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## REVIEW ARTICLE

## Ecology and long-term history of fire in New Zealand

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**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 pyrophylllic 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

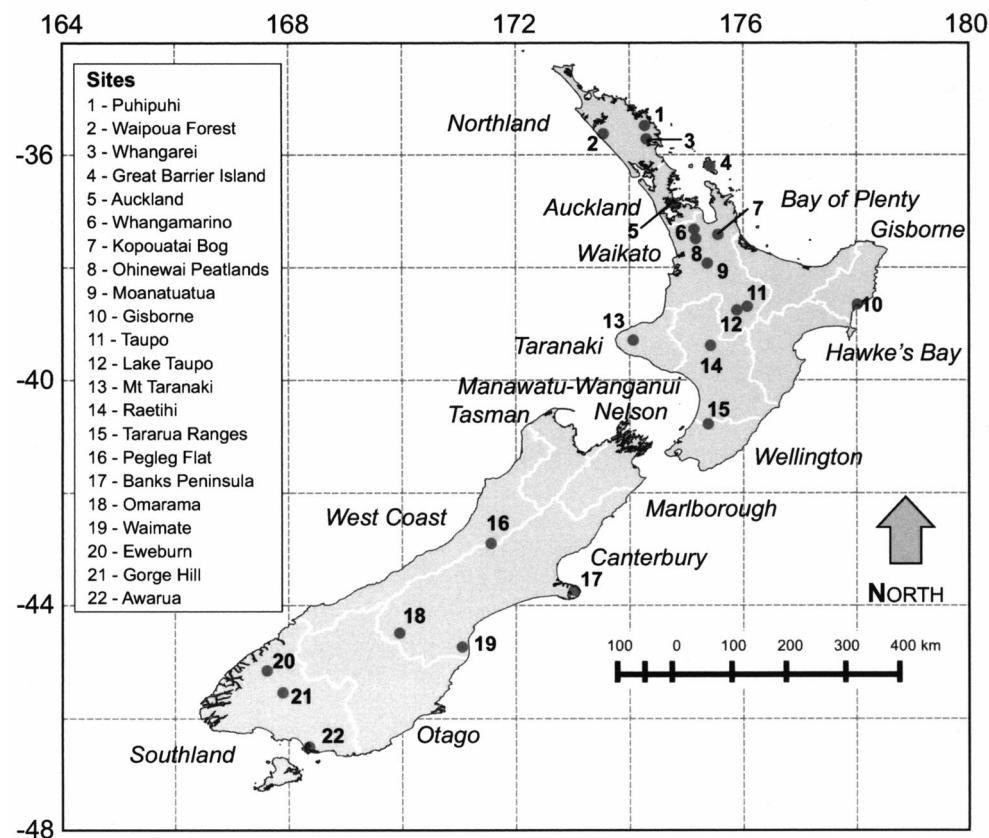
#### Physico-chemical process

Wildfires integrate processes from the sub-second (the physics and chemistry of combustion) to the centuriel (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 Wagendonk 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 Wagendonk 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 Wagendonk 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

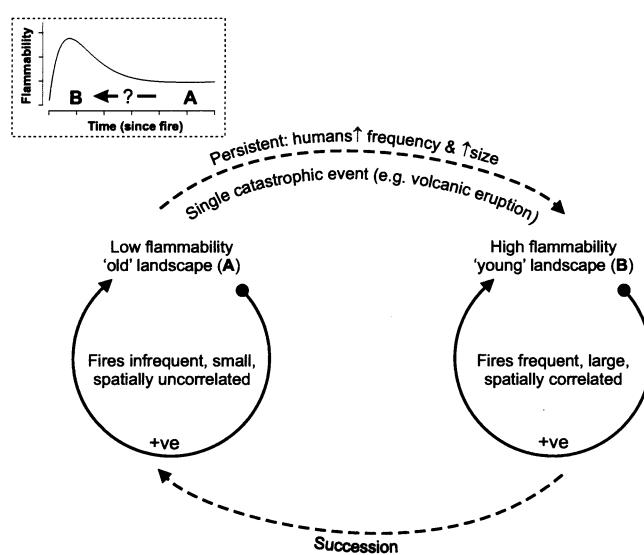
communities dominated by species such as *Leptospermum scoparium* (mānuka) and *Kunzea ericoides* (kānuka) – both flammable Myrtaceous species of Australian origin<sup>1</sup> before declining (Fig. 2). This relationship, which, in the specific statistical context of hazard rates McCarthy et al. (2001) 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.

<sup>1</sup> 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–sedge/land 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, reafforestation 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).

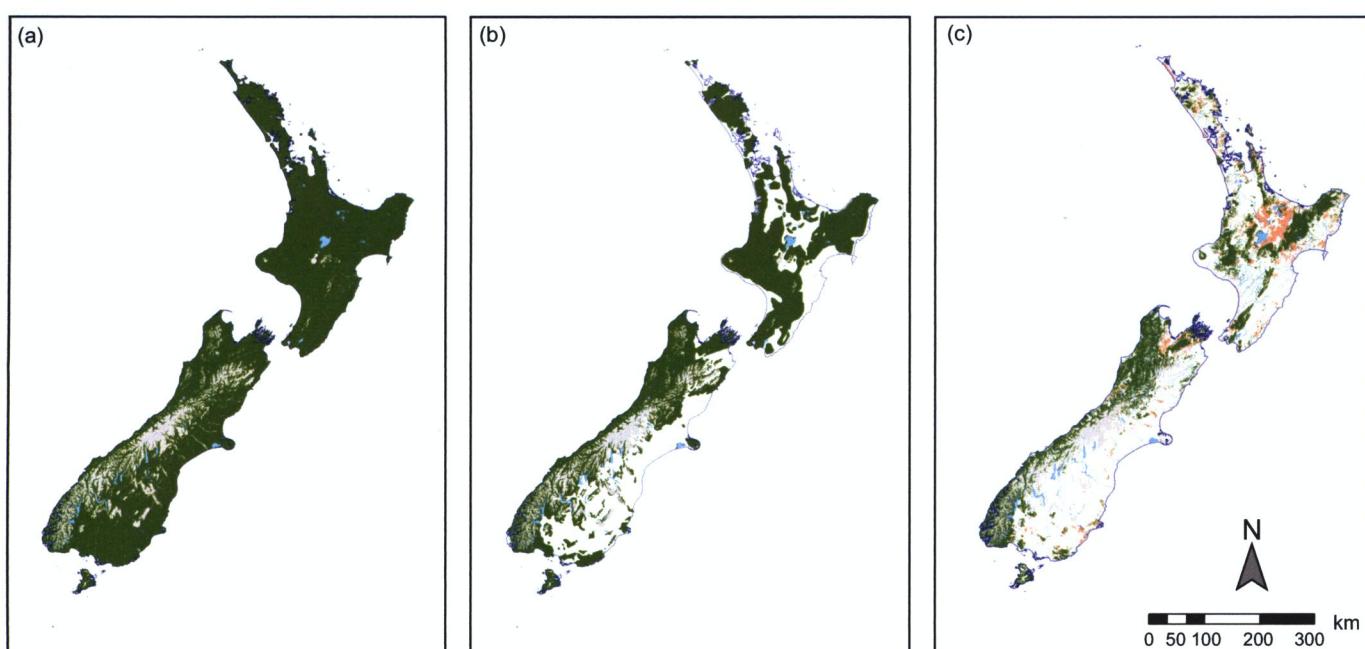
Lowland wetlands may also have been subject to repeated natural fires. Restiad bogs in the northern part of New Zealand have undoubtedly been foci for fire for a considerable period (McGlone et al. 1984c; Newnham et al. 1995; McGlone 2009). Such bogs would have had a woody (scrubby) component and so, 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 centurial 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<sup>-1</sup>, 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>Fuscopora</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)<sup>2</sup>, 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  $7.5 \times 10^7$  board ft [ $1.5 \times 10^6$  m<sup>3</sup>] 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.<sup>3</sup>

<sup>2</sup> 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=IIt0ONZe1dc&feature=channel> (accessed 10 May 2013).

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

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

both islands (Pearce et al. 2005). If pyrophyllitic (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*

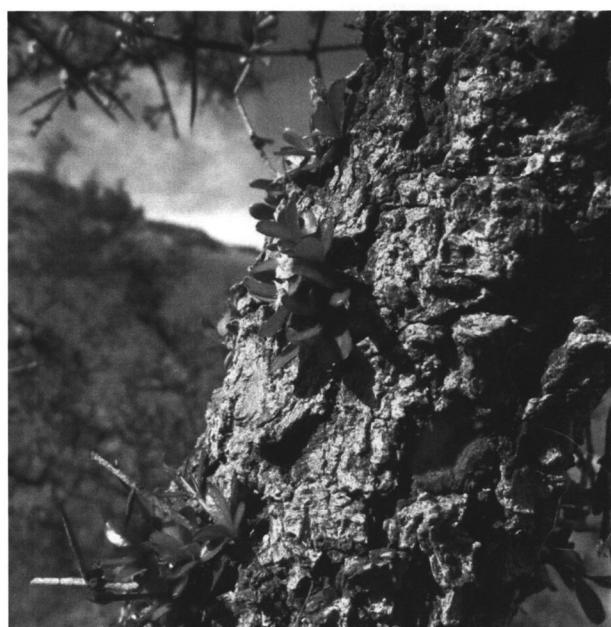
Plants show a range of adaptations to fire, including serotiny (the storage of seeds in a seedbank and their release post-fire), post-fire resprouting, heat and smoke-triggered germination, thick bark, seed adaptations (e.g. hard-seededness) and traits elevating flammability (Midgley & Bond 2013). In 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 rigidula* 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
<b>1. Fire-adapted</b>						
<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 <sup>1</sup>
<i>Pteridium esculentum</i> (bracken)	Dennstaedtiaeae	Fern <sup>2</sup>	N	Y		High
<i>Cordyline</i> spp. (cabbage trees)	Asparagaceae	Monocot trees	N	Y		High
<b>2. Fire-tolerant and/or favoured</b>						
<i>Weinmannia racemosa</i> (kāmahi)	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>Melicytus 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> (tau hinu)	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
<b>3. Fire-sensitive</b>						
<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) <sup>3</sup>
<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) <sup>4</sup>
<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) <sup>5</sup>
<i>Prumnopitys taxifolia</i> (mataī)	Podocarpaceae	Large tree	N	N	2	Moderate

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

including the Stypheliae 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*, *Histiopteris*, *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 pakihi<sup>4</sup> 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

<sup>4</sup>Wetland 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  $3.0 \times 10^5$  seeds m<sup>-2</sup>. 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*

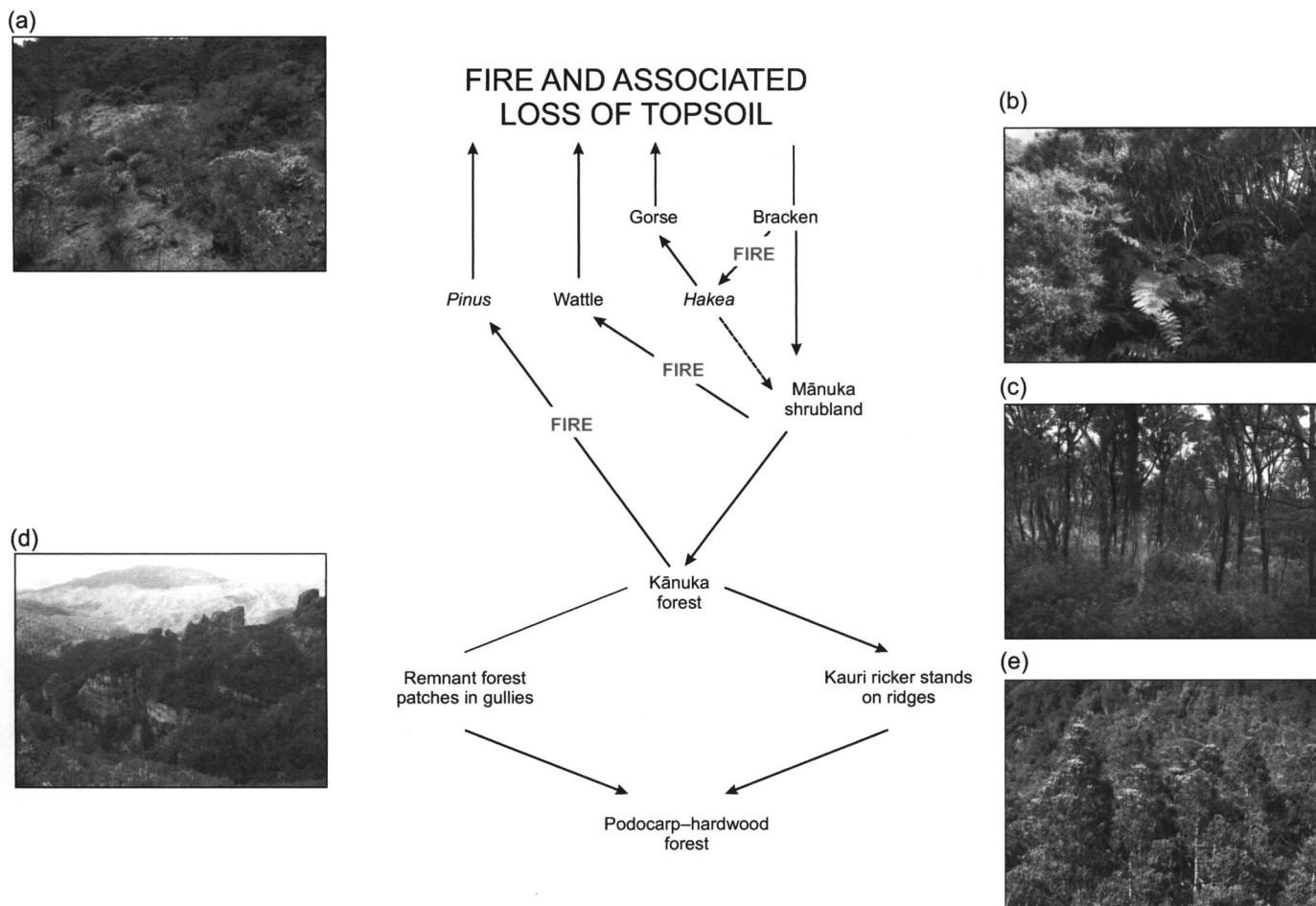
**Forests:**—Post-fire successions have been described for *Nothofagus*-dominated forest (Allen 1988; McQueen 1991; Wiser et al. 1997), kauri forest (Mirams 1957; Ogden et al. 2003) and for mixed-hardwood and podocarp-hardwood forest (McKelvey 1955; Esler 1967; Payton et al. 1984). A post-fire succession 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 (Wilmshurst & McGlone 1996; Wilmshurst 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; Marrs 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 pyrophyllic 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 pyrophyllic 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 reinvoke 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 pyrophyllic 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 pyrophytic 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 overtapped 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<sup>-1</sup>) 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 ericooides* 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 pyrophylllic 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 pyrophylllic 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 Kawerau (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

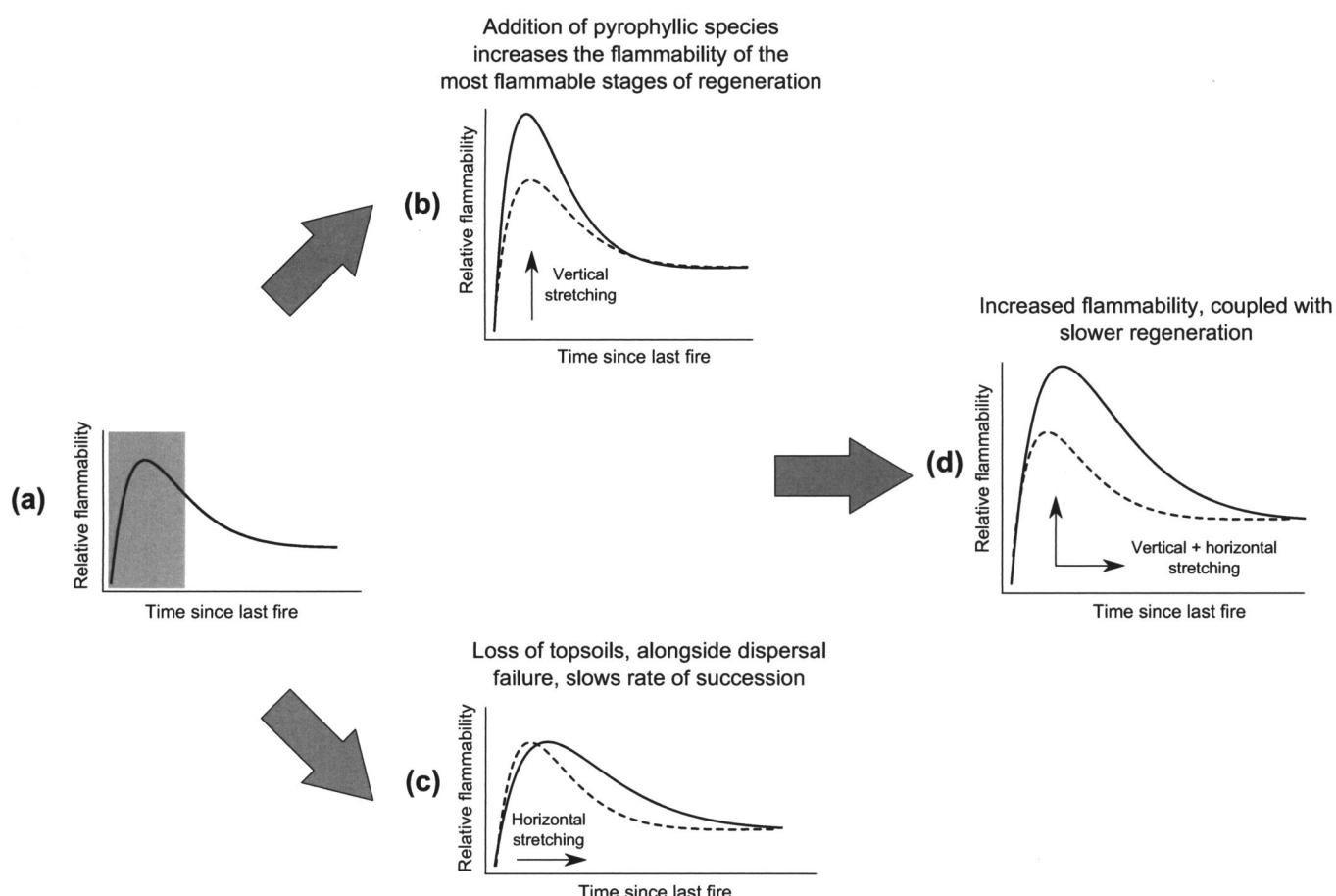
the other hand, vulnerable to invasion by pyrophytic exotics when burned, with such exotic species potentially altering secondary successional trajectories. Heathlands elsewhere in New Zealand are often maintained by fire, in combination with other disturbances such as frost. Smale et al. (2011) describe 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 *Eucalyptus 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 pyrophytic, 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.

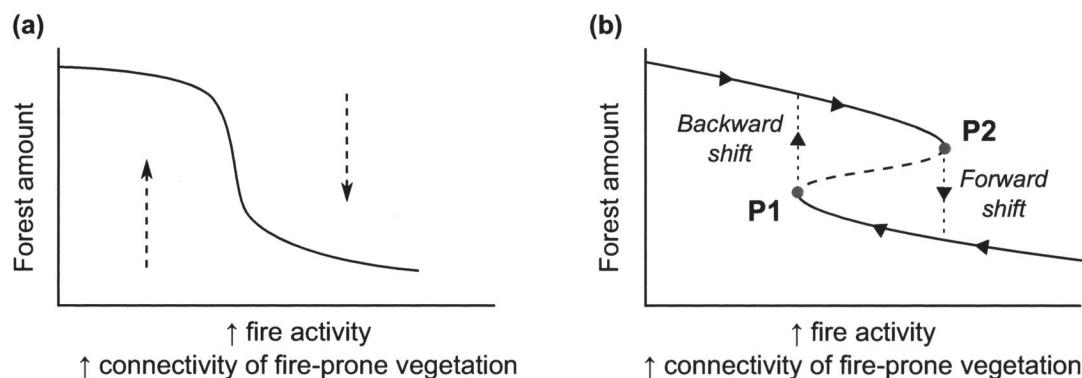
feedback. Although the humpbacked relationship is inherent in New Zealand's forests, human actions have rescaled it. Processes that slow succession, such as the loss of soils and reduced dispersal and pollination services, mean that longer is spent in more flammable early-successional stages, stretching 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 Tararuas. Ragamuffin ecosystems, comprising early-successional native species (such as *Leptospermum scoparium* and *Kunzea ericoides*), alongside pyrophyllitic 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 pyrophyllitic 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 pyrophyllitic 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).

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