still under-studied (Smale et al. 2011). However, New Zealand's ecosystems afford a unique opportunity to evaluate the ecological responses and re-sorting caused by such shifts in disturbance regime (as noted 80 years ago by Cockayne and Calder (1932)). In the context of fire in New Zealand, attention has been focused on the 'losers' in terms of vegetation distribution and community composition, with less consideration given to those species – native and exotic – that have been favoured by the shifts in fire regimes. Despite fire being naturally recurrent, if infrequent, in prehuman New Zealand (e.g. Wilmshurst et al. 1997, 1999), in post-settlement ecosystems it is largely regarded as a destructive tool of transformation rather than as an ecological

process. In short, there is a need to develop a more considered view of the place of fire in New Zealand's ecosystems. In this review we aim to outline what we know about the ecological history of fire in New Zealand (see Fig. 1 for locations), and the response of indigenous ecosystems to fire, with a focus on the flora rather than the fauna. Our review comprises three parts. First, in order to understand the physical basis for the fragility of New Zealand's ecosystems to anthropic fire we begin by considering the fundamentals of fire as a physical process. We then survey what is known about fire regimes prior to and following human settlement, placing this history in the contexts of New Zealand's biogeographic past, and of the shifts in vegetation pattern and composition that natural and human fire has induced across New Zealand's forests, wetlands and grasslands. Finally we consider the modern fire regime and the management challenges fire poses, especially in novel ecosystems where invasive plant and animal species are dominant and there is a risk of large areas falling into landscape 'traps' from which escape will require interventionist management. Throughout we highlight key areas of uncertainty in our understanding and discuss the opportunities that the human-induced rescaling of New Zealand's fire regime provides for ecological research.

The process of fire

Physico-chemical process

Wildfires integrate processes from the sub-second (the physics and chemistry of combustion) to the centurial (the accumulation of fuels over succession). Fire starts with ignition, which may be natural (e.g. lightning strike) but in many modern landscapes, including New Zealand, is overwhelmingly human in origin. The spread of fire through a fuel bed involves three components

(Sullivan & Ball 2012): (1) heating of fuels prior to ignition, (2) flaming spread, and (3) smoulder behind the active flaming front. The passage of a flaming front through a fuel bed is driven by convective and radiative heat transfer driving water out of the fuels, releasing volatile gases (pyrolysis), and igniting them (Ward 2001; van Wagtenonk 2006). The outcomes of a fire can be described by (following the terminology of Keeley (2009)): (1) fire intensity – the energy released in the event, which is correlated with flame height and temperature, (2) fire (burn) severity – the total amount of organic matter consumed in the event, and (3) ecosystem responses – changes in hydrology, soils and vegetation resulting from the fire.

Plant mortality is the fundamental ecological outcome of the spread of fire through vegetation; Michaletz & Johnson (2007) and Butler & Dickinson (2010) provide thorough overviews of the biophysical links between fire and plant death. As a rule of thumb, a temperature of between 50° and 60°C is the threshold for cell death (Whelan 1995; Jones et al. 2006). There is, however, a close relationship between the heat required to cause necrosis and the length of time that a plant is subjected to the heating: as temperature increases, the required exposure time drops exponentially (Bond & van Wilgen 1996). While cellular necrosis is often considered the main source of fire-induced tree mortality, heat-induced deformation and cavitation of the xylem have recently been identified as another potential mortality source (Michaletz et al. 2012).

Mortality eventuates from heat-related damage to the trunk, crown or roots (Dickinson & Johnson 2001; Michaletz & Johnson 2007; Michaletz et al. 2012). During a fire event the heating of tree trunks and stems is primarily driven by radiation and convection, with most of this occurring via conduction (Butler & Dickinson 2010). This heat transfer can be reduced

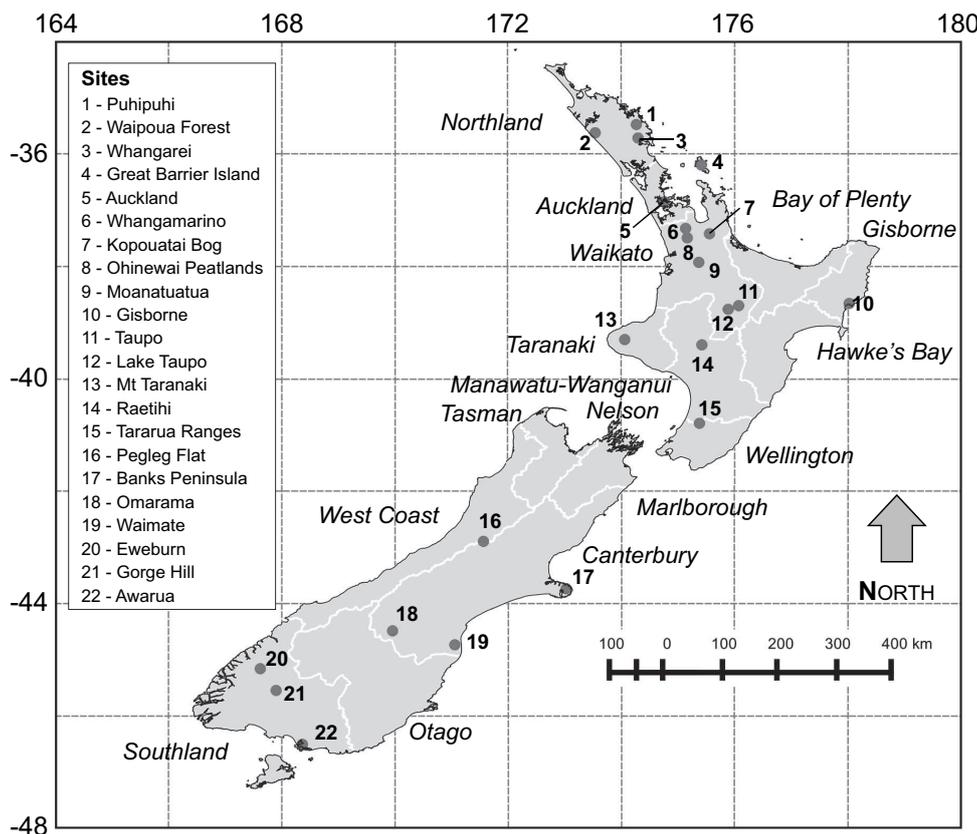


Figure 1. Location of the studies mentioned in the text (numbers, ordered north to south); regions are identified in italics and follow the New Zealand regional council boundaries of 2012 (white lines).

by possessing thick bark, as the heating time required for plant mortality increases with bark thickness (Gutsell & Johnson 1996; Dickinson & Johnson 2001). The relationship between bark thickness and trunk diameter varies between species, but thickness tends to increase with diameter whether linearly (Hengst & Dawson 1994) or as a power function (Lawes et al. 2011). Thus, because the thermal properties of bark show little interspecific variation, smaller individuals, irrespective of species, tend to be most susceptible to fire damage (Michaletz & Johnson 2007). As discussed below, by global standards New Zealand's indigenous tree species tend to have thin bark making them vulnerable to fire-induced mortality. Radiative and convective transfer will heat the crown, and the height up to which this heating occurs is an important determinant of the amount of damage and mortality. Finally, root death may occur as heat is transferred to the soil and then the roots, with heat transfer and temperature declining sharply with soil depth (Certini 2005). Because soils, especially peats, may smoulder over long periods, the transfer of heat to the soil, and the associated biological and physical effects, is typically much slower than the flux of heat to the trunk and crown (Michaletz & Johnson 2007; Rein et al. 2008).

The conventional wisdom is that wildfires are driven by fine and dead fuels, such as twigs, bark and litter. Dead fuels hold from 2% to 200% moisture content and live fuels 75–150% (Macias Fauria et al. 2011), with the geometry (surface-to-area ratio) of a fuel particle largely determining the rate at which it attains its equilibrium fuel moisture content (Bond & van Wilgen 1996; van Wagtendonk 2006). At the level of the landscape, fire behaviour is influenced by topography and wind (fires tend to spread upslope and with the wind as the flaming front is tilted towards the fuel bed) and the nature of the fuel bed itself (e.g. the fuel-bed particle packing density ratio, which effects aeration and the effectiveness of radiative transfer at the flaming front; see van Wagtendonk 2006). Thus, the occurrence of large fires depends on an ignition source and a fuel bed that supports fire spread (e.g. a sufficient amount of dead and fine fuels) alongside conducive weather conditions (which act to dry the fuel bed). There is long-standing interest in disentangling the relative importance of top-down climatic (via fuel moisture) vs bottom-up fuel (via available biomass) controls in driving fire events (Whitlock et al. 2010). Recent conceptual models have sought to move beyond the fuel vs climate dichotomy and have attempted to identify the conditions under which different controls are more or less important in determining the fire regime (Meyn et al. 2007; Krawchuk & Moritz 2011; McWethy et al. 2013).

Flammability–age relationships in New Zealand's ecosystems

Much of the understanding of landscape-level interactions between fire and vegetation in forest ecosystems is derived from extensive research in the fire-prone ecosystems of North America. In such ecosystems flammability typically monotonically or asymptotically increases (or is independent of stand age) with time since the last fire event. Such relationships are appropriate where biomass (fuel load) is the primary control on fire activity at a given point in time and space, and result in a landscape comprised of a mosaic of patches in different stages of successional recovery, as old patches are more vulnerable to fire. This conceptual model is inappropriate for New Zealand's vegetation. Instead, in New Zealand's forest ecosystems, flammability follows a hump-backed (or more generally declining) relationship with time since fire, such that it peaks 50–100 years after fire (i.e. in successional

communities dominated by species such as *Leptospermum scoparium* (mānuka) and *Kunzea ericoides* (kānuka) – both flammable Myrtaceous species of Australian origin)¹ before declining (Fig. 2). This relationship, which, in the specific statistical context of hazard rates McCarthy et al. (2001) call the 'moisture model', is the result of changes in the structure and composition of the fuel bed and possible accompanying shifts in microclimate conditions over the course of succession, rather than changes in aggregate biomass or fuel load.

While the humpbacked age–flammability relationship has received little attention compared with those where it increases with time (although see Perry & Enright 2002; Kitzberger et al. 2012; Perry et al. 2012a), it has long been recognised in New Zealand's ecosystems (e.g. see Druce 1957). Crucially, this humpbacked relationship carries with it the potential for a positive feedback in which changes in vegetation composition may be self-reinforcing as they influence the fire regime (a dynamic hinted at in Walsh (1910)). Kitzberger et al. (2012) demonstrated the potential for rapid shifts in composition in ecosystems where this dynamic occurs if fire frequency changes (as may result from changes in climate or anthropic fire frequency). Such feedback dynamics are likely also important in other temperate and tropical rainforests experiencing shifts from mesic primary forest to more open secondary forest (Warman & Moles 2009; Lindenmayer et al. 2011; Davidson et al. 2012).

Origins of fire in New Zealand's ecosystems

Biogeography and Quaternary fire history

Wherever there is plant material, there will be fire, and charcoal is found in New Zealand sediments of all ages. However, whether fire is significant in the evolution and ecology of the

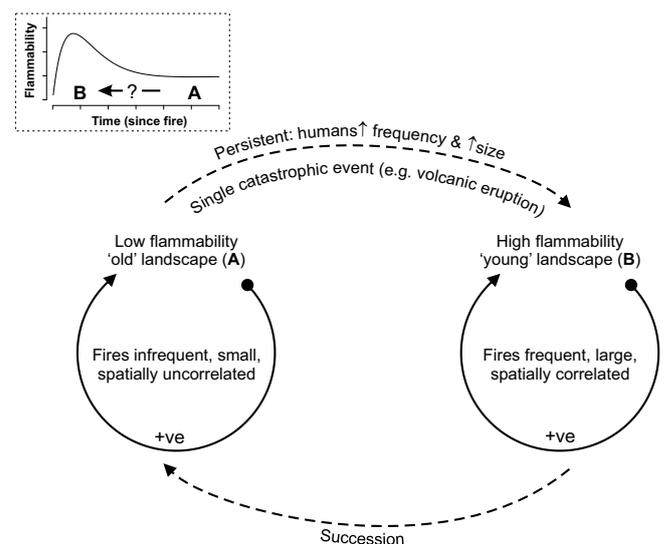


Figure 2. There is an inherent positive feedback between fire and vegetation in New Zealand's ecosystems: post-fire vegetation is more flammable (B in inset) than later successional vegetation (A in inset). Given this feedback the widespread and rapid forest loss that occurred during New Zealand's early prehistory may have been inevitable rather than motivated.

¹ Nomenclature follows the Ngā Tipu o Aotearoa – New Zealand Plants database: <http://nzflora.landcareresearch.co.nz/>.

plant life of a given region depends largely on how frequent it is and how large an area it burns. As Keeley et al. (2011) emphasise, selection for fire adaptations occurs in the context of the fire regime, not individual fire events. Where fire is neither frequent (scaled against typical longevity) nor predictable we would not expect a species to evolve particular adaptations to fire whether in the form of fire tolerance, resistance or recovery. On the other hand, if fire regularly creates distinctive but ephemeral habitats we might expect short-lived, rapid-response species to evolve. The New Zealand flora has few species with specific adaptations to fire, but a number do respond rapidly to the opportunities fire creates. However, as most of the latter group proliferate after any form of disturbance, it is difficult to tell in a meaningful sense if they are fire-adapted. Of the species with distinctive fire adaptations (*Kunzea* spp., *Leptospermum scoparium*, *Pteridium esculentum*, and *Discaria toumatou*) all are closely related to east Australian species (e.g. de Lange et al. 2010) and have a history in New Zealand no earlier than the Pliocene (Mildenhall 1980). New Zealand had a number of taxa from fire-adapted genera (*Acacia*, *Casuarina* and *Eucalyptus*) during the Miocene but all were lost during the Plio-Pleistocene period (McGlone 2006).

Charcoal is the only definitive evidence for fire that is available in New Zealand, although chemical biomarkers have been developed and deployed elsewhere (Conedera et al. 2009) provide a thorough overview of the proxies and methods available to reconstruct palaeofire regimes). Large fragments of charcoal or charred wood are often found in superficial soil deposits (Ogden et al. 1998) or volcanic tephra deposits (e.g. Vucetich & Pullar 1973) but they are only rarely transported far. In lake sediments, nearly all charcoal particles greater than 125 µm in diameter are derived from distances of no more than 1–2 km, and this size is commonly used as a cut-off point for evidence of local fires (Whitlock & Larsen 2001). Smaller particles can travel much longer distances and dust-sized charcoal can disperse thousands of kilometres from its source. Until recently, continuous records of fire have been developed from analysis of charcoal in pollen slides and thus only dust-sized particles recorded (as, during sample preparation, the sediment is sieved to remove particles larger than 100 µm); we will refer to this evidence as ‘pollen-charcoal’. After a fire, charcoal will remain on charred wood, on the ground and in superficial soil layers for many years. Any disturbance in the catchment of the lake such as heavy rain or fluctuations of lake level will lead to a pulse of reworked charcoal (Wilmshurst et al. 1999). It is therefore difficult to clearly distinguish any one fire from others in the sequence, and usually peaks above a background level are used to calculate a ‘fire frequency’ (e.g. Kelly et al. 2011).

There are only a few pre-Holocene-aged records for New Zealand in which pollen-charcoal is systematically documented, although references to charcoal presence are often made. In general terms, forested sites yield little or no pollen-charcoal. Northland sites during the last glaciation are an exception as periods where *Fuscospora* cf. *truncata* dominated are also accompanied by high amounts of pollen-charcoal (Elliot 1998; Newnham 1999; Elliot et al. 2005). A glacial forested sequence from swamp sediments in Gisborne also has a high input of pollen-charcoal (McGlone et al. 1984a). The Northland sites are restiad bogs, and the Gisborne site dominated by *Leptospermum* and *Coprosma*, and it is most likely that the high pollen-charcoal levels are associated with these highly flammable wetland systems, rather than the forest, as forest taxa do not decline with charcoal. Sites in similar partly forested

landscapes on the Auckland Isthmus 230 km to the south did not record pollen-charcoal, or only occasional isolated peaks (Sandiford et al. 2002, 2003). However, as these are lakes, the absence of charcoal may reflect the absence of a flammable shrub–sedgeland on the bog surface. Conifer shrubland and *Coprosma–Myrsine–Dracophyllum* shrubland sites were common during the last glaciation in the central and southern North Island and were nearly always associated with pollen-charcoal (McGlone & Topping 1983; McGlone et al. 1984b; Bussell 1990). While the same proviso regarding flammable wetlands applies to these shrubland sites there seems a much higher probability that the surrounding landscape burned as well. For example, a set of palynological sites beneath the Kawakawa Tephra (25 360 ± 160 cal yr BP; Vandergoes et al. 2013) on the Volcanic Plateau represent scrub-grassland on moist sites rather than true wetlands, with pollen-charcoal common in the profiles and one site containing layers of macro-charcoal (McGlone & Topping 1983).

Around 18 000 years ago, reforestation of the New Zealand landscape began, a process that was largely complete by 15 000 years ago as far south as the northern South Island, and essentially finished by 8000 years ago with the spread of forest in the central south-eastern South Island (Newnham et al. 1999; McGlone et al. 2003). New Zealand forest trees appear to be ill-adapted to fire and tend to succumb to even low-intensity ground-fires. Modern observations show that from time to time ridge tops or individual trees may be struck by lightning and burn, even in some of the wettest forests, but any more widespread fire resulting from this is extremely rare. New Zealand has low rates of lightning strike (Christian et al. 2003) and those storms that do carry lightning tend to be associated with wet fronts (Ogden et al. 1998) and occur predominantly in wetter ecosystems (see fig. 6 in Rogers et al. 2007).

Volcanism is often mentioned as a potential fire source, which, unlike lightning, is not usually accompanied by rain. However, pollen sequences close to volcanoes or even on their upper flanks (McGlone et al. 1988; Lees & Neall 1993; Horrocks & Ogden 1998, 2000) record little charcoal aside from that under ignimbrites. Large ignimbrite deposits and ash showers in the North Island may have been an exception: for example, following the Taupo eruption (c. 1800 years BP) the palynological record suggests widespread fires for several decades after the eruptive event, with areas as far away as 170 km experiencing damage, but with almost complete recovery of tall-forest within 150–200 years (Wilmshurst & McGlone 1996). However, such eruptions were rare. As a general rule then, soil macro-charcoal and/or pollen-charcoal are infrequent where Holocene forests remained intact, even in dry areas (McGlone & Basher 1995; Wilmshurst et al. 1997; McGlone 2002).

Ogden et al. (1998) suggested that prior to human settlement of New Zealand fire frequencies in both the North and South Island were in the order of centuries, but possibly millennia apart at the same site. This general conclusion was supported by Rogers et al. (2007). But, as far as we are aware, no studies in which a systematic search has been made for macro-charcoal exist outside of the eastern South Island. Nearly all prehuman, non-volcanic-related macro-charcoal comes from the east coast of the South Island (Molloy et al. 1963; Ogden et al. 1998; Rogers et al. 2007) and this is a biased sample on which to make general conclusions for New Zealand. Using the driest Level 1 environments (N, J & B) of Leathwick et al. (2002), which also cover most of the area within which soil charcoal has been recovered, about 12% of the New Zealand land area was exposed to prehuman fire.

Fire nevertheless was widespread throughout the drier regions—especially where there was scrub or open forest (Leslie & McGlone 1973; McGlone et al. 1995, 1997; McGlone & Moar 1998; Pugh & Shulmeister 2010). Fire was especially common in *Phyllocladus alpinus* and *Halocarpus bidwillii*-dominated systems (e.g. in the eastern interior of the South Island); of these two groups *Phyllocladus* is very sensitive to fire, but *Halocarpus* perhaps less so as it is known to have regenerated after fire in some sites. McGlone and Moar (1998) describe increases in fire activity from around 5000 years BP at Duncan Stream (near Omarama, Mackenzie Basin) and an accompanying shift from open *Phyllocladus* forest to shrub–tussockfield.

A key question is how frequent was fire? A number of lines of evidence converge on relatively long time intervals between fires. Many sites have sequences of dated charcoal layers (e.g. Burrows et al. 1993; Burrows 1996; McGlone & Moar 1998; McGlone & Wilmshurst 1999b; Wardle 2001) but typically there are long gaps of many hundreds of years between fire episodes. Charcoal layers only preserve in the case of rapid burial, and in turn that necessitates steep slopes and substantial loss of vegetation (Wardle 2001). It is possible that fires were more frequent than indicated by the charcoal layers. However, a limit is imposed by the slow regeneration of forest and the intolerance to fire of most of the constituent species. For instance, the presence of *Podocarpus cunninghamii* tree trunks unbranched for 3–4 m in Central Otago, unlike the multi-stemmed individuals found in patches on the current landscape, suggests that even in fire-prone regions, trees of considerable age had themselves regenerated in closed-canopy forests (Wells 1972).

Lowland wetlands may also have been subject to repeated natural fires. Restiad bogs in the northern part of New Zealand have undoubtedly been foci for fire for a considerable period (McGlone et al. 1984c; Newnham et al. 1995; McGlone 2009). Such bogs would have had a woody (scrubby) component and so, given ignition, provided an abundance of fine fuels to

carry fire. These sites also have physical conditions conducive to fire: they are raised, have a low and uniform vegetation cover (i.e. no natural firebreaks), endure a summer dry period, and the restiad cover generates a dry and heated surface (Campbell & Williamson 1997). McGlone et al. (1984c) found charcoal, probably deriving from surface fires, in records from the Ohinewai peatland (Waikato lowlands) throughout the Holocene and other bogs in the region show a similar pattern (e.g. Kopouatai Bog; Newnham et al. 1995). There is, however, little evidence that fire spread from these bogs to surrounding forests in prehuman New Zealand. Fire is not recorded from raised bogs in the southern South Island, and this is likely because of the uniform distribution of rainfall at those latitudes, which differs from the marked seasonal contrast between wet winters and dry summers in the North Island.

A number of studies suggest an increase in fire activity from the mid-Holocene onwards in the east of both islands (McGlone & Moar 1998; Horrocks et al. 2001; McGlone 2001; Rogers et al. 2007; Pugh & Shulmeister 2010). This increase is possibly the result of strengthening summer insolation and the greater frequency and intensity of ENSO events and associated droughts at this time. Irrespective of prehuman fire activity, these dry, open forest types did not persist in the face of anthropic fire regimes, as the widespread abundance of burned wood and charcoal across the South Island attests (Molloy et al. 1963). While some forest systems may have had some resilience to fire (at centennial frequencies), they were vulnerable in the face of the greatly elevated frequencies that accompanied human settlement (Perry et al. 2012b).

Prehistoric fire in New Zealand

Human settlement of New Zealand commenced around AD 1280 when the first Polynesians (Māori) arrived (Wilmshurst et al. 2008). At this time most of the country, other than areas above the alpine treeline, was cloaked with forest (Fig. 3a). The palaeoecological record describes widespread environmental changes coincident with human settlement, including increased

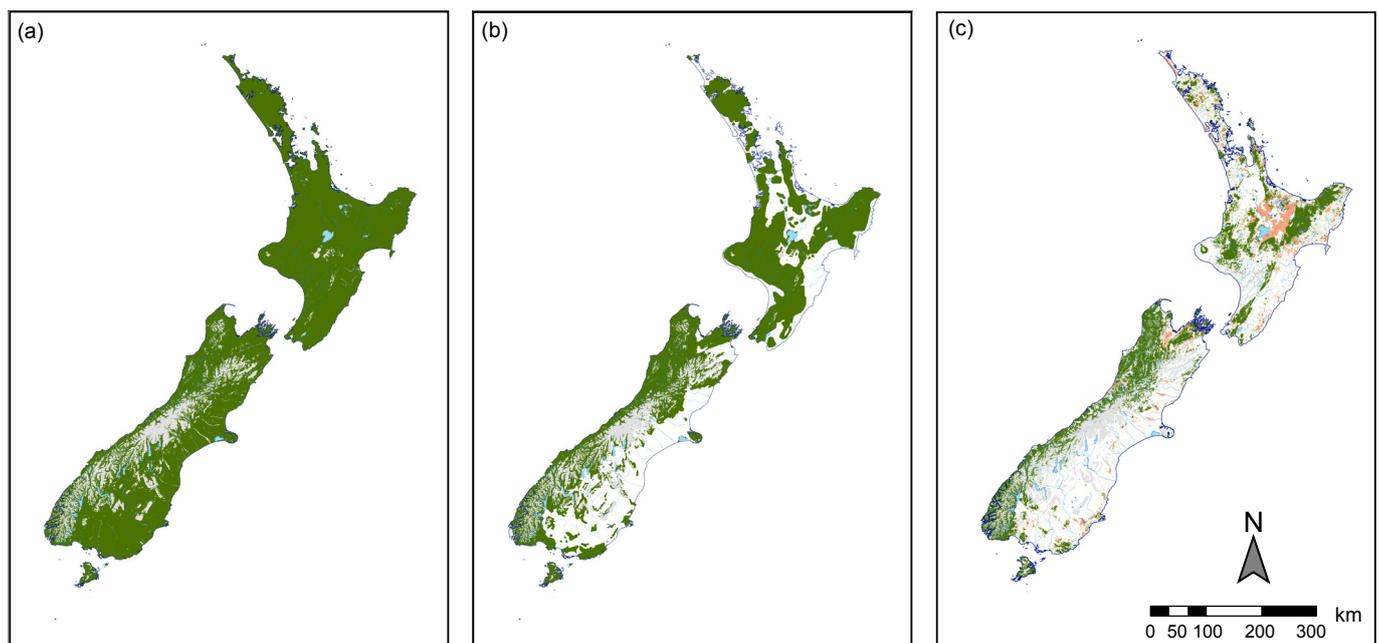


Figure 3. (a) Inferred forest cover (green) in New Zealand c. 3000 years BP; other than areas above treeline (light grey), New Zealand was covered in a range of forest types. (b) Forest cover in New Zealand at the end of the prehistoric period (c. AD 1840) based on maps in McGlone (1989). (c) Native (green) and exotic (orange) forest cover in contemporary New Zealand (data from LINZ 1:50 000 maps).

macro-charcoal in the sediment record, the widespread loss of tall forest and its replacement with seral vegetation and especially bracken (*Pteridium esculentum*), and a massive wave of extinctions in the vertebrate fauna, which is best documented in the avifauna (Worthy & Holdaway 2002). Recent high-resolution sediment-charcoal records from lakes in the South Island describe an 'initial burning period' (IBP) in which large areas (predominantly drier lowland forest) were burned rapidly (McWethy et al. 2009, 2010). In some of the drier eastern areas of the North Island, the duration of the IBP is estimated to have been less than 60 years (Wilmshurst 1997). This fire activity was not temporally synchronous across sites, but extensive dated pollen and charcoal records suggest deforestation was underway in the drier regions in the 13th century (Newnham et al. 1998), and later in wetter sites such as coastal Taranaki (Wilmshurst et al. 2004). The onset of deforestation does not appear to be related to broad-scale climatic shifts: rather, it marks the introduction of anthropic fire to New Zealand's ecosystems. McGlone (1983) argued that forest loss was limited or occurred later on sites where rainfall exceeds around 1600 mm year⁻¹, but increased as rainfall declines. Whether or not a given part of the landscape was burned during the prehistoric period is most strongly related to gradients relating to climate and topography rather than human activity or presence (Perry et al. 2012b). Lower, dry sites on gentle slopes were most vulnerable (especially in the South Island); in the North Island the presence of humans, as measured by proximity to bodies of freshwater (important food and transport resources), was also important in determining whether a site was burned, but not overwhelmingly so. These variables are also among the suite of best predictors of bracken spore abundance in Holocene sediment profiles (McGlone et al. 2005) and are similar to those identified by Rogers (1994) as important in explaining patterns of prehistoric fire in North Island tussocklands. Thus, at the time of human settlement, New Zealand's landscapes and ecosystems seem to have been conducive to widespread fire, but the occurrence of fire was apparently limited by the absence of an ignition source.

During the IBP it seems likely that more than 40% of the existing forest cover was burned (Fig. 3b), with nearly all

lowland and montane dry forest disappearing, and wetter upland forest (e.g. as dominated by *Fuscospora* and *Lophozonia*) less affected, but by virtue of landscape position rather than an inherent lack of sensitivity. As a result some montane and lowland dry podocarp–hardwood forest types have been all but extirpated (Molloy et al. 1963; McGlone 1989, 2001). Table 1 outlines important shifts in the fire regime at this time: fires not only became more frequent, but almost certainly became more spatially correlated (i.e. repeatedly burned the same parts of the landscape) and some vegetation types were affected much more than others. There is, however, a paradox in these patterns in that fire-driven forest loss appears most pronounced in places where human populations were small and resources apparently limited. This apparent decoupling of fire activity from human population density begs the question of why such forest loss might have occurred. Was it intentional? Or, given the inherent positive feedbacks in the system (between fire and vegetation), was such loss inevitable once fire was introduced to fire-vulnerable ecosystems – whether desired or not? Simulation modelling suggests that if humans targeted ignitions in the most flammable vegetation, perhaps also taking advantage of climatically favourable conditions, rapid and widespread forest loss was easily achieved (Perry et al. 2012a). The nature of the feedbacks between flammability and fire means that once sufficient forest was lost, a positive feedback may have become entrained where fire resulted in further fire (Fig. 2). The answer to the long-standing question of the motivation for the dramatic clearance of forest undertaken by Māori may be that there was none. Instead, widespread loss may have been inevitable once fire was introduced to such fire-sensitive and non-adapted ecosystems. Although Māori actively transformed the landscape (e.g. for horticulture and habitation), such widespread prehistoric forest loss was not necessarily simply a direct outcome of such activities.

Early European fire in New Zealand

The European period saw New Zealand experience a second wave of forest loss (Fig. 3c and Table 1), with fire being a primary tool for clearing forest, scrub and fernland for agricultural activities. Beaglehole (2012) estimates that 90%

Table 1. Contrasting (inferred) nature of the fire regime in prehuman New Zealand (i.e. before AD 1280), the initial burning period (IBP) that followed Polynesian settlement (AD 1280), and the European era (1840 onwards).

	Prehuman Holocene fires	IBP fires (c. 750 years BP)	European fires (c. 1840 onwards)
Dating	Timing of larger events under-studied	Events well-dated	Events well-dated
Fire frequency	Under-studied; relatively low	High	High, but declining since mid-20th century
Outcome	Small-scale, short-term disturbance with no major shifts in forest composition	Rapid and large-scale loss of forest, increase in charcoal and bracken. Massive changes in sedimentation regimes	Large-scale loss of forest including areas previously unburned and areas burned during the IBP. Increased sedimentation including remobilisation of sediments first moved in the IBP
Post-fire dynamic	Rapid regeneration (150–200 years)	Forest regeneration rare	Forest regeneration rare
Spatial pattern	Fires equally common in conifer and angiosperm forests, similar impacts	Dry lowland conifer forests more vulnerable than wetter angiosperm-dominated forests	<i>Agathis</i> forest, drier <i>Fuscospora</i> and <i>Lophozonia</i> forests and successional shrubland vulnerable. Wet angiosperm-dominated forests survived

of this forest loss occurred during the early European period, reckoning that some 3.3 million hectares of forest were burned in the period 1830–1873. However, despite interest from social and environmental historians there has been surprisingly little ecological research focused on this phase of New Zealand's fire history. In some areas (e.g. the South Island high country) fire was used to clear land for 'exploitative pastoralism'; much of this burning may have occurred in systems recovering from previous Māori fires and so probably transformed previously burned scrubland, rather than forest, to grassland (O'Connor 1982, 1984). However, Europeans also burned large areas of previously intact forest, such as the kauri (*Agathis australis*) forests of the far north of the North Island (Ogden et al. 1998) and the forests of Banks Peninsula (Wood & Pawson 2008), and remobilised sediments first moved during the early prehistoric period (Wilmshurst 1997; Ogden et al. 2006). Fires during the early European period were sometimes huge, persisting over days if not weeks, and burned both young successional and older less disturbed forests (Wardle 2001). The Forest and Rural Fires Association of New Zealand (2012) lists particularly significant fire events occurring in the early European period. Guild and Dudfield (2010) describe fires in the Wairarapa burning more than 8000 ha of forest (and various infrastructure) in the summer of 1897; in a similar vein McLean (1992) and Beaglehole (2012) describe significant fires in 1878 at Waimate, 1918 at Raetihi and 1946 near Taupo (under extremely dry conditions)², and both highlight that such events were often associated with drought conditions and railways, sawmilling and other forestry activities. Dick (1956) also notes the close association between years of high fire activity and low rainfall (at least for *Fuscospora-Lophozonia* forest in the eastern South Island). The year 1946 was particularly bad with drought conditions prevalent and more than 280 000 ha of vegetation burning of which 6600 ha was state forest (half of which was indigenous) with the remainder comprising privately owned exotic plantations, indigenous forest and regenerating scrub (Guild & Dudfield 2010; Beaglehole 2012).

By the 1930s foresters (e.g. Smith & Wastney 1935) were expressing concern about the threat posed to forest assets from the ongoing pastoral use of fire for secondary clearance and the associated accumulation of flammable fuels (bracken and scrub). Fires in indigenous forests and plantations were ecological and economic catastrophes. In early 1888 fires at Puhipuhi kauri forest (north of Whangarei, Northland), possibly started by gum-diggers, burned more than 2000 ha (equivalent to some 7.5×10^7 board ft [1.5×10^6 m³] of timber) with an estimated 2008 value of more than \$560 million (Thode 1983; Guild & Dudfield 2010). Fires continued after the initial burn during (unsuccessful) timber salvage (Hutchins 1919) and newspaper reports of the time comment on the fire risk posed by resin-soaked downed branches in the post-fire forest:

The ground is strewn thickly with masses of fallen branches, with here and there a prostrate stem, over which the eye wanders through vistas of magnificent columns in countless numbers, whose beautiful symmetry cannot but strike the most unobservant. It is in these fallen branches, saturated as they are with kauri resin, that the great danger lies of future fires. Should the forest ignite again the result will be that the trees themselves will burn.³

The legacy of these early losses persists both ecologically and economically. As Thode (1983, p. 223), in describing the loss of kauri forest in Northland in the mid- to late 19th century, laments:

What was originally a truly magnificent estate of one million hectares of the best softwoods in the world was virtually annihilated to generate a pastoral economy. Despite the importance of agriculture to Northland today, the poor soils and difficult conditions have not produced the rich pasture dreamed of at the time of original settlement. In fact, large areas have reverted to scrub and bush or become choked with noxious weeds and are not contributing anything to the region's economy.

Current and future situation

Although fires such as that at Puhipuhi provoked some policy response, it was not until the mid-20th century that real emphasis began to be placed on reducing the occurrence and use of fire in New Zealand's landscapes. As early as 1940 the Department of Land and Surveys saw 'burning, especially of winter country, as dangerous' (Moore 1976, p. 17), and there was growing concern from the soil conservation boards about the practice of burning-off (McIntyre 2008). Legislation was enacted through the 1940s and 1950s (the Forest and Rural Fires Acts of 1947 and 1956) and proved reasonably effective in reducing the use of fire in rural landscapes (Guild & Dudfield 2010; Beaglehole 2012).

Current levels of burning are lower than they were during the first part of the 20th century. From 1991/92 to 2006/07, the number of rural wildfires (i.e. excluding prescribed burn-offs) increased from 1200 to a little over 4000 events per year, but the amount of burned area remained relatively constant (Anderson et al. 2008). These figures are comparable with those reported by Beaglehole (2012) for the period 1940–1945 of 5800 ha per year across a range of forest types and by Cooper (in Guild & Dudfield 2010) for the 1970s (280 fires per year burning c. 4100 ha; average fire size of 14.6 ha). There are currently relatively few fires in forests (6%), with more than 90% occurring in scrub or grass fuel beds; fires in Otago accounted for more than 40% of the national burned area over the period 1991/92 to 2006/07 (Anderson et al. 2008). Lightning (natural ignition) is responsible for just 0.1% of fire events and burned area, with escaped fires from land clearance being the most common source (20%) and responsible for most burned area (47%). On the conservation estate, Rogers et al. (2005) estimate around 2400 ha per year are burned with an average fire size around 14 ha (averages over period 1987–1998). The area burned in controlled burn-offs (around 60 000 ha per year) dwarfs that occurring in unplanned fire events (Guild & Dudfield 2010). The current focus in rural fire management is on fire prevention in plantation forests (Cooper & Ashley-Jones 1987; Pearce et al. 2008), with around \$8–\$10 million per year spent on fire protection in this setting (Cameron et al. 2007).

Just as fire regimes have changed in response to climate change in the past, they are likely to do so in the future. Estimating how specific fire regimes will respond to changing climates is difficult, but, in general, it is likely that any response will be rapid and substantial (Flannigan et al. 2009; Macias Fauria et al. 2011; Moritz et al. 2012). While altered fire activity may not be the most pressing climate-related concern faced by New Zealand's ecosystems (McGlone & Walker 2011), the drier and warmer conditions that much of the country may experience are likely to result in increased fire activity in the most fire-prone parts of the country, i.e. the eastern parts of

² Archival movie footage of these fires held by Archives New Zealand, Te Rua Mahara o te Kāwanatanga is available at: <http://www.youtube.com/watch?v=IIt00NZe1dc&feature=channel> (accessed 10 May 2013).

³ Northern Advocate 13 July 1889 – <http://paperspast.natlib.govt.nz>

both islands (Pearce et al. 2005). If pyrophyllic (fire-loving) exotic species are favoured by future climates then this too has the potential to affect future fire regimes.

To summarise, considerable effort has gone into reconstructing the nature of changes in New Zealand's ecosystems over the Holocene and earlier. We can now be certain that a relatively small number of people, perhaps fewer than 100 (Murray-McIntosh et al. 1998), settled New Zealand around 750 years ago, and that rapid and widespread forest loss followed immediately thereafter. Fire was the primary agent of this transformation. The European period has received rather less ecological attention but the patterns of forest loss and vegetation change are clear. Surprisingly, however, we know relatively little about the ecological responses to the rescaling of the fire regime and the resilience, or otherwise, of the remaining indigenous vegetation to fire. These issues are the subject of the remainder of this review.

A fire ecology of New Zealand's ecosystems

Fire-adaptation in the New Zealand flora

Plants show a range of adaptations to fire, including serotiny (the storage of seeds in a seedbank and their release post-fire), post-fire resprouting, heat and smoke-triggered germination, thick bark, seed adaptations (e.g. hard-seededness) and traits elevating flammability (Midgley & Bond 2013). In ecosystems where disturbance by fire is recurrent a fundamental response axis is how species regenerate post-fire. In such systems, species can be broadly described either as fire-killed obligate seeders or as fire-surviving resprouters (Lamont et al. 1991; Whelan 1995; Bond & van Wilgen 1996; Clarke et al. 2013). Obligate seeders store seeds between fires (e.g. in aerial and soil seedbanks) and release them immediately post-fire; resprouters, on the other hand, survive fire via, for example, underground lignotubers, and thus, despite low levels of sexual reproduction, persist from fire to fire.

A challenging issue in making inferences about the adaptive response of species to fire is in teasing apart adaptations (in the strict sense) from exaptations (i.e. adaptations to some other selective pressure that have been co-opted for another purpose; Gould & Vrba 1982). While some traits such as

serotiny and the retention of dead leaves (which elevates flammability) seem to be direct adaptations to fire (Midgley & Bond 2013), others such as resprouting and the possession of volatile leaf chemicals may be exaptations – resprouting has a range of benefits and occurs as a response to disturbances other than fire (Clarke et al. 2013) and volatile leaf chemicals such as terpenoids also act as anti-herbivore defences (Paré & Tumlinson 1999).

Given the long-term nature of the fire regime in New Zealand (long and unpredictable return intervals; Table 1) it is not surprising that very few of its indigenous plant species show clear adaptations to fire (Table 2 and Fig. 4). The main adaptations in the indigenous flora relate to post-fire resprouting (see Burrows 1994) although this is a more general disturbance response; some species may show fire-triggered reproductive responses (e.g. *Chionochloa rigida* narrow-leaved snow tussock, *Leptospermum scoparium* mānuka), but classic seedbank strategies (long-lived and hard seeds) are almost non-existent (Rowarth et al. 2007), as is serotiny other than in mānuka (Burrell 1965; Bond et al. 2004). Some unusual traits in the New Zealand flora, e.g. a high incidence of leaf-shedding in some grass groups, may be a response to the *absence* of ecologically significant fire in prehuman New Zealand (McGlone et al. 2014). There is, nevertheless, a group of species that has been more favoured by fire than others, and some species are more flammable than others, but neither of those should be taken as evidence of fire-adaptation *sensu stricto*. We can divide New Zealand's flora into three broad classes based on their response to fire: (1) fire-adapted species, (2) long-lived fire-tolerant species, and (3) long-lived fire-susceptible species (Table 2).

Those indigenous species that are fire-adapted tend to be of Australian origin and are fast growing; they include *Leptospermum scoparium* (mānuka; Myrtaceae), *Kunzea ericoides* (kānuka; Myrtaceae), *Pteridium esculentum* (bracken; Dennstaedtiaceae) and *Discaria toumatou* (matagouri; Rhamnaceae). The fire ecology of mānuka is considered further below and McGlone et al. (2005) review how bracken has been favoured by fire since human settlement. Some other groups show weaker fire-adaptation (or exaptation),

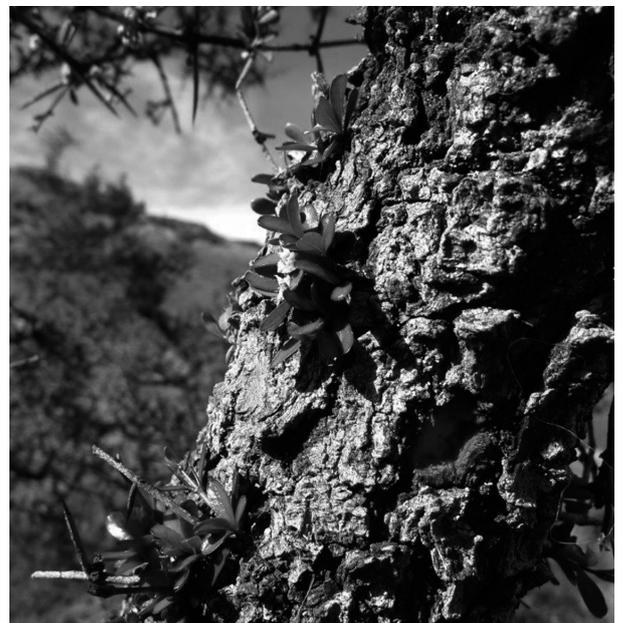


Figure 4. Although the New Zealand flora shows few specific fire-adaptations (see Table 2) two species that do are (left) *Leptospermum scoparium* (mānuka) – in the form of serotiny (Bond et al. 2004) – and (right) *Discaria toumatou* (matagouri) – in the form of thick bark (here c. 22% of stem radius) and epicormic resprouting (Daly 1969). Image of mānuka is from the Denniston Plateau (West Coast, South Island) and matagouri from Kaituna Valley (Banks Peninsula; matagouri photo courtesy of Sarah Richardson).

Table 2. Traits of selected indicative species falling into each of the three fire-response classes (arranged by life-form as per the Landcare Ecological Traits of New Zealand Flora database: <http://ecotraits.landcareresearch.co.nz/>). Flammability classes as per Fogarty (2001) where available, with the number in brackets the rank from among the 42 species Fogarty assessed (higher rank indicates higher flammability). Resprouting includes above-ground (e.g. epicormic buds) and below-ground (e.g. rhizomes–corms) mechanisms (derived in part from Burrows 1994). Bark thickness values (1 = thin to 3 = thick) derived from 32 species measurements (made nationally) described in Lawes et al. (2014).

Species	Family	Life-form	Serotinous?	Resprouting?	Bark thickness	Flammability
1. Fire-adapted						
<i>Kunzea ericoides</i> (kānuka)	Myrtaceae	Large tree	N	N	2	High (2)
<i>Leptospermum scoparium</i> (mānuka)	Myrtaceae	Small tree	Y	N	2	High (1)
<i>Discaria toumatou</i> (matagouri)	Rhamnaceae	Tall shrub	N	Y	3	High ¹
<i>Pteridium esculentum</i> (bracken)	Dennstaedtiaceae	Fern ²	N	Y		High
<i>Cordyline</i> spp. (cabbage trees)	Asparagaceae	Monocot trees	N	Y		High
2. Fire-tolerant and/or favoured						
<i>Weinmannia racemosa</i> (kāmahī)	Cunoniaceae	Large tree	N	Y	1	Low / moderate (17)
<i>Aristotelia serrata</i> (makomako; wineberry)	Elaeocarpaceae	Medium tree	N	Y	2	Low / moderate (26)
<i>Fuchsia excorticata</i> (kōtukutuku)	Onagraceae	Medium tree	N	Y	1	Low (39)
<i>Meliccytus ramiflorus</i> (māhoe)	Violaceae	Medium tree	N	Y	2	Low / moderate (27)
<i>Pittosporum tenuifolium</i> / <i>colensoi</i> (kōhūhū)	Pittosporaceae	Medium tree	N	Y	1	Moderate (13)
<i>Ozothamnus leptophylla</i> (tauhinu)	Compositae	Tall shrub	N	Y		Moderate
<i>Dracophyllum</i> spp.	Ericaceae	Shrubs - trees	N	N		High
<i>Gleichenia dicarpa</i> (tangle fern)	Gleicheniaceae	Fern	N	Y		High
<i>Histopteris incisa</i> (mātātā; water fern)	Pteridaceae	Fern	N	Y		Low / moderate
<i>Baumea teretifolia</i> / <i>rubiginosa</i>	Cyperaceae	Junciform perennials	N	Y		Low / moderate
<i>Schoenus brevifolius</i>	Cyperaceae	Junciform perennials	N	Y		Low / moderate
<i>Chionochloa</i> spp.	Poaceae	Graminiform-tufted grass	N	Y		High
3. Fire-sensitive						
<i>Agathis australis</i> (kauri)	Araucariaceae	Large tree	N	Y	3	Moderate (11)
<i>Beilschmiedia</i> spp. (tawa, taraire)	Lauraceae	Large trees	N	Y	1	Moderate (8) ³
<i>Dacrycarpus dacrydioides</i> (kahikatea)	Podocarpaceae	Large tree	N	N	1	Moderate (13)
<i>Dacrydium cupressinum</i> (rimu)	Podocarpaceae	Large tree	N	N	3	Moderate (12)
<i>Halocarpus</i> spp.	Podocarpaceae	Large trees	N	N	3	Moderate
<i>Fuscospora</i> spp. and <i>Lophozonia</i> (southern beeches)	Nothofagaceae	Large tree	N	N	2	Moderate (19) ⁴
<i>Podocarpus totara</i> (tōtara)	Podocarpaceae	Large tree	N	N	3	Moderate / high (6)
<i>Phyllocladus</i> spp.	Podocarpaceae	Large trees	N	N	3	Low / moderate (17) ⁵
<i>Prumnopitys taxifolia</i> (mataī)	Podocarpaceae	Large tree	N	N	2	Moderate

¹Nitrogen fixer. ²In many contexts bracken is functionally a shrub. ³Based on *Beilschmiedia tawa* (tawa). ⁴Based on *Lophozonia menziesii* (silver beech). ⁵Based on *Phyllocladus glaucus* (toatoa).

including the Styphelieae shrubs (*Acrothamnus*, *Leptecophylla*, *Leucopogon*), *Coriaria* (Coriariaceae), *Dracophyllum* spp. (Ericaceae), *Veronica* spp. (Plantaginaceae), some of which release seeds post-fire, and *Ozothamnus* (Asteraceae). Some non-woody species display fire-adaptations (e.g. the tree fern *Dicksonia squarrosa*; ferns *Paesia*, *Histopteris*, *Gleichenia*, the monocots *Phormium*, *Cordyline*) and some members of the Liliaceae, Orchidaceae and Gentianaceae show post-fire resprouting from underground rhizomes or bulbs/corms that are protected during fire (ferns, lilies and orchids), or a deep tap-root (*Cordyline*). Of the graminoids, some sedges show post-fire resprouting via underground rhizomes (e.g. *Baumea teretifolia*, *B. rubiginosa* and *Schoenus brevifolius*) and some members of the *Chionochloa* also demonstrate positive (short-term) growth, productivity and regeneration responses to burning (Mark 1965, 1994).

Of all of New Zealand's indigenous tree species, mānuka shows the strongest and clearest fire-adaptations. The bipartite *Leptospermum* group is Australian in origin and appeared in the early Miocene. *Leptospermum scoparium* is in the group of

Leptospermum characterised by retained woody-valved fruit, and Thompson (1989, p. 335) argues that its non-primitive nature suggests that it is a 'relatively recent' import to New Zealand. Mānuka shows considerable ecotypic variation across its range in New Zealand and in south-east Australia and Tasmania where it also occurs (Ronghua et al. 1984; Thompson 1989). The New Zealand ecotypes are quite different from those found in Australia where post-fire resprouting and serotiny are common (Bond et al. 2004). In some places in New Zealand mānuka forms an important component of post-fire successions (e.g. Mirams 1957; Burrell 1965; Esler 1967; Atkinson 2004; Perry et al. 2010) and on low fertility sites, such as the northern gumland heathlands (Clarkson et al. 2011) or pakihī⁴ bogs (Williams et al. 1990), it can dominate communities over long periods. Mānuka's small, wind-dispersed seeds enable it to rapidly colonise early-successional sites such as recent burns (Burrell 1965; Grant 1967), with Burrell (1965) noting that

⁴Wetland areas, without forest, usually on low-fertility soils, and sometimes used to describe the northern gumland heathlands (Mew 1983).

mānuka seed is resistant, if not responsive, to moderate heat shock. Mānuka is the only one of New Zealand's indigenous species to show serotiny, with massive seed release occurring after fire; Ogden (1985) estimates canopy seedbanks of up to 3.0×10^5 seeds m^{-2} . The strength of serotiny varies between mānuka populations, however, with some populations releasing seed within a year (i.e. are non-serotinous) and others holding it for much longer periods. Mohan et al. (1984) found that capsule age had no effect on germination success. Harris (2002) describes a north–south gradient in serotiny based on growth trials conducted on seeds sourced from 61 mānuka populations across the North and South Islands. Bond et al. (2004) and Johnson (2005), on the basis of in situ assessments limited to the South Island, describe a bimodal distribution of serotiny both at the individual (i.e. plants have either few or most capsules closed) and the population (i.e. either few or most plants in a population have closed capsules) levels, with landscape position an important predictor (as a proxy for fire activity) of the strength of serotiny.

The vast majority of New Zealand's seral species are, however, disturbance-adapted but fire-susceptible and are relatively slow-growing; taxa in this category could be considered 'long-lived tolerators' and include *Pittosporum*, *Knightia*, *Aristotelia*, *Fuchsia*, *Myrsine*, *Hedycarya*, *Melicytus* among others. Many of these taxa show vegetative resprouting (Burrows 1994) but this cannot be interpreted primarily as a response to fire as it also occurs in response to other disturbances such as wind-damage (see Martin & Ogden 2006). Some taxa in this category (e.g. *Dracophyllum*) are highly flammable and have no doubt been favoured by fire, especially where they are able to disperse and colonise new sites rapidly, but again it is important not to interpret this as a fire-adaptation.

Finally there are a group of long-lived taxa that are highly susceptible to fire, including *Halocarpus* spp., *Phyllocladus* spp., *Podocarpus* spp., *Prumnopitys* spp., *Agathis* (despite having relatively thick bark and sprouting abilities), *Beilschmiedia* spp., *Fuscospora* spp. and other angiosperms.

Post-fire successional dynamics

Forests:—Post-fire successions have been described for *Nothofagus*-dominated forest (Allen 1988; McQueen 1991; Wiser et al. 1997), kauri forest (Mirams 1957; Ogden et al. 2003) and for mixed-hardwood and podocarp–hardwood forest (McKelvey 1955; Esler 1967; Payton et al. 1984). A post-fire succession that was initiated in the 19th century in subalpine *Libocedrus bidwillii* (kaikawaka) forest near Arthur's Pass is the longest longitudinal study of fire in New Zealand (Cockayne 1898; Cockayne & Calder 1932; Calder & Wardle 1969; Haase 1986). While these sequences differ in their details they typically start with mānuka or kānuka 'scrub' (often with bracken or *Gleichenia*), which is sequentially invaded by later-successional species loosely following a trend of small wind-dispersed → small bird-dispersed → large(r) bird-dispersed species (Bray et al. 1999; Atkinson 2004). Similar trajectories are seen in pollen records describing post-fire successions, both natural and human (Wilmschurst & McGlone 1996; Wilmschurst et al. 1997, 2014). In many modern settings these successional pathways are slowed and diverted by exotic mammalian herbivores (e.g. red deer) and seed predators (e.g. rats and mice).

Secondary successions following fire have also resulted in 'novel' or 'ragamuffin' ecosystems (Hobbs et al. 2006; Marris 2009) in which native (often fire-sensitive) and exotic (often fire-tolerant and demanding) species sit alongside each

other (Cockayne & Calder 1932; Druce 1957; Williams 1983; Partridge 1992). For example, Perry et al. (2010) describe the invasion of recurrently burned and now highly eroded slopes on Great Barrier Island (Aotea) by *Hakea* spp., *Erica* spp. and *Pinus* spp. – all fire-adapted and highly flammable taxa. Invasion by pyrophylllic species, coupled with slowed, and possibly dispersal-limited, succession on slopes denuded of topsoils, potentially amplifies the fire-begets-fire cycle described earlier (Figs 2 and 5). Although they carry an inherently higher fire risk, Sullivan et al. (2007) and Williams (2011) note that until recently some exotic pyrophylllic species such as *Ulex europaeus* (gorse) have been seen as (almost) desirable in early-successional communities as they may act as nurse crops and facilitate the entry of native species. Recent studies, however, suggest that there are important differences in succession through mānuka as opposed to gorse, with species richness lower under gorse and little evidence for long-term convergence of successional pathways (Sullivan et al. 2007). In other settings gorse may inhibit succession; Wilson (1994), for example, describes a failure of *Fuscospora fusca* to reinstate through gorse after fire on Banks Peninsula (see also Williams 2011). While in terms of its successional effects gorse is the most studied invasive species, there is no reason that other exotic species would not stall or divert succession in a similar way. For example, a number of studies have described the invasion of burn sites in formerly *Fuscospora* forest by exotic grasses, such as *Agrostis capillaris* (browntop), and the subsequent failure – even after fertilisation and oversowing of native species – of woody shrubs and *Nothofagus* to establish (Dick 1956; Wardle 1984; Wiser et al. 1997; Sessions & Kelly 2000; Ledgard & Davis 2004).

Wetlands and bogs:—Wetlands were foci for fire before the human settlement of New Zealand and so contemporary successions in such systems typically start from a fire-induced state. A number of studies have described post-fire vegetation change in wetlands (Timmins 1992; Clarkson 1997; McQueen & Forester 2000; Johnson 2001, 2005; Norton & de Lange 2003). A common theme in the recovery of wetlands from fire is the very rapid vegetative regeneration of some species (e.g. *Baumea* spp. and bracken) via rhizomes, followed by species, such as mānuka, that rely on seed to regenerate. Johnson (2005) found that 16 years after fire wetlands at Awarua (Southland) and Eweburn (Te Anau) had returned to approximately pre-fire conditions (see also Timmins 1992). Clarkson (1997) found that wetlands in the Waikato took 6–12 years to recover, and describes a general sequence of succession from eutrophic fens to oligotrophic bogs with an accompanying decline in species richness. Fire intensity and the height of the water table largely explain the rate of recovery in wetlands, with succession slowing with the depth of peat burn and associated mortality of underground plant components. As with forests, recurrent fire in wetlands provides opportunities for invasion by pyrophylllic species such as gorse, *Hakea* and *Acacia* (wattle) (McQueen & Forester 2000; Johnson 2001).

Grasslands and tussocklands:—The montane and subalpine grasslands and tussocklands are probably New Zealand's best understood ecosystems in terms of their fire ecology and response to repeated burning (Allen et al. 1996). In prehuman New Zealand grasslands were largely restricted to areas above treeline. Small areas of grassland below treeline in the North Island likely occurred as a function of edaphic and climatic conditions coupled with recurrent geomorphic disturbance

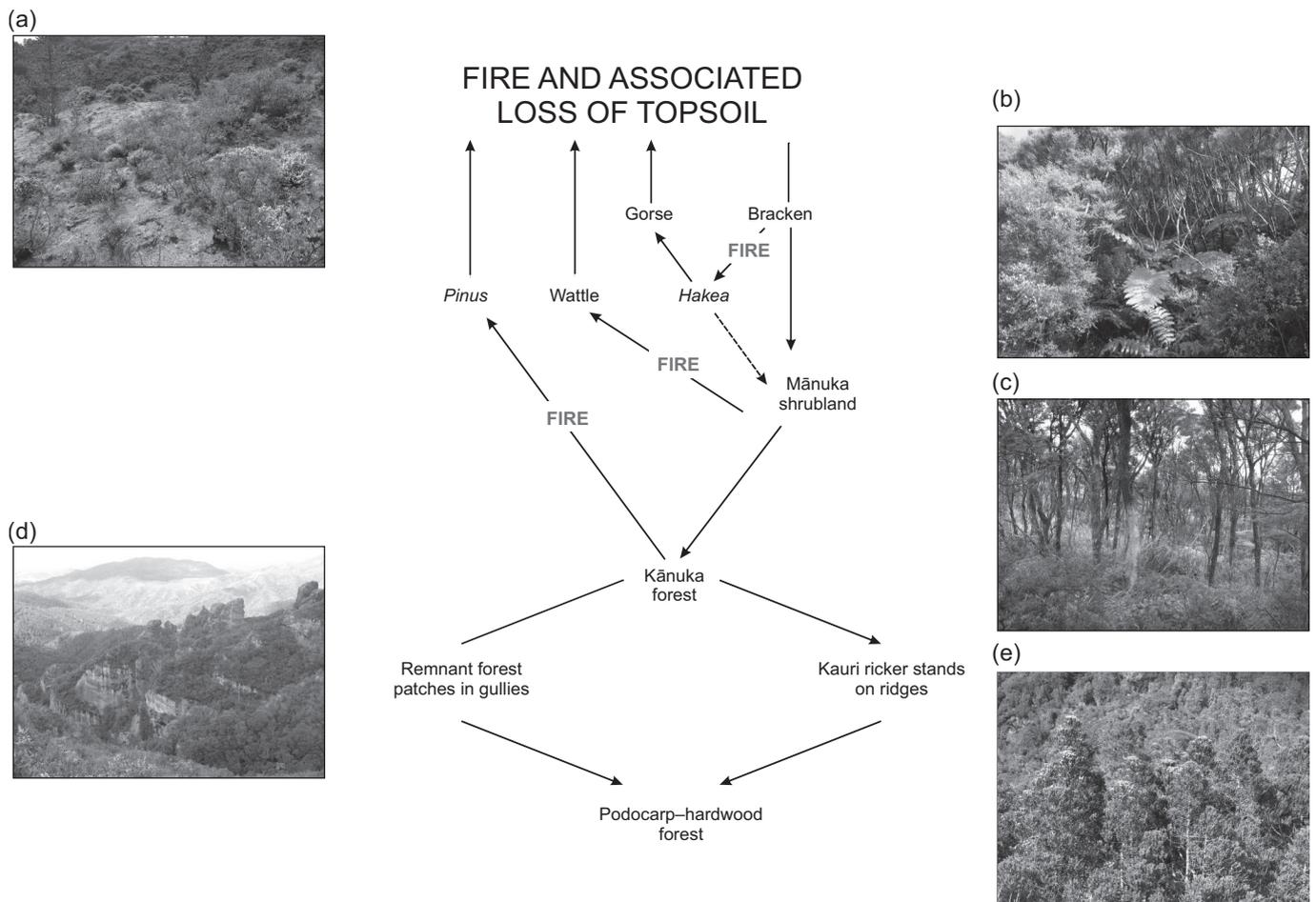


Figure 5. Post-fire successional pathways on Great Barrier Island (see GBICT 2010; Perry et al. 2010). After fire the system moves through bracken and mānuka scrubland (b) to kānuka forest (c) and eventually via various pathways (d and e) to podocarp–hardwood forest. Recurrent fires, however, slow this process by removing topsoil and so slow the growth of species such as mānuka and hence favour the invasion of invasive pyrophyllitic plant species (a), which promote fire so potentially entraining a positive feedback. Such dynamics occur over large spatial scales in much of lowlands New Zealand and are analogous to the ‘landscape traps’ described by Lindemayer et al. (2011). Photo (e) courtesy of John Ogden.

(Rogers 1994) and those in the South Island, rather than being pure grassland, formed part of a complex mosaic of grass, trees and shrubs (McGlone 2001). Since the arrival of humans in New Zealand there has been a considerable expansion of the extent of grasslands (Hobbs et al. (2006) use them as exemplar novel ecosystems), as is evidenced by the massive increase in the abundance of grass and herb pollen and charcoal, accompanied by a commensurate decline in the pollen of tree and shrub taxa. Māori fire resulted in considerable expansions of grasslands in both islands (Rogers 1994; McGlone 2001) and so too has the pastoral use of fire since European arrival (O’Connor 1984). There have not only been changes in the extent of grassland ecosystems but also in their composition (although disentangling fire and grazing is difficult), with *Chionochloa* spp. now forming a more important component than in prehuman times (McGlone 2001). While grasslands have been favoured by fire they are not resilient to recurrent burning in the face of grazing (Gitay et al. 1992). In one of very few experimental studies of fire in New Zealand’s ecosystems, Payton and Pearce (2009) burned *Chionochloa rigida* tussocklands at two sites to evaluate their response to different timings of fire. They found that the moisture conditions

at the time of fire are crucial in determining the vegetation response. Deliberate fire in tussockland usually occurs in spring when soil and biomass moisture levels are higher and tussock tillers may still be dormant. Experimental fires under high moisture (spring) as compared with low moisture (later summer) conditions resulted in much lower tiller loss, lower mortality levels, considerably reduced biomass and nutrient losses and minimised the effects on the tussock’s reproductive behaviour and regeneration. Payton and Pearce (2009) found no evidence of nutrient return to the soil following fire, suggesting that post-fire environments will not necessarily support enhanced plant growth.

The anthropic origin of much of New Zealand’s lowland and montane grassland poses difficult management and conservation questions (McGlone 2001; Mark & McLennan 2005). In the absence of repeated fire, areas of grassland will eventually return to their previously forested state. Calder et al. (1992) describe the invasion of *Chionochloa rigida* grassland by woody shrubs such as mānuka and note that in the absence of further disturbance (burning) the tussock will be overtopped and will decline in importance in around 30 years. Likewise, at the Gorge Hill Red (Copper) Tussock Conservation Area

the *Chionochloa rubra* ssp. *cuprea* tussocklands described by Grove et al. (2002) are steadily being invaded by *Olearia bullata* (Alan Mark, pers. comm. 13 May 2013). Rogers and Leathwick (1994) estimate that in the North Island similar invasion processes will take around 30–55 years depending on site conditions. In such situations prescribed burning provides one potential tool for holding the system in what is effectively an early-successional state, although it brings with it the risk of weed invasion and other deleterious effects (Rogers & Leathwick 1994).

Novel fire regimes: winners and losers

The rescaling of the fire regime that has occurred in New Zealand's ecosystems has resulted in winners and losers. In terms of indigenous species obvious winners are bracken, mānuka and kānuka, all of which are now abundant in many New Zealand landscapes. All three species are highly flammable (Fogarty 2001) and so their increased abundance renders modern landscapes more susceptible to large fire events. These, and other fire-adapted species such as *Discaria toumatou* (Daly 1969), are now widespread in areas where pollen and macrofossil evidence suggests that they were absent (or rare) before the onset of anthropic fire (Wood & Walker 2008). Likewise, many pollen records show raupō (*Typha orientalis*) to be a clear benefactor of anthropogenic fire in swamps and at lake margins (McGlone & Wilmshurst 1999a).

From an indigenous perspective the losers are those species associated with the dry and open forests (areas where rainfall is less than 1000 mm year⁻¹) that once occurred across much of lowland eastern New Zealand (McGlone 2001; Rogers et al. 2007). Mataī (*Prumnopitys taxifolia*) and tōtara (*Podocarpus totara*) were abundant as canopy dominants in these dry forests accompanied by angiosperm canopy trees *Hoheria angustifolia*, *Plagianthus regius*, *Elaeocarpus hookerianus*, and *Sophora microphylla*. In the semi-arid inland basins of the eastern South Island *Phyllocladus alpinus*, *Kunzea ericoides* and small-leaved shrubs formed low forest, probably in association with open grassland–shrubland on the most stressed sites (Wardle 2001). These dryland forests were among the first burned and only small and scattered remnants of them persist, having generally been replaced by fire-tolerant and fire-adapted taxa. Nevertheless, most of these dryland species are still relatively common as scattered stands although large patches of dryland forest are now rare. Rogers et al. (2005) estimate a post-settlement reduction in forest cover of drylands from 84.1% to just 1.1%, largely by fire. One of the most extreme examples of dryland species reduction is the near obliteration of mataī (*Prumnopitys taxifolia*) and *Phyllocladus alpinus*, which were abundant in inland eastern South Island palynological records up until the point of human settlement, and then all but disappeared after deforestation.

Globally, there is concern over the potential for invasive plant species to dramatically alter fire regimes by changing fire itself (e.g. via increased intensity due to higher fuel loads) and the post-fire environment (Brooks et al. 2004). Given that fire-adaptations are much more common in exotic plant species than in New Zealand's indigenous flora, exotic species are likely to be favoured over indigenous ones under New Zealand's rescaled fire regimes. For example, *Ulex*, *Hakea*, *Banksia*, *Pinus*, *Erica*, *Cytisus*, *Chrysanthemoides* – all classed 'environmental weeds' by Howell (2008) – are more strongly fire-adapted than any indigenous species other than possibly mānuka. These exotic taxa are all pyrophyllic and depend upon fire for their persistence in the landscape; Enright (1989), for

example, comments on the role of recurrent fire in the invasion of far northern heathlands by *Hakea gibbosa*. Within weeks of a fire in early 2013 on Great Barrier Island *Paraserianthes lophantha* (brush wattle) and *Phytolacca octandra* (inkweed) had germinated, and burned *Hakea sericea* trees had many freshly opened capsules (John Ogden, pers. comm. March 2013). Other invasive species show reproductive adaptations to fire; for example, gorse (which is hard-seeded) has a positive germination response to heating (McAlpine et al. 2009) and both it and broom (*Cytisus scoparius*) establish vigorously after fire (Partridge 1989). Most of the pyrophyllic exotic species noted above are relatively short-lived and tend to be reasonably rapidly replaced in the absence of fire. The fire-adapted exotic species that pose potentially the greatest threat to indigenous vegetation assemblages are long-lived, shade-tolerant, fire-promoting trees such as *Pinus* spp. and *Acacia* spp.

In some circumstances of repeated fire disturbance, dense stands of fire-dependent exotic species can become self-sustaining – possibly reflecting a stalling in succession in the absence of seed dispersal (Williams 2011); large stands of broom in inland Canterbury provide a possible example. Gorse, in particular, forms an 'alternative post-disturbance system' (Sullivan et al. 2007, p. 23) across broad swathes of New Zealand. Despite the (apparent) dependence of many exotic plant species on fire, or at least disturbance of some sort, to persist, Timmins and Williams (1991) did not find fire history to be a useful predictor of the number of invasive species in a series of reserves across New Zealand other than in the Gisborne region (although not all the reserves they consider may have harboured fire-adapted exotic species). In short, there seems little doubt that recurrent fire tends to favour many exotic plant species.

Favoured and novel vegetation assemblages

Changes in the fire regime have resulted in the expansion of ecosystem types such as grasslands (as described previously), and the northern gumlands (heathlands) and pakihi mires. Large areas (c. 300 000 ha) of northern New Zealand were covered with mānuka-dominated gumlands at the time of European settlement (Burrows et al. 1979). Esler and Rumball (1975, p. 434) describe the vegetation of the gumlands as basically comprising 'tea tree, wiwi rushes, and umbrella fern (*Gleichenia*)' and they are generally associated with low fertility soils (Burrows et al. 1979). While much of this area was once kauri forest, there is evidence (e.g. the persistence of *Leptospermum*-type pollen and charcoal in the sediment record) that heathlands in the far north occupied the landscape long before Polynesian arrival (Dodson et al. 1988; Bond et al. 2004). In a survey of gumland vegetation in northern New Zealand Clarkson et al. (2011) found a range of different vegetation types along a gradient from low (*Gleichenia* fernland) to high(er) fertility (mānuka shrubland) with various intermediate types in between, and noted a positive association between site fertility and fire frequency. Likewise, Jamieson (1989) found that drainage and time since fire were important predictors of vegetation composition in regenerating mānuka scrubland at Kawerua (Waipoua Forest). As Enright (1989) notes, the interesting ecological questions about these heathland communities surround their long-term persistence, which, in turn, requires separating human-induced from older formations. The (northern) heathland communities probably represent successional states which, given sufficient time, may return to forest and so their persistence requires recurrent disturbance (Enright 1989; Clarkson et al. 2011). Such systems are, on

the other hand, vulnerable to invasion by pyrophyllic exotics when burned, with such exotic species potentially altering secondary successional trajectories. Heathlands elsewhere in New Zealand are often maintained by fire, in combination with other disturbances such as frost. Smale et al. (2011) describe post-fire successions in frost-flat heathlands in the central North Island and found that within 25 years of fire the key species have re-established.

Pakihi are in some ways analogous to the northern gumlands (McGlone 2009). While some areas of pakihi are not the result of fire, having formed as a result of the infilling of low-lying bodies of water or due to failed succession to forest on low fertility sites (Burrows et al. 1979), others are almost certainly fire-induced (Williams et al. 1990). Although some pakihi may have experienced prehuman fire, Mew (1983) notes that since human settlement fire has played an important role in establishing and maintaining them. Irrespective of the source of such fires (although low rates of fire on the South Island West Coast strongly suggest anthropogenic origin), the boundaries between pakihi and surrounding forest are likely fire-mediated (Mark & Smith 1975). Nevertheless, in the absence of fire, pakihi appear to slowly succeed to forest (Wardle 1977), which means that if maintaining them in the

landscape is desired then prescribed fire may be necessary (Williams et al. 1990; Miller 1993).

Landscape-level fire dynamics in contemporary landscapes

Drawing on ideas surrounding alternate stable states (Beisner et al. 2003), Lindemayer et al. (2011) described the concept of ‘landscape traps’, i.e. conditions under which ecosystems are massively structurally and functionally altered and from which escape is difficult. Lindemayer et al. describe traps in *Eucalptyus regnans* (mountain ash) forest in south-eastern Australia where a positive feedback loop between increasing fire frequency and severity and landscape condition, triggered by logging activities and declining rainfall, has resulted in large-scale and difficult-to-reverse shifts in vegetation composition and structure. It could be argued that anthropic fire has caused large swathes of New Zealand, especially dry, lowland areas, to fall into a fire-induced landscape trap. As described earlier, New Zealand’s forests are characterised by a humpbacked, rather than increasing, relationship between flammability and vegetation age (Fig. 2). An important implication of this humpbacked relationship is that because the early-successional stages are vulnerable to fire, if ignitions occur a short-interval fire cycle may eventuate, carrying with it a fire-begets-fire

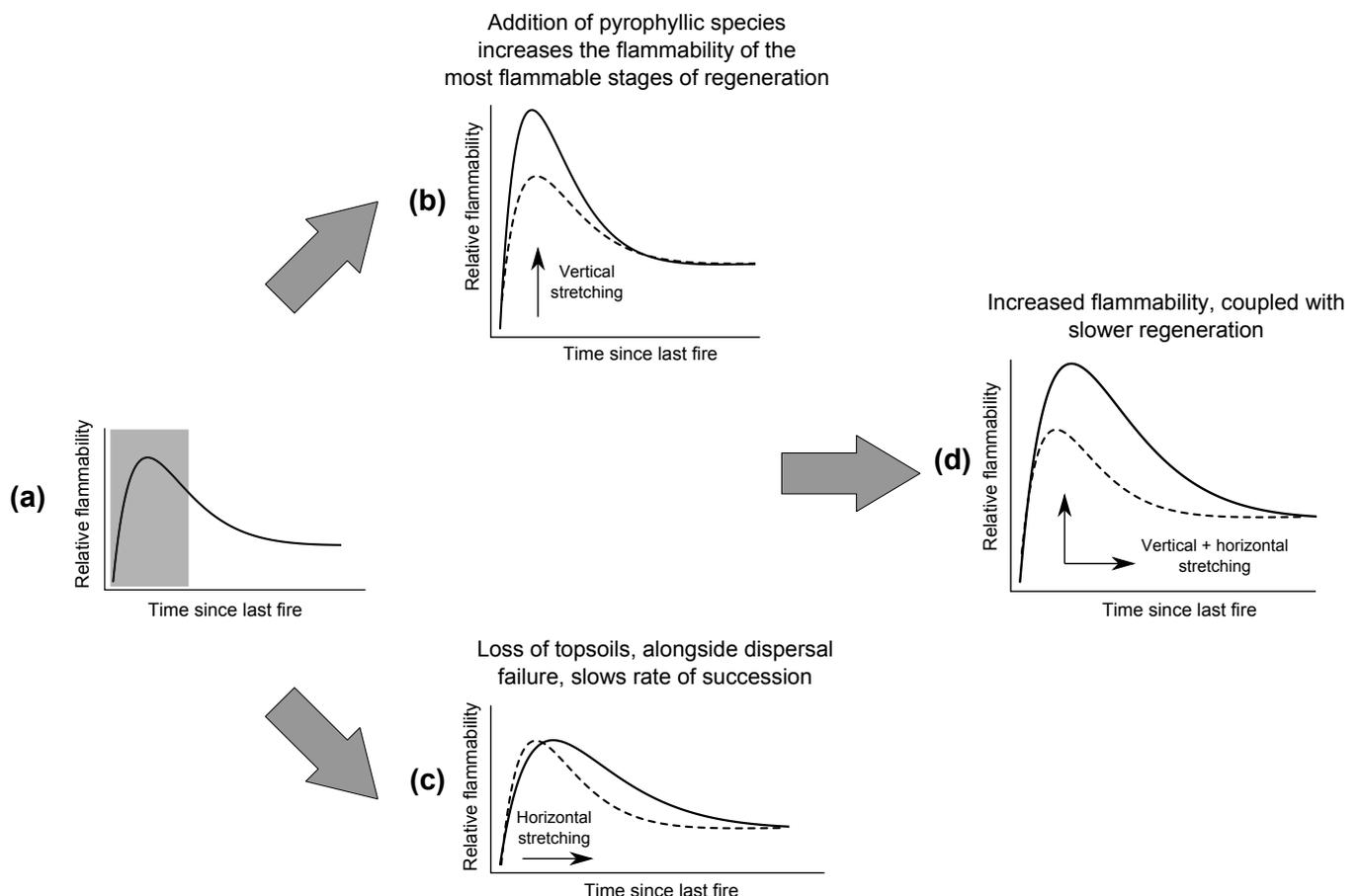


Figure 6. New Zealand ecosystems are characterised by a humpbacked relationship between flammability and time since fire, with ecosystem flammability peaking early in the succession (a). The addition of pyrophyllic, fire-promoting species has increased the absolute flammability of the most flammable parts of the successional sequence (b) and the loss of topsoils, coupled with dispersal and pollination failure (in part an indirect outcome of fire-driven habitat loss), has slowed the rate of succession (c). Combined, these two effects vertically and horizontally ‘stretch’ the humpbacked relationship between flammability and vegetation age (d). As a result succession is slowed and so longer is spent in more flammable early-successional states (shaded box in leftmost figure); navigating the system through these conditions is critical for restoration and conservation.

feedback. Although the humpbacked relationship is inherent in New Zealand’s forests, human actions have rescaled it. Processes that slow succession, such as the loss of soils and reduced dispersal and pollination services, mean that longer is spent in more flammable early-successional stages, stretching the flammability–age relationship on the time (horizontal) axis (Fig. 6). In some cases successions appear to have been stalled for long periods, with, for example, Esler (1963) describing a failure of regeneration following prehistoric fires in the late 1700s in the northern Tararua. Ragamuffin ecosystems, comprising early-successional native species (such as *Leptospermum scoparium* and *Kunzea ericoides*), alongside pyrophyllic exotic species (such as *Ulex europaeus*, *Pinus* spp. and *Hakea* spp.) are now common across much of northern New Zealand (e.g. Perry et al. 2010) and are probably much more flammable than uninvaded communities. The presence of these exotic species stretches the curve on the flammability (vertical) axis. As Druce (1957) recognised nearly 60 years ago, this rescaling of disturbance regimes has significant implications for forest regeneration and efforts to restore areas that were once forested.

Whether ragamuffin communities are quasi-stable or whether they will inevitably move towards either high-flammability exotic-dominated communities or lower flammability native forest is unclear. Many of New Zealand’s regenerating forest ecosystems may sit near a tipping point (Fig. 7a) with small shifts in fire frequency potentially triggering dramatic changes in community composition, structure and function. In effect the two endpoints represent alternative stable states (sensu Beisner et al. 2003) that, once occupied, are difficult to escape from. The long-term trajectories are, however, quite clear. Under (continued) elevated fire frequencies many regenerating systems will remain as early-successional shrubland, increasingly vulnerable to invasion by pyrophyllic exotic species and potential changes in soils. On the other hand, if fire frequencies fall then a return to closed forest may (slowly) eventuate. By holding the system in the vulnerable state for longer, high levels of seed and seedling predation (e.g. by rodents) and/or mammalian browsing will likely act to shift the critical fire frequency at which landscapes tip from one state to the other. If succession is slowed then lower fire frequencies are required to tip the landscape towards fire-induced ‘traps’. In other words, herbivore and predator control may potentially help to reduce long-term fire risk as it will act to speed succession. Forest systems that have been

subjected to elevated fire frequencies may exhibit hysteresis effects where the timescales over which recovery occurs and the effort (external subsidies) required to effect such a recovery may be much greater than those needed to initially ‘degrade’ them (Fig. 7b). The positive feedback dynamics described in Figs 2 and 6 suggest that if early-successional communities are subjected to fire then they will remain in that state in perpetuity with succession occurring at an ever slower rate. The counterpoint to this is that once closed forest begins to regenerate, and so the system moves over the hump of the flammability–age curve, then it may become increasingly resilient to fire. To conclude, it seems unlikely that fire-sensitive and fire-dependent species can stably coexist alongside each other but this question requires more focused attention.

Future challenges and unresolved questions

New Zealand’s fire-prone, but not fire-adapted, vegetation provides opportunities to explore the reorganisation of entire landscapes in the face of a novel disturbance regime. The ecological transformation wrought by the introduction of fire to New Zealand’s landscapes has brought with it important conservation and restoration challenges such as those surrounding the long-term dynamics of novel ragamuffin communities containing fire-persistent exotic and fire-sensitive indigenous species. Given the possibility that future climate change may render some landscapes more fire-prone, and the threats posed to biodiversity by pyrophyllic exotic species, understanding the longer-term dynamics of these mixed-composition ecosystems is important. At least in the first instance the control of potentially undesirable fire-favoured weed species depends on the adequate control of fire, although the effects of introduced mammalian species on regeneration via seed and seedling predation is a complicating factor. On the other hand, the persistence of some valued communities such as tussocklands, pakihi, and gumlands is dependent on fire and so may require carefully considered prescribed burning. Understanding the place of fire in New Zealand ecosystems requires a long-term view that recognises the legacies of both natural and anthropogenic fires. We now have a thorough description of changes in fire activity over the last 1000 years but the mechanisms underpinning those changes and their implications for modern landscapes and ecosystems remain less clear. Nevertheless the imaginative fusion of empirical and model-based studies with the many palaeoenvironmental records available promises to get us closer to the understanding

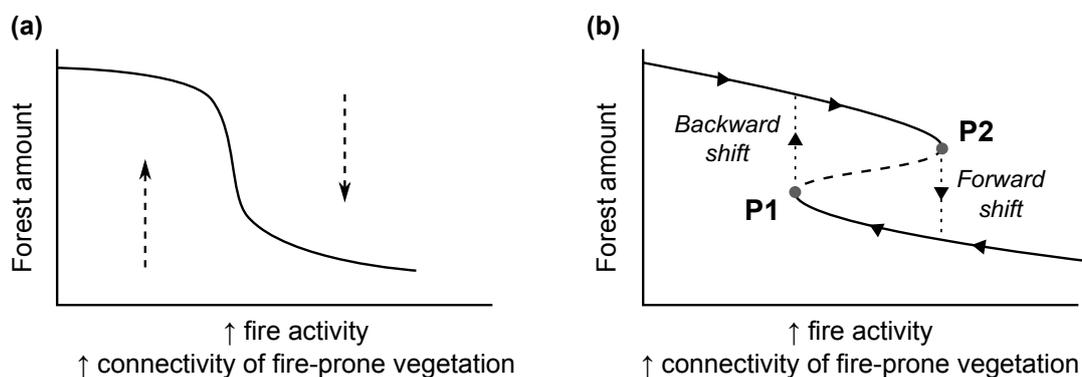


Figure 7. Small increases in fire activity may push ecosystems across tipping points inevitably triggering rapid forest loss (a); systems with tipping points (P1 and P2) show complex dynamics such as hysteresis effects where returning systems to previous states (‘backward shifts’) after change (‘forward shifts’) is difficult, here exacerbating forest loss (b). Figure adapted from Scheffer et al. (2001) with permission of Macmillan.

of the place of fire in New Zealand's ecological systems called for by Cockayne and Calder (1932) and McKelvey (1963).

Acknowledgments

This research was supported by Core funding for Crown Research Institutes from the New Zealand Ministry of Business, Innovation and Employment's Science and Innovation Group. We thank the editor and two anonymous referees for their helpful comments that improved an earlier draft of this manuscript. Thanks to Sarah Richardson for providing information and data on bark thickness. Timothy Thrippleton prepared Fig. 7.

References

- Allen RB 1988. A forest succession in the Catlins Ecological Region, south-east Otago, New Zealand. *New Zealand Journal of Ecology* 11: 21–29.
- Allen RB, Basher LR, Comrie J 1996. The use of fire for conservation management in New Zealand. *Science for Conservation* 23. Wellington, Department of Conservation.
- Anderson SAJ, Doherty JJ, Pearce HG 2008. Wildfires in New Zealand from 1991 to 2007. *New Zealand Journal of Forestry* 53(3): 19–22.
- Atkinson IAE 2004. Successional processes induced by fires on the northern offshore islands of New Zealand. *New Zealand Journal of Ecology* 28: 181–193.
- Beaglehole H 2012. *Fire in the hills: a history of rural fire-fighting in New Zealand*. Christchurch, Canterbury University Press. 343 p.
- Beisner BE, Haydon DT, Cuddington K 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1: 376–382.
- Bond WJ, van Wilgen BW 1996. *Fire and plants*. London, Chapman and Hall. 263 p.
- Bond WJ, Dickinson KJM, Mark AF 2004. What limits the spread of fire-dependent vegetation? Evidence from geographic variation of serotiny in a New Zealand shrub. *Global Ecology and Biogeography* 13: 115–127.
- Bowman DMJS, Haberle SG 2010. Paradise burnt: How colonizing humans transform landscapes with fire. *Proceedings of the National Academy of Sciences (USA)* 107: 21234–21235.
- Bowman DMJS, Balch J, Artaxo P, Bond WJ, Cochrane MA, D'Antonio CM, DeFries R, Johnston FH, Keeley JE, Krawchuk MA, Kull CA, Mack M, Moritz MA, Pyne S, Roos CI, Scott AC, Sodhi NS, Swetnam TW 2011. The human dimension of fire regimes on Earth. *Journal of Biogeography* 38: 2223–2236.
- Bray JR, Burke WD, Struik GJ 1999. Propagule dispersal and forest regeneration in *Leptospermum scoparium* (manuka) - *L. ericoides* (kanuka) forests following fire in Golden Bay, New Zealand. *New Zealand Natural Sciences* 24: 35–52.
- Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, Ditomaso JM, Hobbs RJ, Pellant M, Pyke D 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54: 677–688.
- Burrell J 1965. Ecology of *Leptospermum* in Otago. *New Zealand Journal of Botany* 3: 3–16.
- Burrows C 1994. Do New Zealand forest trees regenerate from sprouts? *Canterbury Botanical Society Journal* 28: 63–68.
- Burrows CJ 1996. Radiocarbon dates for Holocene fires, and associated events, Canterbury, New Zealand. *New Zealand Journal of Botany* 34: 111–121.
- Burrows CJ, McQueen DR, Esler AE, Wardle P 1979. New Zealand heathlands. In: Specht RL ed. *Ecosystems of the World 9A. Heathlands and related shrublands*. Amsterdam, Elsevier Science. Pp. 339–364.
- Burrows CJ, Randall P, Moar NT, Butterfield BG 1993. Aranaian vegetation history of the Arrowsmith Range, Canterbury, New Zealand III. Vegetation changes in the Cameron, upper South Ashburton, and Paddle Hill Creek catchments. *New Zealand Journal of Botany* 31: 147–174.
- Bussell MR 1990. Palynology of oxygen isotope stage 6 and substage 5e from the cover beds of a marine terrace, Taranaki, New Zealand. *Quaternary Research* 34: 86–100.
- Butler BW, Dickinson MB 2010. Tree injury and mortality in fires: developing process-based models. *Fire Ecology* 6: 55–79.
- Calder JA, Wilson JB, Mark AF, Ward G 1992. Fire, succession and reserve management in a New Zealand snow tussock grassland. *Biological Conservation* 62: 35–45.
- Calder JW, Wardle P 1969. Succession in subalpine vegetation at Arthur's Pass, New Zealand. *Proceedings of the New Zealand Ecological Society* 16: 36–47.
- Cameron G, Dudfield M, Pearce G 2007. Fire management in commercial plantations: a New Zealand perspective. In: *Proceedings of the 4th International Wildland Fire Conference*. Seville, Spain. 12 p. [On CD-ROM.]
- Campbell D, Williamson J 1997. Evaporation from a raised peat bog. *Journal of Hydrology* 193: 142–160.
- Certini G 2005. Effects of fire on properties of forest soils: a review. *Oecologia* 143: 1–10.
- Christian HJ, Blakeslee RJ, Boccippio DJ, Boeck WL, Buechler DE, Driscoll KT, Goodman SJ, Hall JM, Koshak WJ, Mach DM, Stewart MF 2003. Global frequency and distribution of lightning as observed from space by the Optical Transient Detector. *Journal of Geophysical Research* 108: 4005.
- Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197: 19–35.
- Clarkson BR 1997. Vegetation recovery following fire in two Waikato peatlands at Whangamarino and Moanatuatua, New Zealand. *New Zealand Journal of Botany* 35: 167–179.
- Clarkson BR, Smale MC, Williams PA, Wisser SK, Buxton RP 2011. Drainage, soil fertility and fire frequency determine composition and structure of gumland heaths in northern New Zealand. *New Zealand Journal of Ecology* 35: 96–113.
- Cockayne L 1898. On the burning and reproduction of subalpine scrub and its associated plants; with special reference to Arthur's Pass district. *Transactions of the Royal Society of New Zealand* 31: 398–419.
- Cockayne L, Calder JW 1932. The present vegetation of Arthur's Pass (New Zealand) as compared with that of thirty-four years ago. *Journal of Ecology* 20: 270–283.
- Conedera M, Tinner W, Neff C, Meurer M, Dickens AF, Krebs P 2009. Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quaternary Science Reviews* 28: 555–576.
- Cooper AN, Ashley-Jones C 1987. Economics of fire prevention in New Zealand plantations. *New Zealand Journal of Forestry* 31(4): 14–18.

- Daly GT 1969. The biology of matagouri. Proceedings of the NZ Weed and Pest Control Conference 22: 195–200.
- Davidson EA, de Araújo AC, Artaxo P, Balch JK, Brown IF, Bustamante MMC, Coe MT, DeFries RS, Keller M, Longo M, Munger JW, Schroeder W, Soares-Filho BS, Souza CM, Wofsy SC 2012. The Amazon basin in transition. *Nature* 481: 321–328.
- de Lange PJ, Smissen RD, Wagstaff SJ, Keeling DJ, Murray BG, Toelken HR 2010. A molecular phylogeny and infrageneric classification for *Kunzea* (Myrtaceae) inferred from rDNAITS and ETS sequences. *Australian Systematic Botany* 23: 309–319.
- Dick RD 1956. Sixty years after a mountain beech forest fire. *New Zealand Journal of Forestry* 7(3): 104–108.
- Dickinson MB, Johnson EA 2001. Fire effects on trees. In: Johnson EA, Miyanishi K eds *Forest fires: behavior and ecological effects*. San Diego, CA, Academic Press. Pp. 477–525.
- Dodson JR, Enright NJ, McLean RF 1988. A late Quaternary vegetation history for far northern New Zealand. *Journal of Biogeography* 15: 647–656.
- Druce AP 1957. Botanical survey of an experimental catchment, Taita, New Zealand: the central catchment at Taita Experimental Station. Lower Hutt, DSIR.
- Elliot MB 1998. Late Quaternary pollen records of vegetation and climate change from Kaitaia Bog, far northern New Zealand. *Review of Palaeobotany and Palynology* 99: 189–202.
- Elliot M, Neall V, Wallace C 2005. A Late Quaternary pollen record from Lake Tangonge, far northern New Zealand. *Review of Palaeobotany and Palynology* 136: 143–158.
- Enright NJ 1989. Heath land vegetation of the Spirits Bay area, far northern New Zealand. *New Zealand Journal of Ecology* 12: 63–75.
- Esler AE 1963. The influence of pre-European fires in the Tiritea catchment, northern Tararua. *Proceedings of the Ecological Society of New Zealand* 10: 8–12.
- Esler AE 1967. The vegetation of Kapiti Island. *New Zealand Journal of Botany* 5: 353–393.
- Esler AE, Rumball PJ 1975. Gumland vegetation at Kaikohe, Northland, New Zealand. *New Zealand Journal of Botany* 13: 425–436.
- Flannigan MD, Krawchuk MA, de Groot WJ, Wotton BM, Gowman LM 2009. Implications of changing climate for global wildland fire. *International Journal of Wildland Fire* 18: 483–507.
- Fogarty LG 2001. A flammability guide for some common New Zealand native tree and shrub species. *New Zealand Fire Service Commission Research Report 20*. Wellington, NZFS Commission. 18 p.
- Forest and Rural Fires Association of New Zealand 2012. Rural fire history of New Zealand. <http://www.ruralfirehistory.org.nz/>
- GBICT 2010. Great Barrier Island (Aotea) state of environment report 2010. Great Barrier Island Charitable Trust. <http://www.gbict.co.nz/SOE.htm>
- Gitay H, Lee WG, Allen RB, Wilson JB 1992. Recovery of *Chionochloa rigida* tussocks from fires in South Island, New Zealand. *Journal of Environmental Management* 35: 249–259.
- Gould SJ, Vrba ES 1982. Exaptation—a missing term in the science of form. *Paleobiology* 8: 4–15.
- Grant DA 1967. Factors affecting the establishment of manuka (*Leptospermum scoparium*). *Proceedings of the NZ Weed and Pest Control Conference* 20: 129–134.
- Grove PB, Mark AF, Dickinson KJM 2002. Vegetation monitoring of recently protected tussock grasslands in the southern South Island, New Zealand. *Journal of the Royal Society of New Zealand* 32: 379–414.
- Guild D, Dudfield M 2010. A history of fire in the forest and rural landscape in New Zealand - Part 2, post 1830 influences, and implications for future fire management. *New Zealand Journal of Forestry* 54(4): 31–38.
- Gutsell SL, Johnson EA 1996. How fire scars are formed: coupling a disturbance process to its ecological effect. *Canadian Journal of Forest Research* 26: 166–174.
- Haase P 1986. A study of a *Libocedrus bidwillii* population at Pegleg Flat, Arthur's Pass, New Zealand. *New Zealand Journal of Ecology* 9: 153–156.
- Harris W 2002. Variation of inherent seed capsule splitting in populations of *Leptospermum scoparium* (Myrtaceae) in New Zealand. *New Zealand Journal of Botany* 40: 405–417.
- Hengst GE, Dawson JO 1994. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research* 24: 688–696.
- Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vilà M, Zamora R, Zobel M 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15: 1–7.
- Horrocks M, Ogden J 1998. Fine resolution palynology of Erua Swamp, Tongariro, New Zealand, since the Taupo Tephra eruption of c. 1718 B.P. *New Zealand Journal of Botany* 36: 285–293.
- Horrocks M, Ogden J 2000. Evidence for Lateglacial and Holocene tree-line fluctuations from pollen diagrams from the Subalpine zone on Mt Hauhungatahi, Tongariro National Park, New Zealand. *The Holocene* 10: 61–73.
- Horrocks M, Deng Y, Ogden J, Alloway BV, Nichol SL, Sutton DG 2001. High spatial resolution of pollen and charcoal in relation to the c. 600 year BP Kaharoa Tephra: Implications for Polynesian settlement of Great Barrier Island, northern New Zealand. *Journal of Archaeological Science* 28: 153–168.
- Howell C 2008. Consolidated list of environmental weeds in New Zealand. DOC Research & Development Series 292. Wellington, Department of Conservation. 42 p.
- Hutchins DE 1919. *New Zealand forestry. Part 1, Kauri forests and forests of the north and forest management*. Wellington, Dept. of Forestry. 200 p.
- Jamieson AR 1989. Gradients in the Kawerua scrublands, Waipoua Forest, Northland, New Zealand. Unpublished MSc thesis, University of Auckland, Auckland, New Zealand. 88 p.
- Johnson PN 2001. Vegetation recovery after fire on a southern New Zealand peatland. *New Zealand Journal of Botany* 39: 251–267.
- Johnson PN 2005. Fire in wetlands and scrub vegetation: studies in Southland, Otago, and Westland. DOC Research & Development Series 215. Wellington, Department of Conservation. 42 p.
- Jones JL, Webb BW, Butler BW, Dickinson MB, Jimenez D, Reardon J, Bova AS 2006. Prediction and measurement of thermally induced cambial tissue necrosis in tree stems. *International Journal of Wildland Fire* 15: 3–17.

- Keeley JE 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18: 116–126.
- Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* 16: 406–411.
- Kelly D, Ladley JJ, Robertson AW, Anderson SH, Wotton DM, Wiser SK 2010. Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit dispersal in New Zealand. *New Zealand Journal of Ecology* 34: 66–85.
- Kelly RF, Higuera PE, Barrett CM, Hu FS 2011. A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. *Quaternary Research* 75: 11–17.
- Kitzberger T, Araújo E, Gowda JH, Mermoz M, Morales JM 2012. Decreases in fire spread probability with forest age promotes alternative community states, reduced resilience to climate variability and large fire regime shifts. *Ecosystems* 15: 97–112.
- Krawchuk MA, Moritz MA 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 92: 121–132.
- Lamont BB, Le Maitre DC, Cowling RM, Enright NJ 1991. Canopy seed storage in woody plants. *The Botanical Review* 57: 277–317.
- Lawes MJ, Adie H, Russell-Smith J, Murphy B, Midgley JJ 2011. How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. *Ecosphere* 2: art42. DOI: 10.1890/ES10-00204.1.
- Lawes MJ, Richardson SJ, Clarke PJ, Midgley JJ, McGlone MS, Bellingham PJ 2014. Bark thickness does not explain the different susceptibility of Australian and New Zealand temperate rainforests to anthropogenic fire. *Journal of Biogeography*: DOI: 10.1111/jbi.12292.
- Leathwick J, Morgan F, Wilson G, Rutledge D, McLeod M, Johnston K 2002. Land environments of New Zealand: A technical guide. Auckland, Ministry for the Environment. 237 p.
- Ledgard N, Davis M 2004. Restoration of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest after fire. *New Zealand Journal of Ecology* 28: 125–135.
- Lee WG, Wood JR, Rogers GM 2010. Legacy of avian-dominated plant–herbivore systems in New Zealand. *New Zealand Journal of Ecology* 34: 28–47.
- Lees CM, Neall VE 1993. Vegetation responses to volcanic eruptions on Egmont volcano, New Zealand, during the last 1500 years. *Journal of the Royal Society of New Zealand* 23: 91–127.
- Leslie DM, McGlone MS 1973. Relict periglacial landforms at Clarks Junction, Otago. *New Zealand Journal of Geology and Geophysics* 16: 575–583.
- Lindenmayer DB, Hobbs RJ, Likens GE, Krebs CJ, Banks SC 2011. Newly discovered landscape traps produce regime shifts in wet forests. *Proceedings of the National Academy of Sciences (USA)* 108: 15887–15891.
- Macias Fauria M, Michaletz ST, Johnson EA 2011. Predicting climate change effects on wildfires requires linking processes across scales. *Wiley Interdisciplinary Reviews: Climate Change* 2: 99–112.
- Mark AF 1965. Effects of management practices on narrow-leaved snow tussock, *Chionochloa rigida*. *New Zealand Journal of Botany* 3: 300–319.
- Mark AF 1994. Effects of burning and grazing on sustainable utilization of upland snow tussock (*Chionochloa* spp.) rangelands for pastoralism in South Island, New Zealand. *Australian Journal of Botany* 42: 149–161.
- Mark AF, McLennan B 2005. The conservation status of New Zealand's indigenous grasslands. *New Zealand Journal of Botany* 43: 245–270.
- Mark AF, Smith PMF 1975. A lowland vegetation sequence in South Westland: Pakihi bog to mixed beech-podocarp forest Part 1: The principal strata. *Proceedings of the New Zealand Ecological Society* 22: 76–92.
- Marris E 2009. Ecology: Ragamuffin Earth. *Nature* 460: 450–453.
- Martin TJ, Ogden J 2006. Wind damage and response in New Zealand forests: a review. *New Zealand Journal of Ecology* 30: 295–310.
- McAlpine KG, Timmins SM, Westbrooke I 2009. Bone-seed (*Chrysanthemoides monilifera* ssp. *monilifera*) invasion effects on native regeneration in New Zealand coastal plant communities. *New Zealand Journal of Ecology* 33: 72–82.
- McCarthy MA, Gill AM, Bradstock RA 2001. Theoretical fire-interval distributions. *International Journal of Wildland Fire* 10: 73–77.
- McGlone MS 1983. Polynesian deforestation of New Zealand: a preliminary synthesis. *Archaeology in Oceania* 18: 11–25.
- McGlone MS 1989. The Polynesian settlement of New Zealand in relation to environmental and biotic changes. *New Zealand Journal of Ecology* 12 (supplement): S115–S129.
- McGlone MS 2001. The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. *New Zealand Journal of Ecology* 25: 1–15.
- McGlone MS 2002. A Holocene and latest Pleistocene pollen record from Lake Poukawa, Hawke's Bay, New Zealand. *Global and Planetary Change* 33: 283–299.
- McGlone MS 2006. Becoming New Zealanders: immigration and the formation of the biota. In: Allen RB, Lee WG eds *Biological invasions in New Zealand*. Ecological Studies 186. Berlin, Heidelberg, Springer. Pp. 17–32.
- McGlone MS 2009. Postglacial history of New Zealand wetlands and implications for their conservation. *New Zealand Journal of Ecology* 33: 1–23.
- McGlone MS, Basher LR 1995. The deforestation of the Upper Awatere Catchment, Inland Kaikoura Range, Marlborough, South Island, New Zealand. *New Zealand Journal of Ecology* 19: 53–66.
- McGlone MS, Moar NT 1998. Dryland Holocene vegetation history, Central Otago and the Mackenzie Basin, South Island, New Zealand. *New Zealand Journal of Botany* 36: 91–111.
- McGlone MS, Topping WW 1983. Late Quaternary vegetation, Tongariro region, central North Island, New Zealand. *New Zealand Journal of Botany* 21: 53–76.
- McGlone M, Walker S 2011. Potential effects of climate change on New Zealand's terrestrial biodiversity and policy recommendations for mitigation, adaptation and research. *Science for Conservation* 312. Wellington, Department of Conservation. 77 p.
- McGlone MS, Wilmshurst JM 1999a. Dating initial Maori environmental impact in New Zealand. *Quaternary International* 59: 5–16.
- McGlone MS, Wilmshurst JM 1999b. A Holocene record of climate, vegetation change and peat bog development, east Otago, South Island, New Zealand. *Journal of Quaternary Science* 14: 239–254.
- McGlone MS, Howorth R, Pullar WA 1984a. Late Pleistocene stratigraphy, vegetation and climate of the Bay of Plenty

- and Gisborne regions, New Zealand. *New Zealand Journal of Geology and Geophysics* 27: 327–350.
- McGlone MS, Neall VE, Pillans BJ 1984b. Inaha Terrace deposits: A late Quaternary terrestrial record in South Taranaki, New Zealand. *New Zealand Journal of Geology and Geophysics* 27: 35–49.
- McGlone MS, Nelson CS, Todd AJ 1984c. Vegetation history and environmental significance of pre-peat and surficial peat deposits at Ohinewai, Lower Waikato lowland. *Journal of the Royal Society of New Zealand* 14: 233–244.
- McGlone MS, Neall VE, Clarkson BD 1988. The effect of recent volcanic events and climatic changes on the vegetation of Mt Egmont (Mt Taranaki), New Zealand. *New Zealand Journal of Botany* 26: 123–144.
- McGlone MS, Mark AF, Bell D 1995. Late Pleistocene and Holocene vegetation history, Central Otago, South Island, New Zealand. *Journal of the Royal Society of New Zealand* 25: 1–22.
- McGlone MS, Moar NT, Meurk CD 1997. Growth and vegetation history of alpine mires on the Old Man Range, Central Otago, New Zealand. *Arctic and Alpine Research* 29: 32–44.
- McGlone M, Wardle P, Worthy T 2003. Environmental change since the Last Glaciation. In: Darby J, Fordyce RE, Mark A, Probert K, Townsend C eds *The natural history of southern New Zealand*. Dunedin, Otago University Press. Pp. 105–128.
- McGlone MS, Wilmshurst JM, Leach HM 2005. An ecological and historical review of bracken (*Pteridium esculentum*) in New Zealand, and its cultural significance. *New Zealand Journal of Ecology* 29: 165–184.
- McGlone MS, Perry GLW, Houlston GJ, Connor HE 2014. Fire, grazing and the evolution of New Zealand grasses. *New Zealand Journal of Ecology* 38: 1–11.
- McIntyre R 2008. Whose high country? A history of the South Island High Country of New Zealand. Rosedale, North Shore, Penguin. 432 p.
- McKelvey PJ 1955. A note on the forest edge at Te Whaiti. *New Zealand Journal of Forestry* 7: 77–80.
- McKelvey PJ 1963. The synecology of the West Taupo indigenous forest. Wellington, Government Printer. 126 p.
- McLean G 1992. *New Zealand tragedies: fires and firefighting*. Wellington, Grantham House. 216 p.
- McQueen DR 1991. Plant succession and species diversity in vegetation around Lake Pounui, southern North Island, New Zealand. *Tuatara* 31: 43–65.
- McQueen J, Forester L 2000. Succession in the Kaimaumau gumland, Northland, New Zealand, following fire. *Conservation Advisory Science Notes* 280. Wellington, Department of Conservation. 33 p.
- McWethy DB, Whitlock C, Wilmshurst JM, McGlone MS, Li X 2009. Rapid deforestation of South Island, New Zealand by early Polynesian fires. *The Holocene* 19: 883–897.
- McWethy DB, Whitlock C, Wilmshurst JM, McGlone MS, Fromont M, Li X, Dieffenbacher-Kralla A, Hobbs WO, Fritz SC, Cook ER 2010. Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proceedings of the National Academy of Sciences (USA)* 107: 21343–21348.
- McWethy DB, Higuera PE, Whitlock C, Veblen TT, Bowman DMJS, Cary GJ, Haberle SG, Keane RE, Maxwell BD, McGlone MS, Perry GLW, Wilmshurst JM, Holz A, Tepley AJ 2013. A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes. *Global Ecology and Biogeography* 22: 900–912.
- Mew G 1983. Application of the term “pakihī” in New Zealand — a review. *Journal of the Royal Society of New Zealand* 13: 175–198.
- Meyn A, White PS, Buhk C, Jentsch A 2007. Environmental drivers of large, infrequent wildfires: the emerging conceptual model. *Progress in Physical Geography* 31: 287–312.
- Michaletz ST, Johnson EA 2007. How forest fires kill trees: A review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* 22: 500–515.
- Michaletz ST, Johnson EA, Tyree MT 2012. Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. *New Phytologist* 194: 254–263.
- Midgley JJ, Bond WJ 2013. Plant adaptations to fire: an evolutionary perspective. In: Belcher CM ed. *Fire phenomena and the Earth system. An interdisciplinary guide to fire science*. Wiley-Blackwell. Pp. 125–134.
- Mildenhall DC 1980. *New Zealand late Cretaceous and Cenozoic plant biogeography: A contribution*. Palaeogeography, Palaeoclimatology, Palaeoecology 31: 197–233.
- Miller C 1993. *Fire for conservation management of Pakihī*. Conservation Advisory Science Notes 51. Wellington, Department of Conservation. 5 p.
- Mirams RV 1957. Aspects of the natural regeneration of the kauri (*Agathis australis* Salisb.). *Transactions of the Royal Society of New Zealand* 84: 661–680.
- Mohan E, Mitchell N, Lovell P 1984. Environmental factors controlling germination of *Leptospermum scoparium* (manuka). *New Zealand Journal of Botany* 22: 95–101.
- Molloy BPI, Burrows CJ, Cox JE, Johnston JA, Wardle P 1963. Distribution of subfossil forest remains, eastern South Island, New Zealand. *New Zealand Journal of Botany* 1: 68–77.
- Moore LB 1976. The changing vegetation of Molesworth Station New Zealand, 1944 to 1971. *DSIR Bulletin* 217. Wellington, Department of Scientific and Industrial Research. 118 p.
- Moritz MA, Parisien M-A, Batllori E, Krawchuk MA, Van Dorn J, Ganz DJ, Hayhoe K 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3: art49. DOI: 10.1890/ES11-00345.1.
- Murray-McIntosh RP, Srimshaw BJ, Hatfield PJ, Penny D 1998. Testing migration patterns and estimating founding population size in Polynesia by using human mtDNA sequences. *Proceedings of the National Academy of Sciences (USA)* 95: 9047–9052.
- Newnham R 1999. Environmental change in Northland, New Zealand during the last glacial and Holocene. *Quaternary International* 57/58: 61–70.
- Newnham RM, de Lange PJ, Lowe DJ 1995. Holocene vegetation, climate and history of a raised bog complex, northern New Zealand based on palynology, plant macrofossils and tephrochronology. *The Holocene* 5: 267–282.
- Newnham RM, Lowe DJ, McGlone MS, Wilmshurst JM, Higham TFG 1998. The Kaharoa tephra as a critical datum for earliest human impact in Northern New Zealand. *Journal of Archaeological Science* 25: 533–544.
- Newnham RM, Lowe DJ, Williams PW 1999. Quaternary environmental change in New Zealand: a review. *Progress in Physical Geography* 23: 567–610.

- Norton DA, de Lange PJ 2003. Fire and vegetation in a temperate peat bog: implications for the management of threatened species. *Conservation Biology* 17: 138–148.
- O'Connor KF 1982. The implications of past exploitation and current developments to the conservation of South Island tussock grasslands. *New Zealand Journal of Ecology* 5: 97–107.
- O'Connor KF 1984. Stability and instability of ecological systems in New Zealand mountains. *Mountain Research and Development* 4: 15–29.
- Ogden J 1985. An introduction to plant demography with special reference to New Zealand trees. *New Zealand Journal of Botany* 23: 751–772.
- Ogden J, Basher L, McGlone M 1998. Fire, forest regeneration and links with early human habitation: evidence from New Zealand. *Annals of Botany* 81: 687–696.
- Ogden J, Deng Y, Boswijk G, Sandiford A 2003. Vegetation changes since early Maori fires in Waipoua Forest, Northern New Zealand. *Journal of Archaeological Science* 30: 753–767.
- Ogden J, Deng Y, Horrocks M, Nichol S, Anderson S 2006. Sequential impacts of Polynesian and European settlement on vegetation and environmental processes recorded in sediments at Whangapoua Estuary, Great Barrier Island, New Zealand. *Regional Environmental Change* 6: 25–40.
- Paré PW, Tumlinson JH 1999. Plant volatiles as a defense against insect herbivores. *Plant Physiology* 121: 325–332.
- Partridge TR 1989. Soil seed banks of secondary vegetation on the Port Hills and Banks Peninsula, Canterbury, New Zealand, and their role in succession. *New Zealand Journal of Botany* 27: 421–435.
- Partridge TR 1992. Successional interactions between bracken and broom on the Port Hills, Canterbury, New Zealand. *Journal of Applied Ecology* 29: 85–91.
- Payton IJ, Pearce HG 2009. Fire-induced changes to the vegetation of tall-tussock (*Chionochloa rigida*) grassland ecosystems. *Science for Conservation* 290. Wellington, Department of Conservation. 42 p.
- Payton IJ, Allen RB, Knowlton JE 1984. A post-fire succession in the northern Urewera forests North Island, New Zealand. *New Zealand Journal of Botany* 22: 207–222.
- Pearce HG, Mullan AB, Salinger MJ, Opperman TW, Woods D, Moore JR 2005. Impact of climate change on long-term fire danger. *New Zealand Fire Service Commission Research Report* 50. Wellington, NZFS Commission.
- Pearce HG, Cameron G, Anderson SAJ, Dudfield M 2008. An overview of fire management in New Zealand forestry. *New Zealand Journal of Forestry* 53(3): 7–11.
- Perry GLW, Enright NJ 2002. Humans, fire and landscape pattern: understanding a maquis-forest complex, Mont Do, New Caledonia, using a spatial 'state-and-transition' model. *Journal of Biogeography* 29: 1143–1159.
- Perry GLW, Ogden J, Enright NJ, Davy LV 2010. Vegetation patterns and trajectories in disturbed landscapes, Great Barrier Island, northern New Zealand. *New Zealand Journal of Ecology* 34: 311–324.
- Perry GLW, Wilmshurst JM, McGlone MS, McWethy DB, Whitlock C 2012a. Explaining fire-driven landscape transformation during the Initial Burning Period of New Zealand's prehistory. *Global Change Biology* 18: 1609–1621.
- Perry GLW, Wilmshurst JM, McGlone MS, Napier A 2012b. Reconstructing spatial vulnerability to forest loss by fire in pre-historic New Zealand. *Global Ecology and Biogeography* 21: 1029–1041.
- Pugh JM, Shulmeister J 2010. Holocene vegetation history of a high elevation (1200 m) site in the Lake Heron Basin, inland Canterbury, New Zealand. In: Haberle S, Stevenson J, Prebble M eds *Altered ecologies: fire, climate and human influence on terrestrial landscapes*. Terra Australis 32. Canberra, ANU E Press, The Australian National University. Pp. 69–81.
- Rein G, Cleaver N, Ashton C, Pironi P, Torero JL 2008. The severity of smouldering peat fires and damage to the forest soil. *Catena* 74: 304–309.
- Rogers GM 1994. North Island seral tussock grasslands 1. Origins and land-use history. *New Zealand Journal of Botany* 32: 271–286.
- Rogers GM, Leathwick JR 1994. North Island seral tussock grasslands 2. Autogenic succession: change of tussock grassland to shrubland. *New Zealand Journal of Botany* 32: 287–303.
- Rogers G, Walker S, Lee B 2005. The role of disturbance in dryland New Zealand: past and present. *Science for Conservation* 258. Wellington, Department of Conservation. 122 p.
- Rogers GM, Walker S, Basher LM, Lee WG 2007. Frequency and impact of Holocene fire in eastern South Island, New Zealand. *New Zealand Journal of Ecology* 31: 129–142.
- Ronghua Y, Mark AF, Wilson JB 1984. Aspects of the ecology of the indigenous shrub *Leptospermum scoparium* (Myrtaceae) in New Zealand. *New Zealand Journal of Botany* 22: 483–507.
- Rowarth JS, Hampton JG, Hill MJ 2007. New Zealand native seed germination requirements: A review. *New Zealand Journal of Botany* 45: 485–501.
- Sandiford A, Horrocks M, Newnham R, Ogden J, Alloway B 2002. Environmental change during the last glacial maximum (c. 25 000—c. 16 500 years BP) at Mt Richmond, Auckland Isthmus, New Zealand. *Journal of the Royal Society of New Zealand* 32: 155–167.
- Sandiford A, Newnham R, Alloway B, Ogden J 2003. A 28 000–7600 cal yr BP pollen record of vegetation and climate change from Pukaki Crater, northern New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology* 201: 235–247.
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591–596.
- Sessions LA, Kelly D 2000. The effects of browntop (*Agrostis capillaris*) dominance after fire on native shrub germination and survival. *New Zealand Natural Sciences* 25: 1–9.
- Smale MC, Fitzgerald NB, Richardson SJ 2011. Resilience to fire of *Dracophyllum subulatum* (Ericaceae) frost flat heathland, a rare ecosystem in central North Island, New Zealand. *New Zealand Journal of Botany* 49: 231–241.
- Smith CM, Wastney AW 1935. Forest protection against pastoralists' fires. *Te Kura Ngahere* 3: 199–203.
- Sullivan AL, Ball R 2012. Thermal decomposition and combustion chemistry of cellulosic biomass. *Atmospheric Environment* 47: 133–141.
- Sullivan JJ, Williams PA, Timmins SM 2007. Secondary forest succession differs through naturalised gorse and native kānuka near Wellington and Nelson. *New Zealand Journal of Ecology* 31: 22–38.
- Thode PJ 1983. Northland's forest history and present resources. *New Zealand Journal of Forestry* 28: 203–224.
- Thompson J 1989. A revision of the genus *Leptospermum* (Myrtaceae). *Telopea* 3: 301–448.

- Timmins SM 1992. Wetland vegetation recovery after fire: Eweburn Bog, Te Anau, New Zealand. *New Zealand Journal of Botany* 30: 383–399.
- Timmins SM, Williams PA 1991. Weed numbers in New Zealand forest and scrub reserves. *New Zealand Journal of Ecology* 15: 153–162.
- van Wagtenonk JW 2006. Fire as a physical process. In: Sugihara NG, van Wagtenonk JW, Fites-Kaufman J, Shaffer KE, Thode AE eds *Fire in California's ecosystems*. Berkeley, CA, University of California Press. Pp. 38–57.
- Vandergoes MJ, Hogg AG, Lowe DJ, Newnham RM, Denton GH, Southon J, Barrell DJA, Wilson CJN, McGlone MS, Allan ASR, Almond PC, Petchey F, Dabell K, Dieffenbacher-Krall AC, Blaauw M 2013. A revised age for the Kawakawa/Oruanui tephra, a key marker for the Last Glacial Maximum in New Zealand. *Quaternary Science Reviews* 74: 195–201.
- Vucetich CG, Pullar WA 1973. Holocene tephra formations erupted in the Taupo area, and interbedded tephra from other volcanic sources. *New Zealand Journal of Geology and Geophysics* 16: 745–780.
- Walsh P 1910. The effects of the disappearance of the New Zealand bush. *Transactions of the Royal Society of New Zealand* 43: 436–447.
- Ward D 2001. Combustion chemistry and smoke. In: Johnson EA, Miyanishi K eds *Forest fires: behavior and ecological effects*. San Diego, CA, Academic Press. Pp. 55–78.
- Wardle JA 1984. *The New Zealand beeches: ecology, utilisation and management*. Christchurch, New Zealand Forest Service. 447 p.
- Wardle P 1977. Plant communities of Westland National Park (New Zealand) and neighbouring lowland and coastal areas. *New Zealand Journal of Botany* 15: 323–398.
- Wardle P 2001. Holocene forest fires in the upper Clutha district, Otago, New Zealand. *New Zealand Journal of Botany* 39: 523–542.
- Warman L, Moles AT 2009. Alternative stable states in Australia's Wet Tropics: a theoretical framework for the field data and a field-case for the theory. *Landscape Ecology* 24: 1–13.
- Wells JA 1972. Ecology of *Podocarpus hallii* in Central Otago, New Zealand. *New Zealand Journal of Botany* 10: 399–426.
- Whelan RJ 1995. *The ecology of fire*. Cambridge University Press.
- Whitlock C, Larsen C 2001. Charcoal as a fire proxy. In: Smol JP, Birks HJB, Last WM eds *Tracking environmental change using lake sediments*, Vol. 3 Terrestrial, algal, and siliceous indicators. *Developments in Paleoenvironmental Research*. The Netherlands, Springer. Pp. 75–97.
- Whitlock C, Higuera PE, McWethy DB, Briles CE 2010. Paleoecological perspectives on fire ecology: revisiting the fire-regime concept. *The Open Ecology Journal* 3: 6–23.
- Williams PA 1983. Secondary vegetation succession on the Port Hills Banks Peninsula, Canterbury, New Zealand. *New Zealand Journal of Botany* 21: 237–247.
- Williams PA 2011. Secondary succession through non-native dicotyledonous woody plants in New Zealand. *New Zealand Natural Sciences* 36: 73–91.
- Williams PA, Courtney S, Glenny D, Hall G, Mew G 1990. Pakihi and surrounding vegetation in North Westland, South Island. *Journal of the Royal Society of New Zealand* 20: 179–203.
- Wilmshurst JM 1997. The impact of human settlement on vegetation and soil stability in Hawke's Bay, New Zealand. *New Zealand Journal of Botany* 35: 97–111.
- Wilmshurst JM, McGlone MS 1996. Forest disturbance in the central North Island, New Zealand, following the 1850 BP Taupo eruption. *The Holocene* 6: 399–411.
- Wilmshurst JM, McGlone MS, Partridge TR 1997. A late Holocene history of natural disturbance in lowland podocarp/hardwood forest, Hawke's Bay, New Zealand. *New Zealand Journal of Botany* 35: 79–96.
- Wilmshurst JM, Eden DN, Froggatt PC 1999. Late Holocene forest disturbance in Gisborne, New Zealand: A comparison of terrestrial and marine pollen records. *New Zealand Journal of Botany* 37: 523–540.
- Wilmshurst JM, Higham TFG, Allen H, Johns D, Phillips C 2004. Early Maori settlement impacts in northern coastal Taranaki, New Zealand. *New Zealand Journal of Ecology* 28: 167–179.
- Wilmshurst JM, Anderson AJ, Higham TGF, Worthy TH 2008. Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. *Proceedings of the National Academy of Sciences (USA)* 105: 7676–7680.
- Wilmshurst JM, Moar NT, Wood JR, Bellingham PJ, Findlater AM, Robinson JJ, Stone C 2014. Use of pollen and ancient DNA as conservation baselines for offshore islands in New Zealand. *Conservation Biology* 28: 201–212.
- Wilson HD 1994. Regeneration of native forest on Hinewai Reserve, Banks Peninsula. *New Zealand Journal of Botany* 32: 373–383.
- Wiser SK, Allen RB, Platt KH 1997. Mountain beech forest succession after a fire at Mount Thomas Forest, Canterbury, New Zealand. *New Zealand Journal of Botany* 35: 505–515.
- Wood JR, Walker S 2008. Macrofossil evidence for pre-settlement vegetation of Central Otago's basin floors and gorges. *New Zealand Journal of Botany* 46: 239–255.
- Wood V, Pawson E 2008. The Banks Peninsula forests and Akaroa Cocksfoot: explaining a New Zealand forest transition. *Environment and History* 14: 449–468.
- Worthy TH, Holdaway RN 2002. *The lost world of the moa: prehistoric life of New Zealand*. Christchurch, Canterbury University Press. 718 p.

Editorial Board member: Jason Tylianakis

Received 13 June 2013; accepted 18 December 2013