

NEW ZEALAND'S INDIGENOUS FORESTS AND SHRUBLANDS

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ABSTRACT: New Zealand's remaining indigenous forests and shrublands are of immense cultural, environmental, and economic significance. Their composition, structure, and function are driven by a diverse array of factors, many of which are complexly interrelated. The imprint of disturbances is pervasive and it is necessary to understand disturbances to interpret anthropogenic impacts. For example, understanding impacts of exotic browsing mammals is only possible if they are placed in the context of forest development and tree demographic processes. Recently, a representative plot-based sample of the country's indigenous forests and shrublands has allowed an unbiased depiction of their composition and structure that is needed for international reporting, performance assessment and management prioritisation. There are now extensive areas of shrublands successional to forest, often composed of novel mixtures of indigenous and exotic species. These shrublands provide expanded opportunities for ecosystem services from, for example, carbon sequestration to water quality. An increasing area of indigenous forests and shrublands is managed for distinctive Māori aspirations that include sustainable use.

Key words: composition, disturbance, forests, function, management, structure, trends.

INTRODUCTION

New Zealand's indigenous forests and shrublands currently cover c. 23% and 10% of New Zealand's 27-million-hectare land surface respectively (Thompson et al. 2004). These largely evergreen forests have four major physiognomic elements: *Nothofagus* spp. (beech), broadleaved angiosperm trees, *Agathis australis* (kauri), and other conifers (predominantly podocarps) (Cockayne 1928; Wardle 1991). Warm temperate forests in the north give way to cool temperate forests further south (Cockayne 1926) and tree species richness also decreases from north to south (McGlone et al. 2010). Hence some of the dominant trees of warm temperate forests, such as kauri and taraire (*Beilschmiedia tarairi*), are restricted to north of latitude 38°S (Wardle 1991). Subalpine shrublands occupy the zone between montane forests and alpine grasslands and there are also extensive areas of lowland and montane shrublands that are successional to forest (Wardle 1991).

TABLE 1 Factors commonly shown to influence the structure, composition and functioning of forests and shrublands. Some of the variables commonly measured to represent these factors are given, as well as some of the mechanisms through which these factors operate (modified from Allen et al. 2003)

Factors	Variables	Examples of mechanism
Disturbance	Changes in biomass or number of trees	Individuals killed of one or more species
Herbivory	Level of defoliation, individual height growth	Reduced photosynthetic ability, nutrient removal
Species effects	Litter quality, decay resistance of woody debris	Modifies the abilities of seeds of other species to germinate and grow
Climate	Temperature, precipitation	Changes physiological processes
Soil	Texture, N availability, cation availability	Influences resources essential for growth and development
Dispersal	Seed dispersal, available regeneration niches	Seeds do not arrive at an otherwise suitable site
Time	Tree age, relative biomass	Species' differential longevity
Assembly history	Species priority effects	Facilitation

The current forest area represents a >70% reduction from the prehuman state (c. 800 years ago) due to historical fire, forest clearance, and logging (e.g. Wardle 1991). The expanding influence of humans continues to have wide-ranging stand-level, local or regional effects, for example those brought about by invasive species (e.g. Allen and Lee 2006), while others have an even broader influence, for example those brought about by an increasing atmospheric CO₂ concentration. It is often difficult, however, to determine why the structure, composition, and functioning of forests is changing. Such changes can be correlated with many factors (Table 1), some of which are relatively well characterised as they are easy to measure (e.g. precipitation), while others we know little about (e.g. individual species' effects on ecosystems). Often these factors are themselves correlated so it is challenging to define causal relationships. This chapter first describes what we know about how disturbance, and related factors (Table 1), drive change in indigenous forests and shrublands, then defines the structure and composition of current forests, what factors these relate to, and how they are changing, and finally considers the consequences of their management for ecosystem services. Our emphasis is on an ecosystem process perspective, informed by a trait-based approach.

DISTURBANCE, SUCCESSION, AND ECOSYSTEM DEVELOPMENT

Disturbances are a fundamental feature of forest ecosystems, promoting their regeneration and the maintenance of species diversity, population structure and ecosystem function. New Zealand's location at the intersection of large tectonic plates, for example, means that its vegetation is prone to disturbances that can at times be severe and extensive.

Disturbance types and ecosystem responses

Most of New Zealand's current indigenous forests bear the imprints of natural disturbances long past. The current forests, especially in the South Island, still bear the mark of past glaciations. Successive advances of ice sheets in Westland removed beech (*Nothofagus* spp.) from areas where it was present. Beech takes a long time to recolonise from margins because of slow seed spread and dependence on mycorrhizal fungi for establishment and growth (e.g. Baylis 1980). As a consequence, the forests of

central Westland now lack beech. Glaciation also has a rejuvenating effect because the glacial till includes ground bedrock, making key mineral nutrients such as phosphorus more available as glaciers retreat. Hence at Franz Josef a series of forest landscapes have developed, from very recent advances (the Little Ice Age of the 1600s) through to terraces that were last under glaciers more than 100 000 years ago (e.g. Wardle et al. 2004). In this wet climate leaching of mineral nutrients is rapid, and in the absence of glaciation, phosphorus in particular becomes limiting. Thus the forests on recently glaciated soils are highly productive and have a number of species, especially broadleaved species, that depend on ready access to nutrients. In contrast, with all else equal (e.g. climate), the forests on soils last under glaciers 120 000 years ago are dominated by slow-growing conifers that can access scarce nutrients (e.g. Richardson et al. 2004; Holdaway et al. 2011).

In the North Island, the current forests are strongly influenced by the effects of past volcanic eruptions, especially in the central North Island. The Taupō Eruption in AD 232 was one of the largest in the world over the last 5000 years, depositing pumice over most of New Zealand and causing devastating pyroclastic flows and outbreaks of fire that destroyed over 30 000 km² of forest (e.g. Wilmshurst and McGlone 1996). The rhyolitic ignimbrite and pumice deposits from past eruptions are relatively infertile whereas the more common andesitic ash showers produce fertile deposits and these have a large influence on the kinds of forests that develop. The ash showers from more recent smaller eruptions since the Taupō Eruption, such as from Kaharoa in AD 1314 and more recently from Tarawera in AD 1886, devastated forests over hundreds of square kilometres, but the nutrient-rich ash boosted the fertility of soils. The Tarawera Eruption created bare surfaces upon which forest recovery is still taking place (e.g. Walker LR et al. 2003). The larger volcanoes of the North Island, such as Taranaki and Ruapehu, have erupted since human settlement and influenced the forests around them, not only from ash and lava flows, but also from devastating lahars that have swept down their slopes. The forests of the Auckland Isthmus also are strongly influenced by volcanoes, nowhere more apparent than on Rangitoto, which was most recently active only 500 years ago (Shane et al. 2013). On Rangitoto, forests dominated by pōhutukawa (*Metrosideros excelsa*) have colonised the bare lava (Clarkson 1990).

New Zealand's position at the junction of the Australian and Pacific plates produces major earthquakes, not only along the Alpine Fault, but also along faults throughout New Zealand south of Auckland. The largest earthquake since European settlement was the magnitude 8.2 Wairarapa earthquake of AD 1855, which caused the Rimutaka Range to rise 2.5 metres, and formed new land from areas previously below the sea (Rodgers and Little 2006). The earthquake caused large landslides over an area >20 000 km² and some of those landslides have still not been colonised by forest nearly 160 years later. However, debris deposited by landslides at the base of the slopes was rich in nutrients and forests developed rapidly upon them (Robbins 1958). The effects of Alpine Fault movements are even greater. Its movement in c. AD 1615 is estimated to have instantaneously deforested about 49% of the Karangarua catchment in Westland (Wells et al. 2001) and deposited debris metres deep across Westland's floodplains (Cullen et al. 2003). Recolonisation of bare landslide surfaces typically involves colonisation by bryophytes, lichens, nitrogen-fixing herbs and shrubs, and seedlings of many forest trees, so that in the wetter zones of New Zealand forest canopies develop over new landslides within 40 years (e.g. Mark et al.

1989). Finally, some earthquakes, even those very distant from New Zealand, cause tsunamis that have almost certainly caused deforestation in coastal regions (e.g. D'Costa et al. 2011).

The hilly and mountainous regions of New Zealand are prone to landslides caused not only by earthquakes but also by storms and avalanches. Major storms attend prevailing westerly wind patterns, but many intense storms also affect eastern parts of New Zealand. Extra-tropical cyclones affect forests in the northern North Island disproportionately, but periodically intense cyclones track even to high latitudes (Martin and Ogden 2006). All such storms can cause landslides locally, and sometimes over extensive areas, for example during Cyclone Bola of 1988 (Page et al. 1999). Finally, high uplift rates coupled with unstable bedrock can result in large landslides with no obvious triggers. One such event deforested 20 hectares on the slopes of Mt Adams in Westland in 1999 (Hancox et al. 2005). Intense rainfall events in river headwaters, coupled with landslides, and especially the occlusion of gorges by debris and their subsequent breaching, can cause significant damage to riparian and floodplain forests.

The new parent material deposited by rivers across floodplains has high available concentrations of some nutrients, such as phosphorus, but is very low in nitrogen and organic matter. Shrubs such as tutu (*Coriaria arborea*) and native broom (*Carmichaelia* spp.) have symbionts on their roots that overcome nutrient limitation by fixing atmospheric nitrogen. These shrubs are often abundant on young floodplains; their nitrogen-rich litter enhances soil development (e.g. Bellingham et al. 2005). Canopy trees establish on the floodplains, but the material deposited by the floods can shape the composition and structure of future forests. For example, in South Westland, kahikatea (*Dacrydium dacrydioides*) dominates on the fine silts deposited by previous floods whereas rimu (*Dacrydium cupressinum*) dominates on coarser sands (Duncan 1993).

New Zealand's forests are also affected by disturbances that kill trees, sometimes over large areas, but leave soils less disrupted than those subject to glaciation, volcanism, landslides and flooding, providing circumstances for forests to develop from surviving plants as well as new colonisers. For example, in Northland in 1959 storms uprooted or snapped trees over large areas in kauri stands (Conway 1959) and in 1936 an intense cyclone caused extensive uprooting of trees in the Tararua Ranges (Zotov et al. 1938). Heavy snow can break tree crowns (Harcombe et al. 1998). Finally, föhn winds arising from intense westerlies can result in episodic wind-throw of trees over large areas of the eastern side of the axial ranges (Jane 1986). As even-aged forests develop following wind-throw an increasing proportion of ecosystem-level nutrients are sequestered in the aggrading live biomass, with a related decline in the decaying deadwood and soil nutrient-pools (Clinton et al. 2002). This decline in nutrient availability is one reason given for the decline in productivity, and increased susceptibility to pests and disease, as stands age.

Other weather-related events, such as drought, can kill individual trees over large areas (see Wardle 1984). The death of individual or small groups of trees changes the intensity of neighbourhood competition and this can be a major determinant of variation in tree growth within and among stands (e.g. Coomes and Allen 2007). It has been suggested that growth of small trees is more controlled by neighbourhood competition while large-tree growth is more controlled by climate (Easdale et al. 2012). Slow growth resulting from neighbourhood competition leads to high mortality rates in small trees while senescence and disturbance leads to high mortality in large trees, with low mortality in

intermediate-sized trees (e.g. Hurst et al. 2011). Neighbourhood competition is thought to be primarily for light on relatively fertile soils and for soil nutrients on relatively infertile soils (Coomes and Grubb 2000). Of course, responses to disturbance depend not only on site conditions, but also on the ecological traits of component species. For example, mountain beech (*Nothofagus solandri* var. *cliffortioides*) has fast sapling height growth in high light but is only dispersed by seed over short distances when compared with other species (Figure 1).

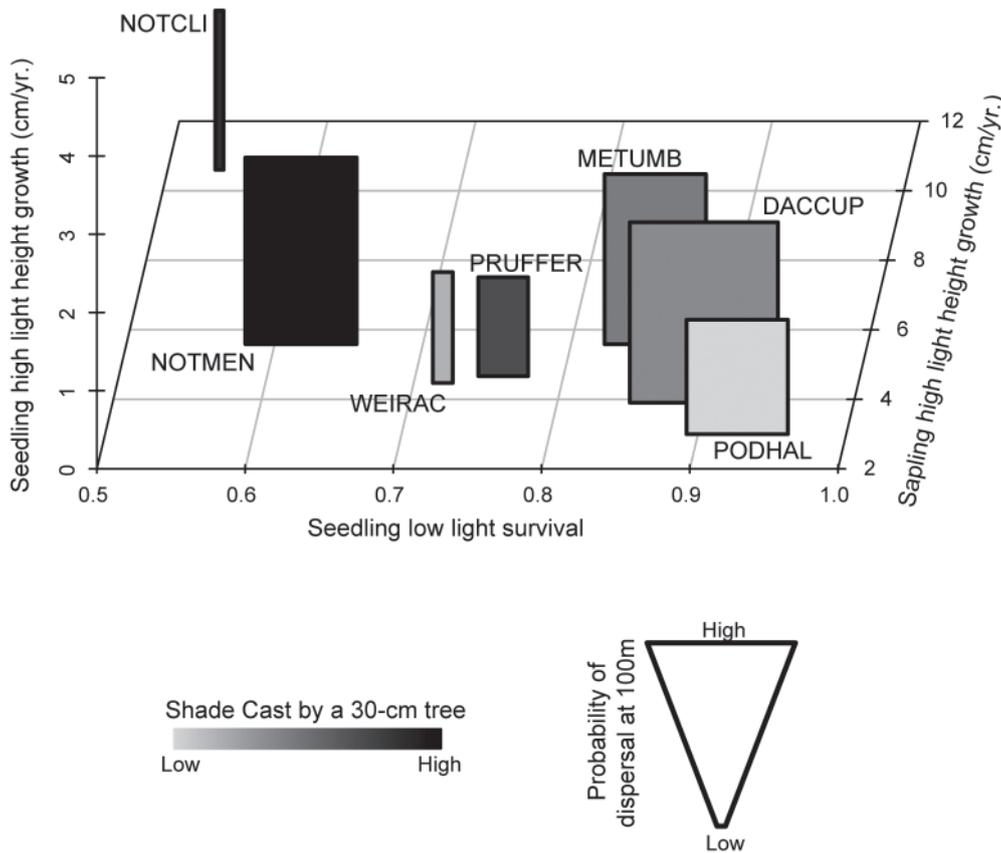


FIGURE 1 Ecological traits affecting stand-level disturbance responses. Horizontal axes show seedling low-light survival and sapling high-light height growth. The vertical axis gives the seedling high-light height growth. Thickness of the bars shows the probability of dispersal at 100 metres. The shading of the bar gives the amount of shade cast by a tree 30 cm in diameter. Component species abbreviations are: DACCUP *Dacrydium cupressinum*; PODHAL *Podocarpus hallii* (Syn. *P. cunninghamii*); PRUFFER *Prumnopitys ferruginea*; NOTCLI *Nothofagus solandri*; NOTMEN *Nothofagus menziesii*; WEIRAC *Weinmannia racemosa*; METUMB *Metrosideros umbellata* (reprinted from Kunstler et al. 2013).

Fire was rare and isolated in New Zealand's ecological history until the arrival of humans, and the vegetation is considered poorly adapted to fire (Ogden et al. 1998). Most tall New Zealand trees are killed by fire and have little capacity to recover by resprouting, although some smaller trees such as mata-gouri (*Discaria toumatou*) resprout after fire and others, such as mānuka (*Leptospermum scoparium*), regenerate profusely from seed after fire. Fires set by Māori caused deforestation of most of the eastern parts of the North Island and South Island within a hundred years of settlement (McGlone and Wilmshurst 1999). Fire disturbances to the wetter parts of New Zealand were less destructive, but areas that were frequently cultivated were burned (e.g. Wilmshurst et al. 2004), so that young forests that developed after fire were locally common. In contrast, Europeans felled and burned large areas of forests in the wetter regions of New Zealand and uncontrolled fires they set destroyed, for example, old-growth kauri forests. Modern fire damage to native forests is often at the margins of larger tracts and mostly affects young forests.

Destruction of original forests in the dry, east of both main

islands has been so complete that by the mid-1800s there were few remnants left. The reduction of seed sources and loss of dispersers, along with an ongoing regime of fire disturbance, meant that forest recovery was limited and much less species-rich than it had been before human settlement. For example, conifers, including mataī (*Prumnopitys taxifolia*) and *Phyllocladus alpinus*, were common respectively in the lowlands and uplands of Central Otago before human settlement but their destruction by fire was so extensive that they scarcely featured in any subsequent

forest successions (McGlone and Moar 1998) and both are now extremely rare in these landscapes. Modern woody successions in this region are dominated by kānuka (*Kunzea ericoides*) and, locally, some of the formerly dominant conifers, for example *Podocarpus cunninghamii* (Walker S et al. 2003). Successions after fire in wetter regions were more rapid, and often proceed through bracken (*Pteridium esculentum*; McGlone et al. 2005) or mānuka and kānuka (e.g. Atkinson 2004) to more species-rich forests. Beech forests in New Zealand are occasionally affected by fires, mostly of human origin. Extensive grasslands found on formerly forested sites in dry, eastern areas are invaded very slowly by beech species, often less than 20 metres a century, although the rate of recovery tends to increase with rainfall (Wardle 1984; Wiser et al. 1997).

Indigenous forests are also subject to disturbances caused by outbreaks of native insects and diseases. Native

insects, such as moths, can cause widespread defoliation of entire canopies in forests where single species of beech are dominant (e.g. Wardle 1984). Other insects, such as pinhole borer beetles (*Platypus* spp.) can attack live trees causing their death (Payton 1989). A recent example of a disease affecting an indigenous tree species is the agent of kauri dieback (*Phytophthora taxon Agathis* (PTA); Beever et al. 2009); although the pathogen may not be indigenous to New Zealand.

Complexities of disturbance

So far the disturbances that affect New Zealand forests have been described as if they were distinct from one another. The reality is, of course, more complex. Interactions between multiple disturbances are commonplace. For example, in mountain beech forests of the Harper–Avoca catchment, heavy snowfalls and wind storms resulted in the deaths of many trees in the 1970s and the dead wood that resulted was a breeding ground for pinhole borer beetles that attacked trees that had survived the storms, causing further mortality (Hurst et al. 2011). In 1994 these same

forests were affected by the M6.7 Arthur's Pass earthquake (Allen et al. 1999). The earthquake damage varied in intensity at a stand-scale (Figure 2) and was often the result of landslides and dislodged boulders, but the landslides also dammed streams that remained intact until snows melted causing the dams to burst and flooding of riparian areas. Widespread generation of dead wood caused by the earthquake did not result in outbreaks of pinhole borer beetles, as observed in beech forest following the 1929 M7.8 Murchison earthquake (Wardle 1984); this may have been because the following years coincided with dry summers that perhaps were not conducive to beetle breeding. A key point that emerges is that the combination of interacting disturbances – the intensity and duration of individual disturbances – may be repeated on the landscape only rarely.

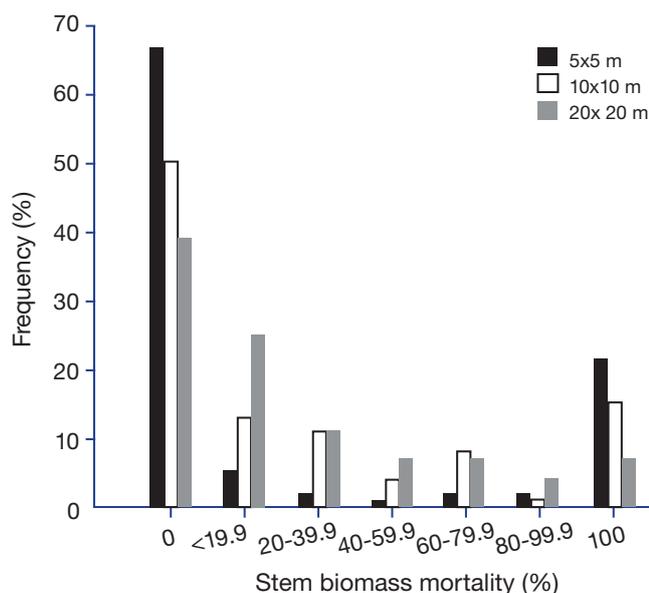


FIGURE 2 Varying intensity of stand-level earthquake damage. Frequency (%) of Basin Creek, Harper–Avoca catchment, plots (20 × 20 m), and subplots (10 × 10 m and 5 × 5 m), in classes of stem biomass mortality (%), assessed immediately before and after the Arthur's Pass Earthquake in 1994 (reprinted from Allen et al. 1999).

Disturbances also need to be defined in terms of human-related impacts. Human-induced climate change may cause more intense cyclones, and more frequent or more intense droughts. Introduced animals and diseases may increase the risk of mortality when forests are subjected to disturbance. For example, mortality of canopy trees of northern rātā (*Metrosideros robusta*) in forests near Wellington was ascribed to a combination of drought and browsing by introduced brushtail possums (*Trichosurus vulpecula*; Cowan et al. 1997). Certainly taking account of other important factors driving tree mortality (e.g. size and neighbourhood competition) should enhance our abilities to distinguish such browsing-animal impacts. Europeans have introduced many trees and shrubs that are adapted to fire, such as many pine species, gorse (*Ulex europeaus*) and *Hakea* spp.. These species create positive feedbacks with fire, so that modern forests and shrublands that contain mixtures of native trees and introduced fire-promoting species (e.g. Clarkson et al. 2011) will support more frequent fire regimes, which in turn may be even more frequent under human-induced climate change. The interactions of multiple disturbances with multiple, interacting human influences make the prediction of the composition and structure of New Zealand's future forests challenging.

STATUS AND TREND IN INDIGENOUS FORESTS

New Zealand's indigenous forests and shrublands provide habitat for a diverse range of biota. Of the 215 tree species ≥ 6 m tall, 171 (80%) are small (≤ 15 m tall), and the leaves of New Zealand's trees are smaller and narrower than those of the temperate Northern Hemisphere (McGlone et al. 2010). McGlone et al. (2004) argue that the relatively mild climate and low nutrient status of most New Zealand forest soils make a deciduous leaf phenology, with its high turnover of foliar nutrients, less competitive than the nutrient-conserving evergreen phenology found in indigenous trees and shrubs. Nevertheless, there are now c. 110 exotic naturalised deciduous trees and shrubs in New Zealand, mostly growing where indigenous forests have been cleared (McGlone et al. 2004). Even with the invasion of exotic species and, in particular, the dramatic historical deforestation, there are no native trees or shrubs known to have suffered extinction (de Lange et al. 2009), although a large mistletoe confined to forests and their margins, *Trilepidia adamsii*, is extinct (Norton 1991). This is not so for the indigenous avifauna, which has had numerous species extinctions and reductions in distribution and abundance (e.g. Innes et al. 2010). Since human arrival 31% of a total of 131 indigenous bird species have become extinct on the two main islands (Duncan and Blackburn 2004). The biotic diversity in forests and shrublands of other groups of organisms has not been fully determined, even at a stand scale, let alone at larger scales. This is largely due to the difficulties of sampling and determining cryptic biota such as invertebrates and microbes. New Zealand forests do have high fungal diversity (Buchanan et al. 2004) and fungal community assembly, for example in deadwood, has strong consequences for community composition and ecosystem processes (Fukami et al. 2010).

Our ability to depict and characterise forests and shrublands at regional and national scales has been dramatically advanced by establishment of the LUCAS (Land Use and Carbon Analysis System) permanent plot network (Coomes et al. 2002; Allen et al. 2003; Wiser et al. 2011) and its subsequent extensions on land managed by the Department of Conservation through its Natural Heritage Management System (MacLeod et al. 2012). This network consists of 1258 plots (established 2002–2007) located on an 8 × 8 km grid throughout the country's indigenous forests and shrublands (one plot every 6400 ha) (<http://www.mfe.govt.nz/publications/climate/carbon-emissions-land-use/measuring-carbon-emissions.pdf>). These plots were established to meet New Zealand's carbon emissions reporting requirements but also included measures of plant species composition, diversity, and structure (MacLeod et al. 2012). The Department's extensions include measures of bird species diversity and composition and introduced mammal distribution and abundance (MacLeod et al. 2012). For example, we now know that indigenous forests support at least twice as many indigenous bird species as exotic ones (mean plot-location species richness: indigenous = 9.49; exotic = 2.95). Of the 12 most widespread bird species, 10 are indigenous. Three species – grey warbler, tomtit, and bellbird – were found in more than 75% of indigenous forests (MacLeod et al. 2012). Brushtail possums occurred on 80% of plot locations. Occupancy was similar in beech and other types of forest. Wild ungulates (deer and goats) occurred in 75% of plot locations. Occupancy was higher on Stewart Island and the North Island than the South Island. LUCAS plot measures have also allowed us to determine the amount of coarse woody debris (CWD) in forests and shrublands. Mean plot CWD biomass was 54 Mg ha⁻¹,

with 65% as fallen CWD, and only 1% of plots had no CWD (Richardson et al. 2009).

Composition and structure of current indigenous forests and shrublands

New Zealand has a long history of collecting quantitative plot data to document the composition and structure of indigenous forests. Data from the National Forest Survey (1946–55), the 1956–69 Ecological Survey, and subsequent surveys conducted by the NZ Forest Service underpinned classifications of North Island (McKelvey and Nicholls 1957) and South Island forests (McKelvey 1984). These classifications defined forest classes using expert interpretation of these data and were based on the presence and abundance of dominant trees judged to determine both the productive capability of the forest and its protection role. The resultant classes underpinned the development of forest class maps that have been used for a wide range of conservation and management purposes. Other vegetation classifications include, for example, the Land Cover Data Base (LCDB 1, 2 and 3; Thompson et al. 2004) and ECOSAT (Dymond and Shepherd 2004). Because lowland, largely transformed landscapes have little indigenous biota there have also been attempts to depict forest and shrublands that potentially could cover cleared areas (e.g. Hall and McGlone 2006).

The LUCAS dataset has underpinned the development of a new classification of New Zealand's woody vegetation (Wiser et al. 2011; Wiser and De Cáceres 2013). This classification's goals included (a) to describe contemporary vegetation patterns given the ongoing impacts of land use change, invasion and fire; (b) to extend the scope of earlier efforts so as to describe not only old-growth forests, but also disturbed forests and shrublands; (c) to incorporate into the typology subordinate plant species occurring at a site; (d) to be both quantitative and extensible; and (e) to allow unbiased, statistically valid estimates of various parameters to be made for each type (i.e. basal area of dominant trees; cover of exotic plants and species vulnerable to browsing by exotic animals) to underpin derivation of ecological indicators.

Analysis of the LUCAS dataset allowed the more extensive types (termed 'alliances' following the International Vegetation Classification; Grossman et al. 1998) of woody vegetation to be recognised. This allowed recognition of a similar number of units as used at a national mapping scale of 1:250 000 for the Forest Class maps (NZ Forest Service Mapping Series 6) and 1:1 000 000 scale of the Vegetative Cover Map of New Zealand (Newsome 1987). Subsequently, the data from an additional 12 374 plots archived in the National Vegetation Survey Databank (NVS; Wiser et al. 2001) were incorporated into the classification to allow new alliances to be defined that were too rare on the landscape to be typified based on the LUCAS plots. The larger dataset also allowed units to be recognised at a finer level of compositional resolution by defining component associations (again following Grossman et al. 1998) within each alliance. This approaches the finer level of resolution of, for example, McKelvey (1984). Here we summarise the alliance-level classification that defined 22 forest and 7 shrubland alliances. Further information about each alliance and component associations is available at <https://www.landcareresearch.co.nz/publications/factsheets/woody-types>.

Forest alliances — Most forest alliances can be broadly grouped by physiognomy as beech, beech–broadleaved, beech–broadleaved–podocarp, broadleaved–podocarp, and podocarp

forests (Table 2; Wiser et al. 2011; Wiser and De Cáceres 2013). Within beech forest, four common alliances were defined that are dominated by black (*N. solandri* var. *solandri*) or mountain beech (two alliances), mountain/black and silver beech (*N. menziesii*), and mountain/black, silver and red beech (*N. fusca*), respectively. These alliances are much more extensive at southern latitudes of the South than North Island, are relatively species poor, have low levels of invasions by exotic plants, and abundant seedlings and saplings of the dominant canopy species. Two rare (i.e. estimated extent < 100 000 ha) alliances were defined. The first is dominated by silver beech with mountain lacebark (*Hoheria* spp.) and weeping matipo (*Myrsine divaricata*) in the subcanopy and occurs in montane and subalpine areas of South Island. The second is the only alliance dominated by hard beech (*N. truncata*) (shared with kāmahi, *Weinmannia racemosa*). It occurs in the north-western South Island and scattered North Island locations.

Three common alliances were defined within beech–broadleaved forest: Silver beech–broadleaf forest, Silver beech–red beech–kāmahi forest and Kāmahi–hardwood forest. These forests are most prevalent in wet areas of the West Coast and in Northwest Nelson, with scattered North Island locations. Species richness is moderate and levels of exotic plant invasion are low. These alliances can include associations where beech is absent (occurring in the 'beech gaps' or on Stewart Island) but share many species associated with beech. The Kāmahi–hardwood forest has a high proportion of species that are preferred by deer and possums (Wiser and Hurst 2010) and size-structure analysis suggests that unpalatable horopito (*Pseudowintera colorata*) may be increasing in importance in these forests. Total basal area tends to be higher in these forests than most others (Table 2).

Four common alliances were defined within beech–broadleaved–podocarp forest: Kāmahi–Southern rātā forest and tall shrubland, Kāmahi forest, Kāmahi–silver fern forest, and Pepperwood–hardwood forest and successional shrubland. Of these, the Kāmahi–Southern rātā forest and tall shrubland is restricted to the South Island and Stewart Island whereas the other kāmahi-dominated alliances are predominantly northern, with all excluded from drier parts of the country.

The broadleaved–podocarp forest group is the most heterogeneous with seven alliances (Table 2). The Kāmahi–podocarp and Mataī forest alliances are restricted to the South Island and Stewart Island, the Māhoe, Tawa, Silver fern–māhoe and Pepperwood–fuchsia–broadleaf forest alliances occur on both the North and South Island, whereas the Tōwai–tawa alliance occurs only on the North Island. Individual podocarp species may be emergent but are not always sufficiently dominant to be included in the alliance name. Species richness in these forests tends to be higher than in most other New Zealand forests (Table 2). The Kāmahi–podocarp and Tawa forest alliances are the most extensive of those defined by the classification, with estimated extents of 575 000 and 544 000 hectares respectively. Three alliances in this group are relatively uncommon. The Mataī forest alliance is largely restricted to the eastern South Island, north of Oamaru, the Tōwai–tawa forest alliance is restricted to the Coromandel and Northland, whereas the successional Pepperwood–fuchsia–broadleaf forest is widespread, but not extensive. Seedlings of podocarps are often present in this alliance, indicating potential successional trajectories.

No forest alliances were defined where the northern, warm temperate kauri was the most dominant tree species or was present in more than half of the plots. However, kauri commonly

TABLE 2 Characteristics of forest and shrubland alliances. Common names of alliances are preceded by a short identifying code comprising an acronym signifying the physiognomic group followed by sequential numbers for each of the alliances within that group. Distribution and elevational ranges are based both on plots used to define the alliances and on those assigned to these alliances in Wiser and De Cáceres (2013). Extent was calculated algebraically using the proportion of the suitable (see Wiser et al. 2011) 1177 grid-based sample plots (LUCAS plots) assigned to that alliance relative to the total area of 8.9 million hectares of mapped forest or shrubland sampled by those plots. For alliances defined by Wiser et al. (2011) it was possible to calculate unbiased means (and their associated standard deviations) using the data collected from the subset of 1177 grid-based sample plots (LUCAS plots) assigned to the alliance. Mean basal area was calculated from stand structural data associated with forested plots. For the alliances defined when the classification was extended by Wiser and De Cáceres (2013; indicated with *) mean species richness and mean % exotic were calculated based on those plots used to define the alliance. Figures may differ from those presented in Wiser et al. (2011) owing to changes in alliance assignment of some of the 1177 grid-based sample plots (LUCAS plots)

Alliance	Distribution	Extent (ha)	Elevational range (m)	Mean basal area	Mean species richness	Mean % exotic	No. component associations
Beech forest							
BF1: Black/mountain beech forest (subalpine)	NI, SI	219 000	220–1520	60 ± 19.1	14 ± 13.1	5 ± 7.6	3
BF2: Black/mountain beech – silver beech forest/subalpine shrubland	NI, SI	265 000	130–1420	67 ± 20.6	31 ± 10.7	2 ± 5.3	5
BF3: Black/mountain beech forest	NI, SI	189 000	100–1350	43 ± 16.0	34 ± 9.0	4 ± 4.1	2
BF4: Silver beech–red beech–black/mountain beech forest	NI, SI	196 600	100–1300	69 ± 25.7	17 ± 9.5	0	2
*BF5: Silver beech–mountain lacebark forest	SI	75 616	460–1260	58 ± 67.8	28 ± 11.3	<1	1
*BF6: Hard beech–kāmahi forest	SI	68 054	50–990	64 ± 18.3	18 ± 8.6	<1	4
Beech–broadleaved forest							
BBF1: Kāmahi–hardwood forest	NI, SI, Stewart	446 000	10–890	84 ± 33.6	56 ± 13	1 ± 1.7	6
BBF2: Silver beech–broadleaf forest	NI, SI	363 000	280–1440	81 ± 25.8	38 ± 10	<1	4
BBF3: Silver beech–red beech–kāmahi forest	NI, SI	454 000	40–1020	74 ± 26.4	36 ± 11	<1	4
Beech–broadleaved–podocarp forest							
BBPF1: Kāmahi–Southern rātā forest and tall shrubland	SI, Stewart	287 000	10–1120	68 ± 24.6	44 ± 9.2	1 ± 1.3	3
BBPF2: Pepperwood–hardwood forest and successional shrubland	NI, SI	287 000	40–1150	69 ± 31.5	41 ± 8.1	1 ± 2.4	4
BBPF3: Kāmahi forest	NI, SI	265 000	110–910	94 ± 34.2	51 ± 10.6	<1	2
BBPF4: Kāmahi–silver fern forest	NI, SI	219 000	140–490	58 ± 22.3	53 ± 12.2	2 ± 3.0	1
Broadleaved–podocarp							
BPF1: Kāmahi–podocarp forest	SI, Stewart	575 000	10–1000	77 ± 35.6	53 ± 8.9	1 ± 1.6	7
BPF2: Māhoe forest	NI, SI	280 000	40–810	65 ± 22.0	50 ± 12.0	3 ± 4.0	2
BPF3: Tawa forest	NI, SI	544 000	30–740	69 ± 23.5	51 ± 10.8	<1	6
BPF4: Silver fern–māhoe forest	NI, SI	371 000	40–480	58 ± 19.4	53 ± 11.6	1 ± 2.6	2
*BPF5: Pepperwood–fuchsia–broadleaf forest	NI, SI	45 370	10–900	56 ± 21.0	39 ± 14.5	2 ± 4.5	2
*BPF6: Mataī forest	SI	15 123	20–680	65 ± 18.3	39 ± 15.7	7 ± 6.0	1
*BPF7: Tōwai–tawa forest	NI	22 685	30–640	67 ± 44.0	50 ± 24	0	1
Podocarp¹							
*PF1: Mountain neinei–inanga low forest and subalpine shrubland	SI	22 685	740–1210	Insufficient data	40 ± 11	<1	2
Other forests							
OF1: Kānuka forest and tall shrubland	NI, SI	204 000	20–370	28 ± 1.7	44 ± 13.1	17 ± 13.5	1
Shrublands							
*S1: Kānuka shrubland with coprosma and prickly mingimingi	NI, SI	120 986	20–1010	NA	27 ± 18.4	14 ± 11.1	2
*S2: Grey scrub with kānuka	NI, SI	75 616	50–700	NA	45 ± 12.4	46 ± 11.3	1
*S3: Mānuka shrubland	NI, SI, Stewart	37 808	10–1020	NA	20 ± 12.4	3 ± 4.8	2
S4: Matagouri shrubland	SI	204 000	110–910	NA	48 ± 8.2	47 ± 14.5	1
*S5: Turpentine scrub – <i>Gaultheria montana</i> shrubland	SI	60 493	730–1360	NA	37 ± 12.4	13 ± 6.5	1
*S6: Gorse shrubland with cabbage trees	NI, SI	15 123	10–570	NA	6 ± 6.6	39 ± 17.8	2
*S7: Grey scrub with cabbage trees	SI	<7562	60–300	NA	3 ± 3.6	6 ± 14.5	1

¹ Included here is an alliance that grades from low forest to subalpine shrubland

occurs in the Tōwai–tāwa forest alliance and can have high cover. The Tawhero–kauri forest with mānuka and rewarewa association also commonly includes stands where kauri is important. An alliance with which this association can be aligned has yet to be described.

Only one alliance was classed as podocarp forest and this one is uncommon. The Mountain neinei–inanga low forest and subalpine shrubland alliance is dominated by the nominal shrubs and *Coprosma pseudocuneata*, *Archeria traversii* and mountain flax (*Phormium cookianum*). Podocarps, including Hall’s tōtara (*Podocarpus cunninghamii*) and pink pine (*Halocarpus biformis*), and also the New Zealand cedar (*Libocedrus bidwillii*), occur in 69% of the sampled stands with the lower-statured species retained in subalpine shrublands.

The Kānuka forest and tall shrubland does not fit clearly into any of the physiognomic groups. This alliance occurs primarily north of 39°S and in scattered locations elsewhere on the North and South Island. The forest is dominated by kānuka, typically with an understorey of *Coprosma rhamnoides*, mingimingi (*Leucopogon fasciculatus*), hangehange (*Geniostoma ligustrifolium*), and silver fern (*Cyathea dealbata*), and is usually successional to forest.

Shrubland alliances — Seven shrubland alliances were defined. Only one of these, the Turpentine scrub – *Gaultheria* montane shrubland, is clearly subalpine or montane; the remaining six all typically occur below treeline. Of these, the most extensive are the Kānuka shrubland with coprosma and prickly mingimingi (*Leptecophylla juniperina*), Matagouri shrubland, and Grey scrub with kānuka (Table 2). The former grades into low forest, but has a more southern distribution than the Kānuka forest and tall shrubland described above. The Matagouri shrubland occurs in areas periodically disturbed by fire, and there is often no evidence of succession to other woody alliances. Nearly half the species present are exotic, with sweet brier (*Rosa rubiginosa*) and grasses such as sweet vernal (*Anthoxanthum odoratum*) and cocksfoot (*Dactylis glomerata*) especially characteristic. The most consistent dominants of the Grey scrub with kānuka alliance are the shrub *Coprosma rhamnoides*, exotic grasses, and exotic herbs such as white clover (*Trifolium repens*), catsear (*Hypochaeris radicata*) and smooth hawksbeard (*Crepis capillaris*). Native woody species are variably dominant in the canopy including kānuka, mānuka, māhoe (*Melicactus ramiflorus*), and tauhinu (*Ozothamnus leptophyllus*). Like the Matagouri shrubland alliance, on average exotics comprise nearly half the species in a given stand (Table 2). Three less common shrublands were defined – Mānuka shrubland, Gorse shrubland with cabbage trees, and Grey scrub with cabbage trees. Given that shrublands are undersampled in NVS relative to forests in proportion to their extents, there is a need for more plot data to be collected from New Zealand shrublands to allow them to be more comprehensively described.

Trends in composition and structure

Changes in the total extent of indigenous forest and shrubland and subordinate mapped classes can be derived from successive versions of LCDB (LCDB1 based on 1996/97 satellite imagery and LCDB2 based on 2001/02 satellite imagery). Between these successive versions of LCDB c. 12 500 hectares of indigenous shrubland and c. 2200 hectares of indigenous forest were converted to non-indigenous cover nationally (Walker et al.

2006). Most of the converted shrublands were broadleaved hardwood and mānuka and were predominantly converted to exotic plantations (Walker et al. 2006). Between these successive versions of LCDB only a very small area (c. 300 ha) nationally changed to an indigenous-dominated class. It should, however, be noted that LCDB has limited success in distinguishing boundaries between some of its mapped classes, particularly shrublands (Coomes et al. 2002; Brockerhoff et al. 2008). For example, LCDB2 estimates total extent of matagouri shrublands to be < 30 000 hectares yet the LUCAS plot-based assessment estimates the extent of matagouri (averaging 40% cover) shrublands to be 204 000 hectares (Table 2). Land cover transformation will vary markedly through time, depending on, for example, drivers of land use change and the spatial scale of analysis. For example, by the early 1920s less than 1% of the Banks Peninsula region’s original 100 000 hectares of indigenous forest remained, but, by 2008 an additional 9000 hectares of broadleaved shrubland and forest had developed (Wilson 2008). Assuming there was little secondary forest in the early 1920s, then indigenous woody cover has increased from <1% to 9.8% over this time.

More-specific trends in the biota of indigenous forests and shrublands at national and regional scales are often inferred from the pooling of local datasets. For example, Forsyth et al. (2011) compiled data on deer faecal pellet counts to investigate decadal-level changes in the relative abundances of deer at the national scale for the period 1952–2010. Pellet frequencies were highest during the 1950s–1970s, declined to minima in the 1980s and 1990s, and then increased in the 2000s. The decline in pellet frequencies was probably caused by increasing commercial deer harvesting, and the recent increases in pellet frequencies are likely a consequence of reduced commercial harvesting.

Changes in indigenous forests and shrublands have also commonly been recorded using time-series data at stand level or local scales. The former NZ Forest Service established vegetation plots at many localities in forests and shrublands. Remeasurement of these plots, and others, continues to contribute to our understanding of, for example, the influence of disturbance on the structure and composition of forests (e.g. Hurst et al. 2011), weed invasions (e.g. Wiser and Allen 2006), and impacts of exotic herbivores (Husheer 2007). There is also a long history of monitoring trends in forest bird populations (see Innes et al. 2010) and the Ornithological Society of New Zealand maintains an expanding database on bird observations. Currently there is considerable interest in how the public can contribute observations of biotic change – and certainly there is room to consider how this can be done in a quantitatively robust way.

As the LUCAS plots are remeasured they provide the unbiased data required to determine national and regional trends in the composition, structure, and function of indigenous forests and shrublands. The plots remeasured to date show, for example, that kāmahī, a species highly palatable to brushtail possums, deer, and goats, was regenerating 10 years ago across indigenous forests on conservation land and is continuing to regenerate now. The diameter-size-class structure of kāmahī did not change between 2002–2007 and 2009–2012, and both distributions followed a ‘reverse J’ shape, indicative of a self-replacing population (MacLeod et al. 2012). Clearly exotic herbivores can have dramatic impacts in some forests but these may not be pervasive and much is to be gained from understanding where, when and why they have impacts (Wardle 1984).

MANAGEMENT AND PROVISION OF ECOSYSTEM SERVICES

About 80% of New Zealand's remaining indigenous forests are publicly owned and managed by the Department of Conservation under the Conservation Act 1987, which requires them to be managed mainly for conservation purposes. A wide range of activities are considered compatible with conservation goals, but timber production is not one of them. There are c. 1.5 million hectares of indigenous forests that are privately owned. Māori organisations own and manage significant, and increasing, areas of these indigenous forests. For example, under Tūhoe's Deed of Settlement for Te Urewera (2013), a new governance structure was defined that empowers Tūhoe to have a greater decision-making role in the management of indigenous forests and shrublands in Te Urewera. More generally iwi have aspirations for kaitiakitanga (guardianship) that include sustainable use guided by the application of mātauranga (traditional knowledge) in decision making and environmental monitoring (e.g. Lyver et al. in press). For example, observations of the flock sizes and harvest of kererū (*Hemiphaga novaeseelandiae*) were used to construct declining trajectories of the abundance of this pigeon in parts of Te Urewera over the last 80 years (Lyver et al. 2008).

Over the last 50 years the area dominated by native woody species has increased in some areas as land that was formerly used for agriculture, or was otherwise deforested, is now following a successional process through shrublands (see shrubland alliance descriptions). Some of the areas on formerly agricultural land are in the eastern South Island (e.g. Matagouri shrubland); these extensive lands are part of the 'tenure review' process. Under this process the government purchased the improvements on leasehold lands from individual farmers, and the lands retired from grazing are now managed by the Department of Conservation. This process is not without tensions, and debate centres on the level of payment made to farmers, the conservation value of these lands, and what management options and ecosystem services are possible from these shrublands (e.g. Brower 2008).

Conservation of biodiversity

In recent decades, there has been a shift from the view that the conservation role of indigenous forests is largely about water catchment protection to the view that forests are important for biodiversity. Current management of indigenous forests for biodiversity is often aimed at restoring a state close to that before either Māori or European settlement. However, at some locations indigenous forests are undergoing century/millennium-level (not long, relative to species' longevity) compositional and structural changes that reflect transient dynamics (e.g. McGlone et al. 1996; Kunstler et al. 2013). There is also increasing recognition that historical impacts of humans have implications for contemporary forests. For example, there is debate about the likely effects of moa (e.g. *Dinornis* spp.) browsing being removed from ecosystems c. 500 years ago (e.g. Atkinson and Greenwood 1989; Forsyth et al. 2010). In general, though, most of the current concern about threats to biodiversity focuses on the elimination or fragmentation of ecosystems, often the result of land-use change and intensification, and degradation through loss or reduced abundance of species, usually as a result of invasive weeds and pests. To these we add threats from climate change, increasing atmospheric CO₂ concentrations, fire, and exploitative industries (e.g. mining). It is of note that human-related impacts on biodiversity may not be reversed merely through the removal of a causal agent (e.g. for exotic herbivores see Coomes et al. 2003). This leads to an

important distinction between those threats that can and should be countered and those that cannot or should not be.

Land-use change and intensification — The transformation and loss of indigenous forest biodiversity has been pronounced as a consequence, mostly historical, of land-use change and intensification. While halting further loss of indigenous forest cover may be seen as a simple challenge, controlled by the Resource Management Act 1991, it is in fact fraught with economic, social, and political barriers. New Zealand has now lost the structural dominants (trees) over extensive areas, and where shrublands reverting to forest occur in production land settings the shrublands are usually a blend of indigenous and exotic species – creating 'novel-ecosystems' (Hobbs et al. 2006). There is a tension between the pressure to clear these shrublands for productive land use versus allowing them to revert to forest with consequent carbon storage and biodiversity benefits. Managing for biodiversity in these shrublands requires an understanding of the complex interactions of indigenous and exotic species and how these interactions play out on the landscape. Exotic species provide essential services to indigenous species, including exotic vertebrates dispersing seeds and fruits of indigenous species (e.g. Dungan et al. 2002) and exotic shrubs facilitating succession to indigenous forest (e.g. Wilson 1994; Bellingham et al. 2005). In fact, exotic birds, insects, and plants are regarded by some as enhancing and diversifying lowland agricultural systems. While there is an increasing interest in enhancing some indigenous biodiversity components in these blended systems, in part orientated around sustainability credentials of industry, there is a critical lack of research and robust biodiversity monitoring in production landscapes (MacLeod and Moller 2006; Moller et al. 2008) when compared with the Natural Heritage Management System established on conservation lands (MacLeod et al. 2012).

Invasive species — Invasive species can have severe deleterious effects on native biodiversity. In New Zealand, the problem is compounded by the high number of introduced species (Allen and Lee 2006). Exotic animal species of greatest concern largely fall within two groups: browsing animals that can alter forest structure and composition; and, animal predators that can deplete the indigenous fauna. There is also increasing recognition that many other introduced organisms may be having significant impacts on ecosystems (e.g. *Vespula* wasps; Beggs and Wardle 2006).

Impacts of introduced browsing animals vary according to the animal's stage of colonisation and abundance, environmental factors, and features of particular indigenous forests and shrublands (Wardle 1984). Modification of the forest understorey is sometimes caused by browsing animals, with the widely distributed red deer (*Cervus elaphus scoticus*) being the most significant animal, although other ungulate species (pigs, goats, and other species of deer) can be important. Forest types are differentially susceptible to browsing by animals and those most modified by red deer, for example, grow on recently disturbed sites and contain a high proportion of palatable species (e.g. Stewart et al. 1987). Throughout the country subjectively located study plots have been fenced to exclude ungulate browsing (exclosures). In some forests ungulates have lowered the abundance of palatable plants in the understorey relative to outside fenced areas (e.g. Smale et al. 1995). Outside others, selective browsing has favoured an increase of some browse-resistant, or tolerant, species in the understorey (Allen et al. 1984). Others show little difference between the insides and outsides of exclosures (e.g. Bellingham

and Allan 2003). Using a national set of such fenced exclosures, Mason et al. (2010) showed that ungulate impacts are less significant in mature than disturbed forest stands. It is worth noting that browsing patterns also vary among deer species; for example, sika deer (*Cervus nippon*) appear to have greater impacts on seedling abundance of tree species than red deer (Husheer et al. 2006). It also remains unclear how often browsing of seedlings by ungulates is demographically significant to the maintenance of palatable tree and shrub species (e.g. Forsyth et al. 2010). This may be important to resolve as LUCAS plots show palatable plants to be widespread and abundant in forest understoreys at a national scale (Peltzer and Mason 2010; Wisser et al. 2011).

Brushtail possums defoliate some canopy and subcanopy tree species (e.g. kāmahī, *Fuchsia excorticata* and some *Pseudopanax* species), and defoliation by brushtail possums may elevate tree mortality rates (e.g. Bellingham and Lee 2006). Selective browsing has resulted in *Peraxilla* and *Alepis* mistletoes becoming locally rare (Wardle 1991). Brushtail possums also eat fruits that are important food sources for the indigenous fauna (e.g. Leathwick et al. 1983). Possum control can, for example, sometimes reduce mortality rates of kāmahī, one of New Zealand's most abundant indigenous tree species, at local scales (e.g. Gormley et al. 2012) – over most of its range, however, there is no possum control yet kāmahī remains abundant (see Trends in Composition and Structure section).

Introduced predators, including brushtail possums, can have a major impact on forest fauna (Clout 2006). The most studied of these is the relationship between periodic heavy beech seeding and predator dynamics. Heavy seeding leads to a rapid build-up of rats (*Rattus rattus*) and mice (*Mus musculus*), which in turn leads to a build-up of stoats (*Mustela erminea*). When rodent numbers decline on depletion of the seed crop the stoats are forced to feed upon the avifauna (King 1983). Such a pattern appears responsible for the decline of several forest bird species, as exemplified by mōhua (*Mohoua ochrocephala*) in the South Island. Control of multiple predators can result in the population recovery of some bird species (e.g. O'Donnell and Hoare 2012). Fortunately, a few simple climate variables can be used to predict most of the variation in tree seeding, although their relative contributions vary with soil fertility, and this may well provide a cue for predator control (e.g. Smaill et al. 2011). Restoration of forest avifauna, severely threatened by predators, may require careful breeding programmes in combination with other activities such as the removal of predators (Jamieson et al. 2009). Depletion of the avifauna can have flow-on consequences for forest ecosystems, for example, predation of ground-nesting seabirds can result in a loss of nutrient subsidies to coastal forest communities (e.g. Fukami et al. 2006).

In New Zealand there are as many naturalised exotic plant species as there are indigenous ones (Williams and Cameron 2006). This results in a large pool of potential weeds to manage in forests, but particularly in shrublands, and, at least for reserves, this is likely exacerbated by human activity (Timmins and Williams 1991). Exotic plant species invading forest were listed by Wisser and Allen (2006), who concluded that the most invaded forests are those that were species-rich or occurred either at low altitudes in the North Island or in the eastern or northern South Island. Successional shrublands can be highly invaded (Wisser et al. 2011) with impacts on ecosystem processes. For example, increasing biomass of the exotic shrub *Buddleja davidii* increased mineral soil P, whereas increasing biomass of

the native shrub *Coriaria arborea* increased soil N (Bellingham et al. 2005). Dickie et al. (2010) contrasted the ectomycorrhizal fungal communities associated with exotic *Pinus contorta* with co-occurring indigenous *Nothofagus* and found fungal communities on *Pinus* were dominated by exotic (93%) and cosmopolitan fungi (7%), whereas *Nothofagus* had native-dominated fungal communities (e.g. *Cortinarius*) and cosmopolitan fungi.

There has been a long history of controlling exotic browsing animals, and to a lesser degree predators and weeds, for biodiversity conservation. The Department of Conservation controlled goats, deer, brushtail possums, and weeds, in various ways, on 1.40, 0.37, 0.24 and 0.48 million hectares respectively in the 2011/12 year (Department of Conservation 2012). The challenge of financing this control is becoming increasingly complex because of a burgeoning number of exotic species, poorly known effects on biodiversity and ecosystem dynamics, complicated interactions between species, and very limited finances. Although information sources such as the Department of Conservation's Natural Heritage Management System will improve the basis for allocating resources and assessing management effectiveness, the conceptual basis for making choices needs to be progressed. One choice is about when and where commercial models (as widely undertaken for venison) are desirable for control rather than recreational, community or governmental models. Certainly partnered models hold potential, and exotic animal control operations to combat agriculturally important diseases such as bovine tuberculosis could enhance biodiversity benefits in combination with control motivated by community action.

Fire — Although remaining forests are now often found only in steep, high rainfall areas, there is still a potential for anthropogenic fires to destroy forests and arrest succession during dry years. The Department of Conservation maintains a database of ignitions occurring within one kilometre of conservation land boundaries, and this totals over 3000 ignitions dating back to the early 1990s. The average cost for the Department's fire management in recent years is \$7.4 million a year, with about 700 hectares of public conservation land being burnt (<http://www.doc.govt.nz/conservation/threats-and-impacts/fire/>). Increased regulation of rural fires, further understanding of the threat of fire, and improved fire-fighting techniques should reduce the potential for fires, but increased accessibility of the public to forests means fire remains a threat. The National Rural Fire Authority is adopting a Wildfire Threat Analysis (WTA) system, which is a systematic method of identifying the level of threat a particular area faces from wildfire. The level of threat is generally related to a combination of ignition potential, potential fire behaviour and the values threatened. The positive feedback caused by fire-supporting and promoting (pyrogenic) exotic species (e.g. *Pinus contorta*, *Cytisus scoparius*) that are invading some deforested localities adjacent to indigenous forests and shrublands adds to the level of threat.

Other issues — The removal of forests and shrublands for the purposes of roading, farming, gold and coal mining is still undertaken today on limited areas. Restoration has been undertaken, for example, to re-establish forest on mined areas (e.g. Langer et al. 1999). There is also an increasing interest more generally, particularly by community groups, to reforest with indigenous species. Although the area planted so far is modest, some areas have garnered intense popular interest, for example Tiritiri Mātangi, an island that was planted with native trees between 1984 and 1994 to create habitat for land birds and is now a major tourist

attraction (Rimmer 2004). This is particularly important to some iwi and, for example, Ngāti Whare's recent Deed of Settlement with the Crown facilitates, with associated funding, the conversion of 750 hectares of pine plantation into podocarp-dominated indigenous forest.

Historically the extraction of timber in some areas has modified biodiversity and influenced many other forest values. The value of natural forests as habitat for birds and other fauna; their ability to produce honey, game and furs; their efficiency in the protection of soil and regulation of water and nutrients; and their aesthetic appeal, were all modified by timber production (Wardle 1984). In 1993, Part 3A of the Forests Act 1949 came into force to protect the values of privately owned indigenous forests managed for timber production (see Timber Production section below).

While the trend of increasing atmospheric CO₂ concentrations over recent decades is globally consistent, the trends in climate are not, and New Zealand has not experienced the marked warming trend found in continental areas of the Northern Hemisphere (see McGlone and Walker 2011). Higher than ambient atmospheric CO₂ concentrations have been shown to increase photosynthesis and decrease transpiration in tree seedlings (Hollinger 1987) and climate envelopes for species distributions have been used to suggest potential consequences of climate change (Leathwick and Mitchell 1992). However, there is little evidence that suggests movement of tree species in New Zealand in response to modern climate change. For example, there has been demonstrable upward movement of treelines in the Northern Hemisphere over the last century, but New Zealand treelines have been stable (Harsch et al. 2012). Moreover, any consideration of climate change effects must account for potential nutrient (e.g. nitrogen) limitation, particularly given the low nutrient status of many forest soils. It may be that climate change effects will be most pronounced in drier eastern parts of the country through alteration of disturbance regimes, for example with increased incidence of wildfire.

Timber production

The extraction of timber from indigenous forests, particularly of kauri and podocarps, has historically been exploitative and has led to much controversy over the last half century (e.g. Benecke 1996). Over this time harvest levels have declined dramatically.

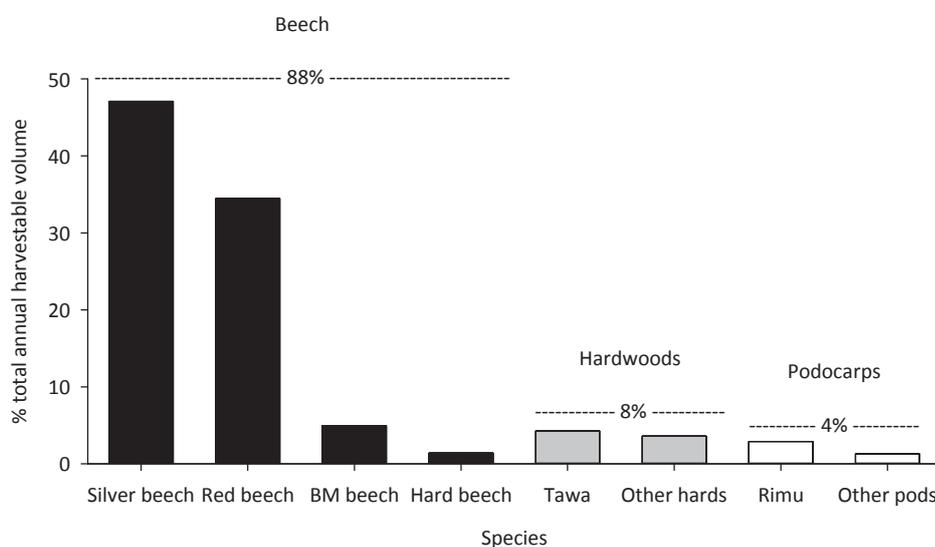


FIGURE 3 Summary of annual harvestable timber volumes (m³) of indigenous tree species (BM = Black Mountain) included on approved sustainable management plans registered with the Ministry for Primary Industries, December 2006. Total volume = 80 007 cubic metres (from Richardson et al. 2011).

Now national demand for high-value timber outstrips supply and imports of such timber have increased dramatically (\$357 million in 2005). Imports are often from unsustainably managed forests and, more alarmingly, are commonly illegally harvested.

In New Zealand, the Forests Act 1993 has provisions specifying how indigenous forests should be managed for timber production. In beech forests the harvested areas can be no greater than half a hectare, unless specific approval has been obtained for a larger area (up to 20 ha; Ministry of Agriculture and Forestry 2009). Further, regeneration must have reached a predominant height of 4 metres and a stocking of the harvested species equal to or greater than pre-harvest levels before adjacent harvesting can occur. The Forests Act also aims to achieve an appropriate balance between productive use and maintenance of the forests' natural values (e.g. native versus exotic dominance). These provisions have been implemented in second-growth beech forest, resulting from historical land clearance and logging, as well as in old-growth forest. In practice, harvest operations tend to be from either selective, group-selection, small-coups (0.1 – 0.2 ha), or coupes of ~0.5 hectare, and typically little silvicultural tending of developing stands is undertaken (Allen et al. 2012). Annual volume increments of up to 6 m³ ha⁻¹ are possible. For podocarps, the Act requires: typically 5% of live standing basal area may be harvested every 10 years; harvesting of only trees >30 cm in diameter at breast height; a proportion of the largest trees shall be retained as wildlife habitat; and, trees shall be harvested as individuals or small groups of up to five trees.

Depending on the ecological characteristics of the constituent species, the size of harvested area will influence the relative growth of species differently and, ultimately, the composition of the developing forest. For example, with increasing size of harvested patch, red beech seedlings have an increasing competitive advantage in terms of height growth over silver beech, so that silver beech will form a smaller proportion of the dominant canopy trees (Wiser et al. 2007). Forest structure is also influenced by the level of compensatory growth by residual trees (e.g. Wiser et al. 2005). The Forests Act provisions so far seem appropriate for maintaining the stand structure of beech forests, although there can be short-term biodiversity changes in understorey plant

(Wiser 2001) and ecto-mycorrhizal (Dickie et al. 2009) communities. The merits of the podocarp provisions are less clear as podocarps are often thought to regenerate following extensive disturbance (e.g. Kunstler et al. 2013). Another challenge is in applying the provisions when a forest owner wishes to convert an already modified forest into a former structure and composition, as for Tūhoe where podocarps have been logged from podocarp-hardwood forest (e.g. Carswell et al. 2012a).

New Zealand timbers, such as silver beech, have distinctive properties (e.g. colour, grain) valued by niche markets in the USA, Australia, and Japan (e.g. Donnelly 2011). Some forest owners recognise this and, notwithstanding the overall decline in harvest, between

1993, when the Forests Act was introduced, and 2006, the area covered by approved plans and permits grew to 120 154 hectares, across 450 properties. Certainly beech species dominate the allowable harvest (Figure 3). Māori are key participants in indigenous forestry and many of the plans and permits approved by the Ministry for Primary Industries are for Māori-owned forests. Māori owners often have broad (social and environmental) sustainability goals and seek management solutions sensitive to their needs. Increasing demand for high-value timber will only translate into an expanded indigenous forest industry if it meets legislated environmental sustainability requirements, international agreements, and forest owner aspirations. Market expectations are becoming increasingly selective through product certification.

Carbon storage and sequestration

Forests store, and can sequester, significant amounts of carbon and in recognition of this the United Nations Framework Convention on Climate Change requires parties to report on carbon emissions from such vegetation. This requirement is part of the rationale for establishing the LUCAS plots to provide a basis for unbiased estimates of carbon stocks. Holdaway et al. (2010) have estimated there are 5611.7 megatonnes of CO₂ equivalents (CO₂e) currently stored in the live stem and coarse woody debris pools in New Zealand's indigenous forest and shrubland. There is also considerable potential for carbon sequestration through restoration of indigenous forest on lands marginal for pastoral agriculture (Trotter et al. 2005). Holdaway et al. (2010) have gone on to model potential carbon stocks as 7485.8 Mt CO₂e, giving a long-term potential increase of 1874.1 Mt CO₂e in existing indigenous forest and shrubland if the effects of historical and ongoing anthropogenic disturbance were removed. Potential carbon sequestration in indigenous forest and shrubland has been estimated at between 6 and 12 Mt CO₂e yr⁻¹ for the period 2010–2022 (Holdaway et al. 2010). Given that New Zealand's gross emissions were 74.7 Mt CO₂e yr⁻¹ in 2008, and are forecast to rise to 83.5 Mt CO₂e yr⁻¹ by 2020 (Ministry for the Environment 2010), indigenous forest and shrublands represent a significant potential sink to offset these increasing emissions.

The potential for indigenous forest and shrubland carbon sequestration, or losses through deforestation and degradation, are spatially and temporally variable (Holdaway et al. 2010). It is currently assumed that indigenous forests are in a steady state with the natural environment, and thus carbon neutral (Ministry for the Environment 2010). This seems unlikely, particularly at regional or local scales, because of the imprint of disturbance. For example, significant (>10%) catchment-scale (10 000 ha) variation in live-tree biomass has been demonstrated as a result of tree death (Coomes et al. 2012), although the level to which this causes temporal variation in total biomass carbon depends upon the decay resistance of woody debris and the growth of residual trees (Mason et al. 2013). Indigenous forests are managed for invasive species and it would be desirable if biodiversity and carbon benefits were congruent. The influence of browsing animals on carbon stocks, however, is context-specific (e.g. Peltzer et al. 2010), difficult to measure (e.g. Holdaway et al. 2012) and carbon benefits do not always correlate with biodiversity benefits (e.g. Wardle et al. 2007).

To maximise carbon sequestration, woody successions are desirable that favour species either with high wood density, fast growth, or large stature (Carswell et al. 2012b). While

carbon accumulation during succession has been often modelled (Holdaway et al. 2010; Mason et al. 2012), few field measurements have been made to allow estimates of its spatial and temporal variability (Carswell et al. 2012b). Sequestration rates of 8.4, 8.4 and 9.2 Mg CO₂e ha⁻¹ yr⁻¹ have been determined for kānuka–red beech, coastal broadleaved hardwood and mānuka shrubland successions respectively (Trotter et al. 2005; Carswell et al. 2012b). Carbon sequestration during succession can be congruent with biodiversity gains (Carswell et al. 2012b) and erosion control. While a significant portion of this sequestration will occur naturally, some organisations and landowners are changing land use and management for carbon sequestration opportunities. For example, the Permanent Forest Sink Initiative promotes the establishment of permanent forests on previously unforested land where this establishment is a direct result of human activities (www.mpi.govt.nz/forestry/funding-programmes/permanent-forest-sink-initiative.aspx) and EBEX21® provides carbon credits from regenerating indigenous forests (www.ebex21.co.nz).

Other values

A wide range of other activities are undertaken in indigenous forests and shrublands, including recreation, tourism, research, mining and commercial hunting (Wardle 1984). While exotic browsing animals are largely treated as pests on conservation lands, they create commercial opportunities with animals harvested for meat and furs, as well as for recreational purposes (e.g. Parkes and Murphy 2003). Indeed, the commercial opportunity for red deer harvesting has led to significant control of that species. Commercial operations have few restrictions and harvest rate largely depends on profit and the resilience of animal populations rather than appropriate levels for conservation values (Parkes 2006). Brushtail possums have been more resilient to commercial activities than red deer and numbers remain relatively high.

While indigenous timber production is currently limited to private lands this is not so for all harvest of indigenous biota, *Sphagnum* moss and honey, for example. The main source of honey from beech forests is honeydew produced from the sap and secreted outside the tree by a scale insect (*Ultracoelostoma assimile*). This is largely harvested from forests in the northern half of the South Island. Honey bees compete with indigenous fauna for the honeydew resource but also potentially provide pollination benefits in the face of a depleted fauna (e.g. Moller and Tilley 1989). There will continue to be pressures for more products from indigenous forests and Māori have long presented a view that it is their traditional right to harvest species such as native kererū.

Recreation and tourism are major economic activities, as many visitors focus on the outdoors and visiting key national parks. With limited road access, most visitors are concentrated into a few well-known areas. For the 1.5 million visitors (2011/12) to lands managed by the Department of Conservation that organisation supports 14 000 kilometres of tracks, 24 visitor centres and 970 huts (Department of Conservation 2012). In some areas there are indications of overuse. The planned expansion of New Zealand's tourist industry will increase pressures on the conservation values of the forests and there is an expanding partnership between the tourism industry and conservation organisations.

The long-held view that forests stabilise slopes and reduce sediment transport in streams was challenged by geomorphologists

in the 1970s. They argued that erosion was primarily controlled by long-term tectonic processes and as such New Zealand had dynamic landscapes with high erosion rates (McKelvey 1995). In 1988 Cyclone Bola struck the East Coast of the North Island delivering a strong reminder of the slope-stabilising benefits of indigenous forests and shrublands at timescales relevant to contemporary society (McKelvey 1995). Indigenous forests and shrublands along riparian margins also provide benefits for stream water quality though woody cover often reduces water quantity.

CONCLUDING REMARKS

We appear to be entering a phase where society is increasingly demanding the multiple services provided by indigenous forests and shrublands. This is an important development as it provides opportunities for partnered support of policy, governance, and management. We expect, at a decadal level, there will only be increasing demands for the services provided by forests and shrublands, accompanied by an expanding range of threats, and competition for the financial resources required to mitigate these threats. Meeting these demands still requires a much greater understanding of the ecological, cultural and economic values ascribed to New Zealand's indigenous forests and shrublands, how these values are interrelated, and what needs to be done to protect them.

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