

REVIEW ARTICLE

New Zealand forest dynamics: a review of past and present vegetation responses to disturbance, and development of conceptual forest models

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Abstract: New Zealand forests have been and are shaped by a suite of disturbance types that vary in both their spatial extent and frequency of recurrence. Post-disturbance forest dynamics can be complex, non-linear, and involve multiple potential pathways depending on the nature of a perturbation, site conditions, and history. To capture the full range of spatial and temporal dynamics that shape forest ecosystems in a given area, we need to use and synthesise data sources that collectively capture all the relevant space-time scales. Here we integrate palaeoecological data with contemporary ecological evidence to build conceptual models describing post-disturbance dynamics in New Zealand (NZ) forests, encompassing large temporal and spatial scales. We review NZ forest disturbance regimes, focussing primarily on geological and geomorphic disturbances and weather-related disturbances but also considering the role of anthropogenic disturbance in shaping present-day NZ forests. Combining information from 58 studies of post-disturbance forest succession, we derive conceptual models and describe forest communities and forest change for conifer-angiosperm (including kauri forest), and beech forests (pure and mixed). The methods used in these studies included chronosequences, assessments of stand dynamics, longitudinal studies, palaeoecological reconstructions, and comparisons with historical observations; the temporal range of the studies extended from 15 years to millennia (c. 14 000 years BP). Our models capture the generalities of NZ forest dynamics, and can be used to support modelling and help guide decision-making in areas such as ecosystem restoration. However, this generality limits model resolution, meaning the models do not always portray the specific features of individual sites and successional pathways. There is, therefore, scope for more detailed, site-specific development and refinement of these frameworks. Finally, our models capture successional pathways and native plant communities from the past and present; invasive species, climate change, and exotic plant pathogens are likely to alter future forest dynamics in novel and unpredictable ways. These models, however, provide us with baselines against which to interpret and assess the impacts of such effects on forest composition and processes.

Keywords: beech forest; conifer-angiosperm forest; forest succession; invasive species; kauri forest; neo-ecology; palaeoecology; vegetation disturbance

Introduction

The forested landscapes of Aotearoa New Zealand (NZ) are shaped by large and infrequent disturbance events that are challenging to describe, but fundamental to forest ecosystem change. Historically, botanists from Cockayne (1928) onwards viewed NZ forests through a classical Clementsian lens, following the guiding paradigm of the time (Clements 1916, 1936), whereby forests were deemed to reach an equilibrium or 'climax' state of long-term stability dominated by broadleaved angiosperms. More recently, however, ecologists such as Ogden (1985), Bray (1989), and Ogden and Stewart (1995), recognised the central role that disturbances play in NZ forests, fundamentally shifting the way we view NZ forest dynamics. It is evident that patterns and processes in NZ's forest ecosystems are expressed and operate across a broad range of spatio-temporal scales, combining the primary and secondary successions that result from disturbances ranging in spatial extent from individual tree-fall gaps (Ogden 1988)

to destructive events covering thousands of square kilometres (e.g. Wilmshurst & McGlone 1996).

Disturbance events can promote complex and non-linear ecosystem dynamics such as path-dependence and, under some conditions, abrupt ecosystem state changes (Filotas et al. 2014; Johnstone et al. 2016). The temporal frequency of disturbances is often related to their size, with localised disturbances such as wind-throw and flooding typically more frequent than disturbances such as catastrophic volcanic eruptions (Delcourt et al. 1983; Fig. 1). Very large and infrequent events may lead to primary successions, and can be disproportionately important in their ecological effects (Turner et al. 1998). Thus, such events must be considered in any model of forest dynamics, although their rarity makes this challenging (Kunstler et al. 2013).

To develop models describing vegetation dynamics that span a broad range of spatial and temporal extents, evidence from different data sources, including palaeoecological records, must be integrated to ensure all relevant scales are captured (Willis et al. 2010). While direct observations of

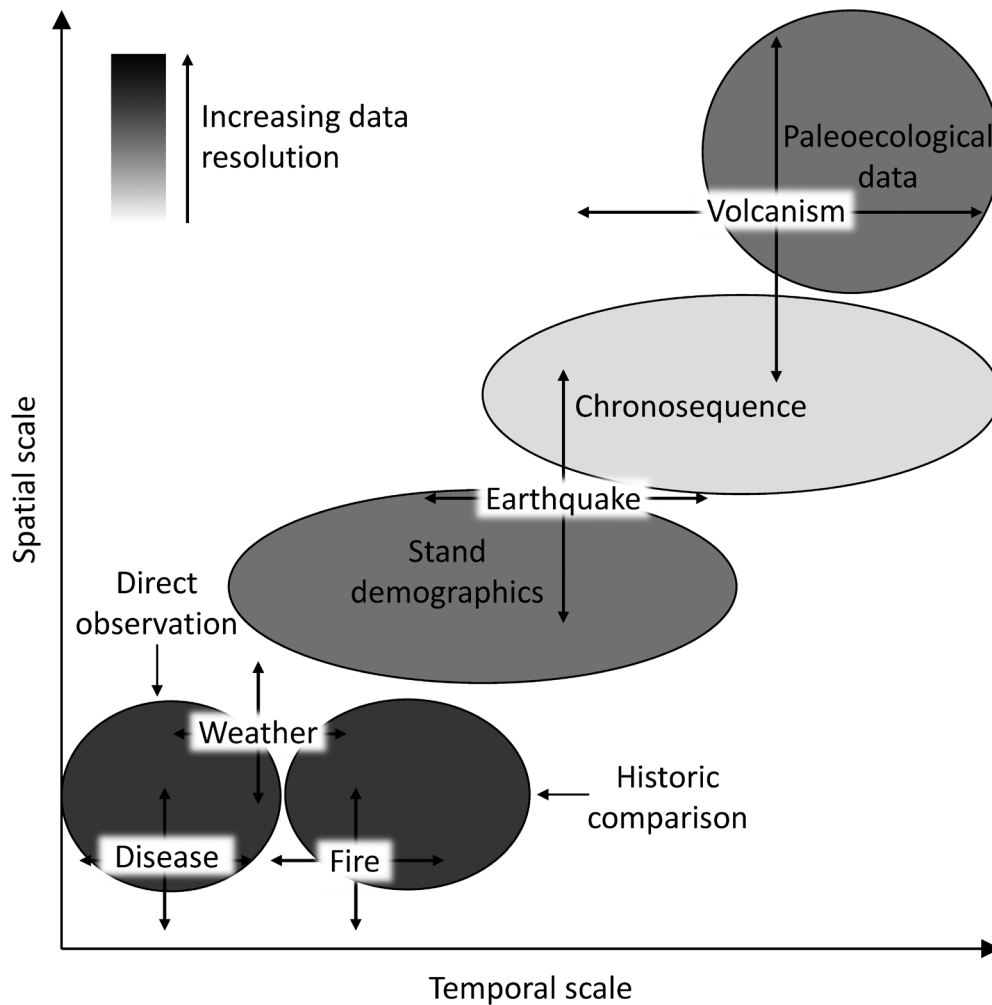


Figure 1. Conceptual diagram indicating the spatial and temporal scales of the dominant disturbance types in New Zealand forests, and the sources of data suited to capturing forest dynamics at these different scales. Shading of the ellipses indicates the resolution of the data.

vegetation change and historical comparisons are appropriate for measuring dynamics in response to relatively small and frequent perturbations, long-term (i.e. palaeoecological or chronosequence [the ‘space for time’ approach]) data are required to capture large, infrequent disturbances and ecosystem responses to them (Delcourt et al. 1983; Lindbladh et al. 2013). These different methods all have their own benefits and drawbacks, with temporal and spatial direct observation and comparison with historical accounts providing detailed and accurate information, but only for small snapshots of successional time. By contrast, palaeoecological data can provide long-term records, but at lower resolution, and typically with little spatial information (Fig. 1). The use of chronosequences has received criticism where observations are used to infer mechanisms or erroneous temporal linkages are assumed, yet when appropriately applied they can allow valuable insight into vegetation dynamics and soil development over time (Johnson & Miyanishi 2008; Walker et al. 2010). Finally, although palaeoecology has much to contribute to the understanding of forest dynamics, the opportunity for increased integration of palaeoecology with forest ecology and conservation science remains (Willis et al. 2007; Lindbladh et al. 2013; Wilmschurst et al. 2015; McGlone et al. 2017).

There has been considerable study of both the long-term history of NZ forests, and their neo-ecology (i.e. the ecology

of the present and recent past, as opposed to the geological timescales that are the subject of palaeoecology). Our goal here is to synthesise the knowledge gained from this prior work to develop conceptual models describing post-disturbance NZ forest dynamics, with particular respect to landscape-level disturbances. We start by briefly describing NZ forest ecosystems and the major disturbances that affect them. We then integrate information from a diversity of methodological approaches in conceptual models for the major NZ forest types, incorporating geological and geomorphic events (volcanic eruptions, earthquake-induced landslides and other mass movements), landscape-level disturbances that result from extreme weather (landslides, wind-throw, flooding, drought-induced mortality, and lightning-initiated fire), and anthropogenic disturbances, particularly human-ignited fire. Our aim is to derive models of NZ forest dynamics that describe baseline vegetation patterns and trajectories of community change. Such baseline models are vital if ecologists are to understand how factors such as changing climatic conditions and novel species assemblages, disturbance regimes, and plant diseases might impact NZ’s forests and the future trajectory of successions. We highlight key community types and transitions that are being altered from these baselines by novel disturbances, exotic weeds, and mammalian browsers, leading to present-day changes in forest structure.

New Zealand forest dynamics

Dominant New Zealand forest types

New Zealand is an archipelago in the South Pacific. The three main islands (Te Ika a Māui North Island, Te Waipounamu South Island, and Rakiura Stewart Island) span c. 1450 km (13°) of latitude from 34°23' S to 47°17' S, while offshore islands extend the latitudinal range north to 29°14' S (Rangitāhua Kermadec Islands) and south to 52°37' S (Motu Ihupuku Campbell Island group). Approximately 60% of the country is above 300 m in elevation, with the highest elevations of over 3000 m occurring in the Southern Alps of the South Island (Molloy 1998). On the main islands, mean annual temperatures at sea-level range from 16 °C in the north of the country to 10 °C in the south. The interception of the prevalent westerly winds by the Southern Alps results in a strong east-west rainfall gradient in the South Island (from < 500 to > 4000 mm yr⁻¹). Edaphic conditions vary across the country, reflecting its diverse geological history (Molloy 1998). Forest composition also varies considerably across NZ as a function of underlying soil, climate, topography, and geology (Singers & Rogers 2014). Nevertheless, NZ's native forests (Fig. 2) can be divided into two broad classes: beech forests

(with Nothofagaceae), and mixed conifer-angiosperm forests (including the northern forests where kauri *Agathis australis* is patchily dominant); these forest types have been described in detail by Wardle (1984), Wardle (1991), Ogden and Stewart (1995), Leathwick (2010), Wisser et al. (2011), Allen et al. (2013) and Singers and Rogers (2014). Our nomenclature here follows the New Zealand Plant Conservation Network (www.nzpcn.org.nz).

Forests where southern beech species (Nothofagaceae, specifically *Fuscopora* spp. and *Lophozonia menziesii*) comprise the major forest element, whether in pure associations or in mixtures with conifers or broadleaved angiosperms, account for approximately 60% of what remains of New Zealand's indigenous forests (Wisser et al. 2011; Allen et al. 2013). Beech-dominated forests are the least floristically diverse of NZ's forest types (Ogden et al. 1996) and are typically associated with higher latitudes and elevations, and lowland areas with infertile and poorly drained soils (Wardle 1984). Mixed conifer-angiosperm forests are characterised by conifers in an emergent tier, and a canopy composed of various broadleaved angiosperms (Ogden & Stewart 1995). Although most common in lowland areas where Nothofagaceae are absent, mixed conifer-angiosperm forest also occupies

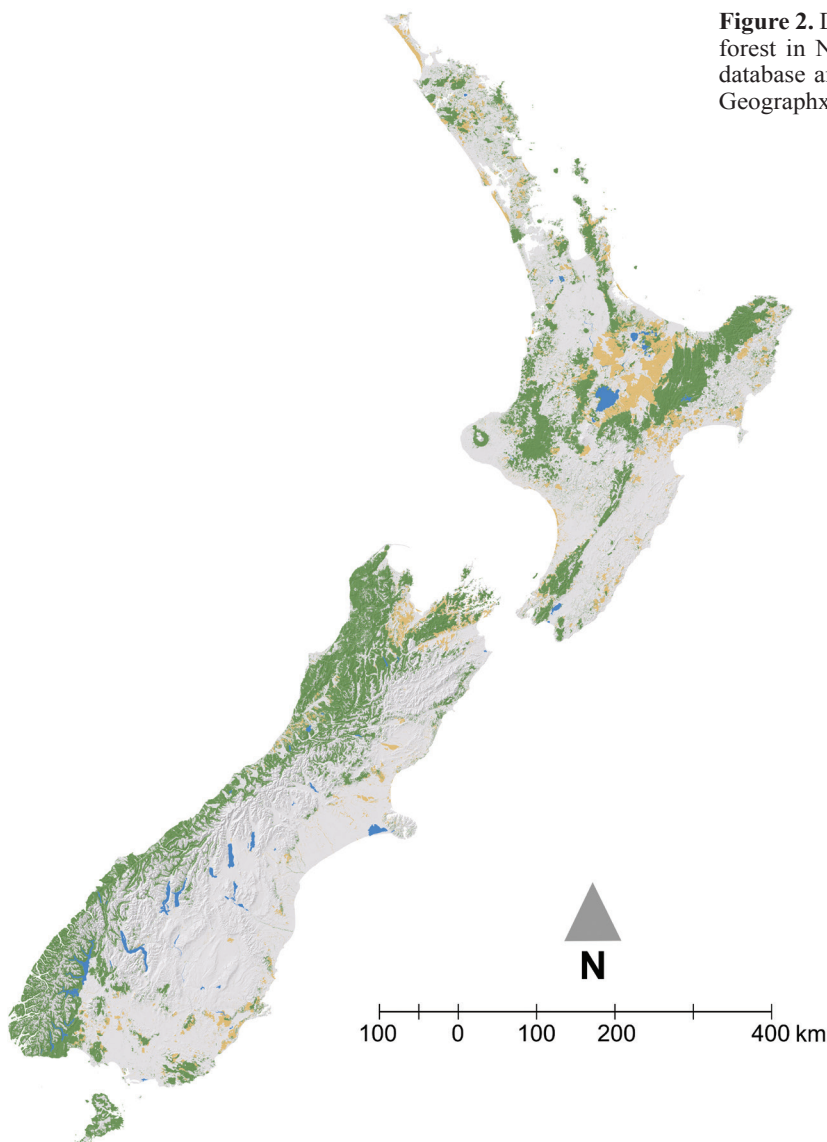


Figure 2. Distribution of indigenous (green) and exotic (orange) forest in NZ. Data: forest data from LINZ 1:50 000 NZTopo database and topographic data 100 m hillshade available from Geographx (www.Geographx.co.nz).

montane and subalpine zones as an alternative to southern beech forests. These mixed forests can be regarded as 'two-component' systems, in which the conifer and angiosperm components often occupy different forest strata and regenerate in response to disturbances of different spatial extents and frequencies (Ogden et al. 1996), implying the importance of disturbance regime characteristics for the co-existence of different plant groups.

New Zealand forest disturbance regimes

Geological and geomorphic disturbances

At ecological time-scales, large and infrequent disturbance events are key agents of state-change in NZ's forests (Table 1); however, the dominant disturbance types vary across the country, based on topography, local climatic patterns, and regional geology (Fig. 3). New Zealand is highly geologically active, and its position on the boundary between the Pacific and Australian Plates has resulted in extensive volcanism in the North Island during the Pleistocene and Holocene (Shane et al. 1996), and the rapid uplift of the Southern Alps in the South Island over the last c. 5 Ma (Cox & Findlay 1995; Heenan & McGlone 2013).

Palaeoecological records show extensive forest disturbance as a result of major volcanic eruptions in the North Island, such as in Auckland, Taranaki, and the Taupō Volcanic Zone (Fig. 3c) (e.g. Nicholls 1959; McGlone et al. 1988; Newnham & Lowe 1991; Lees & Neall 1993; Wilmshurst & McGlone 1996). The 1850 years BP Taupō eruption, for example, overwhelmed 20 000 km² of forest with ignimbrite, and damaged forests up to 170 km east of the vent with wind-blown ash-fall (Pullar et al. 1977; Wilmshurst & McGlone 1996). Primary successions were widespread across the bare

pumice surfaces that formed following the eruption, and fossil charcoal evidence suggests that localised fires continued for some decades after the eruption (McGlone 1981; Wilmshurst & McGlone 1996). Lahars are also a feature of central North Island volcanoes (Cronin et al. 1997; Newnham & Alloway 2004). Such events may occur for decades after an eruption as deposits are remobilised, temporarily damming water courses (Manville et al. 2005), and can cause significant localised forest destruction (Rapson et al. 1998). Minor eruptions from active volcanoes and geothermal areas continue to cause significant localised vegetation damage (e.g. active volcanoes in the central North Island such as Tarawera, Ngāuruhoe, and Ruapehu; Efford et al. 2014).

The major fault-line causing the uplift of the Southern Alps (the Alpine Fault) extends from the far southwest to the far northeast of the South Island. This fault-line and the network of others that traverse the country are the foci for major earthquakes (Fig. 3a), with at least 24 major earthquakes (magnitude $M_w > 7$) on the Alpine Fault in the last 8000 years (Berryman et al. 2012), including three in the last 600 years (Wells et al. 1999). Many earthquakes on smaller fault lines have also caused significant damage to New Zealand forests this century, as evidenced by the November 2016 M_w 7.8 Kaikōura earthquake (Hamling et al. 2017). Earthquakes centred offshore can also lead to forest disturbance, as they can cause tsunami that have almost certainly deforested coastal regions in the past (D'Costa et al. 2011).

Approximately 70% of New Zealand is classified as hilly (12–28° slopes) or steep land (> 28° slopes) (Molloy 1998; Fig. 3b). This steep and dissected terrain experiences frequent landslides, and the creation of landslide-dammed lakes, often in association with major earthquakes; e.g. the 2016 Kaikōura earthquake led to thousands of landslides and multiple new

Table 1. Forest disturbance regimes in pre-human New Zealand. Note that recurrence times indicated are for a region as a whole, rather than the return interval at a specific site.

Disturbance source	Disturbance type	Recurrence time (Y)	Reference	Spatial scale	Range
Volcanism	Pyroclastic flow	c. 2000	Rogers et al. (2005)	Regional	North Is.
	Ash-fall	c. 200–400	Rogers et al. (2005)	Regional	North Is.
	Lava-flow	c. 200–400	Rogers et al. (2005)	Catchment	North Is.
	Fire	c. 200–400	Rogers et al. (2005)	Regional, catchment, stand	North Is.
	Lahar	Variable		Catchment	North Is.
Earthquake	Landslide, debris avalanche	c. 100–200	Wells et al. (1999)	Catchment, stand	NZ-wide
Extreme weather	Landslide	c. 2–6 (site dependent)	Hicks (1991)	Stand	NZ-wide
	Wind-throw	Variable, cyclone frequency: c. 10 years	Shaw (1983)	Stand, individual	NZ-wide
	Snow break	Variable		Stand, individual	Lower North Is., South Is., Stewart Is., NZ-wide
	Flooding	Annual		Stand	NZ-wide
Lightning strike	Fire	Low	Perry et al. (2014),	Catchment, Stand, individual	NZ-wide
Drought	Stand mortality	c. 2–5	Salinger (1979), Burrows and Greenland (1979)	Stand	NZ-wide
Disease, insects	Stand mortality	Variable, may exacerbated by events such as wind-throw, snow break		Stand	NZ-wide

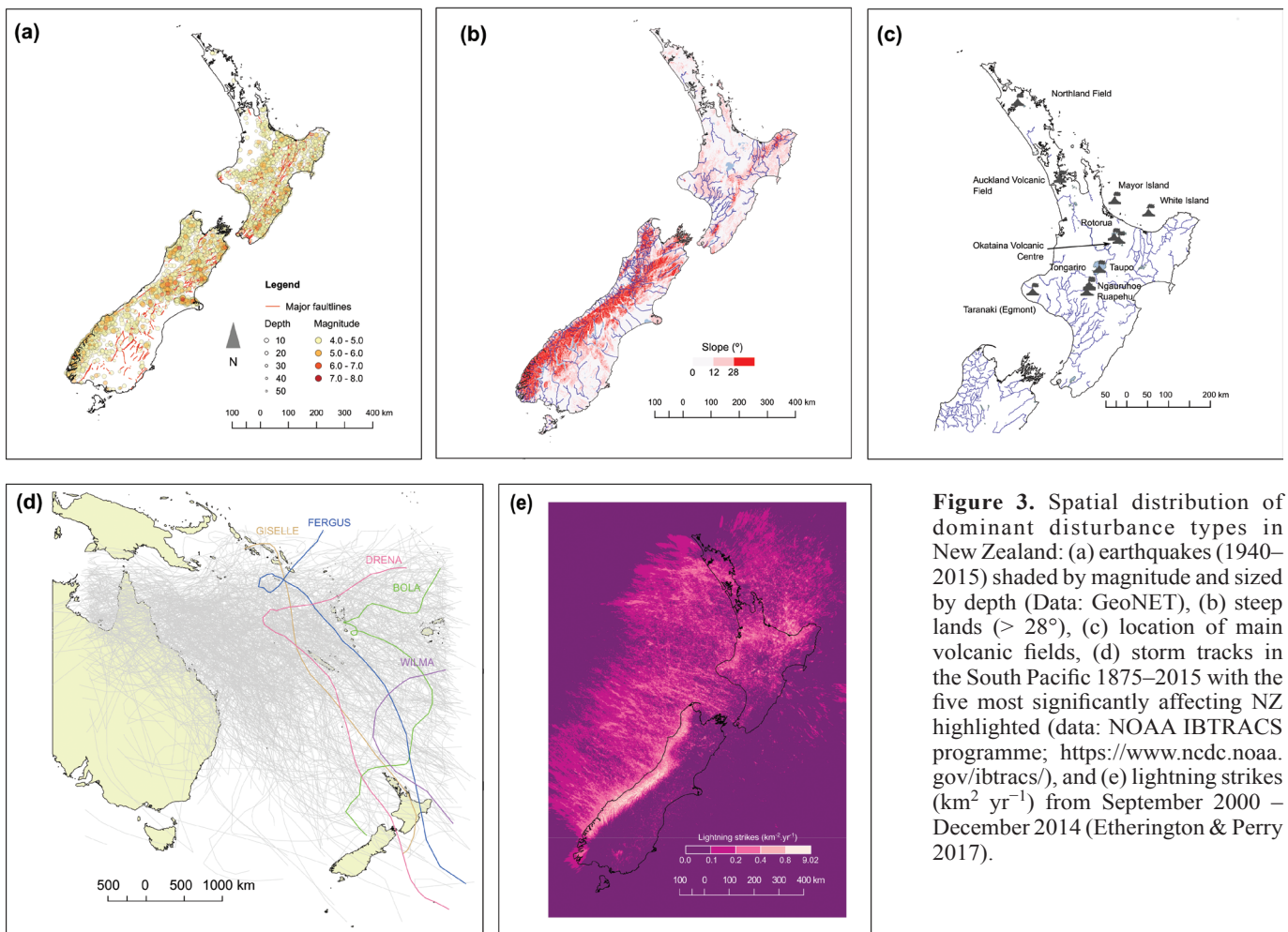


Figure 3. Spatial distribution of dominant disturbance types in New Zealand: (a) earthquakes (1940–2015) shaded by magnitude and sized by depth (Data: GeoNET), (b) steep lands ($> 28^\circ$), (c) location of main volcanic fields, (d) storm tracks in the South Pacific 1875–2015 with the five most significantly affecting NZ highlighted (data: NOAA IBTRACS programme; <https://www.ncdc.noaa.gov/ibtracs/>), and (e) lightning strikes ($\text{km}^2 \text{yr}^{-1}$) from September 2000 – December 2014 (Etherington & Perry 2017).

lakes. The Southern Alps, in particular, have a history of forest disturbance resulting from earthquake-induced landslides (e.g. Allen et al. 1999); these events are evident in the pollen record (e.g. Cowan & McGlone 1991) and in the age structures of extant tree populations (e.g. Wells et al. 1998; Wells et al. 2001). Earthquake triggered activity is not limited to the Alpine Fault; for example, the M_w 8.2 Wairarapa Earthquake (1855) caused 2.5 m of uplift in the Rimutaka Range and triggered landslides up to 400×200 m in extent (Robbins 1958).

Weather-related disturbances

While rainstorm-induced landslides are frequently associated with anthropogenic forest loss and conversion to pasture (Marden & Rowan 1994; Glade 1998), observation of landslides in forested areas suggests that they are also a natural source of forest disturbance during periods of high rainfall (Jane & Green 1983a, b). In northern and central New Zealand, intense rainfall events are usually associated with decaying tropical cyclones (Fig. 3d) (Shaw 1983; Wardle 1991). The return interval of landslide-inducing rainstorms varies based on local weather patterns and may range from a few years in the eastern North Island (Hicks 1991) to centuries in the Taranaki region (Blaschke et al. 1992).

The strong winds associated with storms are likely the single most widespread disturbance agent in many New Zealand forests (Martin & Ogden 2006; Moore et al. 2013; Moore & Watt 2015). The severity of wind-damage relates

to factors such as tree species and size, edaphic conditions, topography, and previous disturbance history (Martin & Ogden 2006). Stands most vulnerable to wind-throw include those that have been recently disturbed by other processes, are on saturated soils, and contain taller trees. Canopy and rooting architecture also influence resistance to wind-throw (Conway 1959; Shaw 1983; Martin & Ogden 2006). Recently, the tail-end of Cyclone Ita caused extensive wind-throw throughout conifer-angiosperm forests in Westland (Platt et al. 2014). Wind-damage can initiate forest dieback in beech forests as the resultant abundant woody debris harbours the larvae of pinhole borer (*Platypus* spp.); the adults of which attack living trees and act as a vector for the fungal pathogen *Sporothrix*, leading to tree death when the beetles are present in sufficient numbers (Ogden 1988; Hosking & Hutcheson 1998).

Other climate-related sources of forest disturbance include snow-break and drought-induced mortality. Snow-break is most prominent in areas of beech forest, where heavy snow can cause canopy breakage and snap or uproot whole trees (Wardle & Allen 1983). Severe summer droughts occur irregularly but, unlike snowfalls, may simultaneously affect forests throughout large areas of the country. Droughts can cause rapid and widespread forest changes, and drought-induced mortality has been recorded in all of New Zealand's major forest types (Atkinson & Greenwood 1972; Skipworth 1981; Grant 1984; Innes & Kelly 1992). The recorded frequency of drought ranges from about twice per decade on average in the

Auckland Region, up to every 2 years in the eastern South Island (Burrows & Greenland 1979; Salinger 1979; Salinger & Porteous 2014; Palmer et al. 2015). As with wind-throw, the effects of both snow-break and drought can act synergistically with insect and pathogen attack, a phenomenon particularly noted in beech forests (Skipworth 1981; Wardle & Allen 1983; Hutcheson & Hosking 1986). Finally, floods, frosts, and hail also act as important climate-related disturbance agents or initiators of stand dieback in many parts of the country, although severe frosts and hail only rarely cause significant changes to forest composition (MacKenzie & Gadgil 1973; Smith & Lee 1984; Kelly 1987; Shaw 1987; Duncan 1993; Redpath & Rapson 2015).

Prior to human settlement, widespread fires were rare in New Zealand's ecosystems and natural ignitions were infrequent and mostly confined to wetlands and to dryland communities in central Otago (Ogden et al. 1998; Perry et al. 2014). Today, lightning strike rates are still extremely low (Etherington & Perry 2017; Fig. 3e). Storms bringing lightning are typically associated with rain-bearing frontal systems and are most common in wetter ecosystems (Ogden et al. 1998), although they can occasionally cause ignitions (e.g. Hinewai Reserve, Banks Peninsula 2011; Perry et al. 2012). While ridge-tops and individual trees may be struck by lightning in such storms, the resulting burns are small and more extensive fires are extremely rare (Perry et al. 2014). Ogden et al. (1998) suggest that prior to human settlement, return times for fires at the same site may have been in the order of centuries or even millennia (see also McGlone 2001; Rogers et al. 2007). As discussed previously, extensive forest fires can also occur in association with volcanic eruptions, but these too were infrequent and limited to the North Island.

Anthropogenic disturbances

Since Māori settlement of NZ in the mid-13th century (Wilmshurst et al. 2008), followed by European arrival in the early 19th century, NZ's disturbance regimes have been rescaled in space (effective size increased due to fragmentation and habitat loss) and time (made more or less frequent). Repeated and widespread fires have been the dominant disturbance agent during the period of human settlement in NZ (Perry et al. 2014), with burning responsible for the largest part of forest loss over this time (from c. 90% forest cover pre-arrival to c. 24% today). Burning favoured indigenous seral species such as *Pteridium esculentum*, *Leptospermum scoparium*, and, in wetlands, *Typha orientalis*. Since European settlement, repeated burning has also facilitated invasion by fire-favoured species such as *Ulex europaeus*, *Cytisus scoparius*, and *Hakea* species. The outcome of widespread fire, alongside loss of pollination and seed dispersal services (Kelly et al. 2010) and increased herbivory by invasive mammals (Gormley et al. 2012), has been arrested successions in some areas (e.g. Te Urewera, Richardson et al. 2014 [field-based study]; northern NZ, Perry et al. 2015 [simulation study]), loss of dryland forest types (Rogers et al. 2005), and altered successional trajectories (Wilmshurst et al. 2014). Additionally, arrested successions can result from exotic grassland inhibiting the regeneration of woody species (West 1980; Standish et al. 2009; Mitchell 2013).

Conceptual models for New Zealand forests

To develop the conceptual models we undertook an extensive literature search of the NZ ecological and palaeoecological literature (including 'grey' literature). We reviewed data from 58 studies that detailed New Zealand forest community change following landscape-level disturbance (see Table S1 in supplementary material). These studies encompassed the full range of New Zealand forest types in locations from the far north (Dodson et al. 1988) to Stewart Island (Veblen & Stewart 1980); our aim was not to compile an exhaustive list of successional studies in NZ, but rather to derive information from a diverse range of studies that allowed us to identify the main stages in forest dynamics across forest and disturbance types. The methods used in the studies we considered included: chronosequences, assessments of stand dynamics, direct observations of change (longitudinal studies), palaeoecological reconstructions, and comparisons with historical observations (Fig. 4a). The temporal scope of the studies ranged from 15 years (1980–1995 AD: Wiser et al. 1997) to millennia (up to c. 14 000 BP: Wardle 1980) (Fig. 4b). The studies covered three major types of disturbance: (1) geological and geomorphological events (volcanic eruptions and earthquake-induced landslides); (2) extreme weather events (wind-throw, landslides and flooding); and (3) fire (Fig. 4c). Although fires were infrequent prior to human occupation they are one of the most-studied disturbances in the literature detailing contemporary forest successions in New Zealand. Of the studies included in this review, the majority of fire successions are anthropogenic in origin, with just one-fifth (Dodson et al. 1988; Newnham 1992; McGlone & Moar 1998) based on the palaeoecological record prior to the arrival of humans. The diverse data we have been able to draw on have allowed us to capture the dynamics of NZ's two broad forest types in response to the three major sources of disturbance listed above, including those that occur only at geological timescales. We also include information from several key studies that describe arrested successions or changes to forest structure that have resulted from modern influences on NZ's forests: invasive plants and animals, and changes in disturbance regimes. The major influences of these factors on modern NZ forests are illustrated with respect to the baseline forest dynamics that we describe.

Using the available data, we attempted to draw broad parallels among different studies and sites in terms of the composition of forest states, the trajectories of forest change, and the length of time for succession to shift a community from one to another state. However, the inherent variation among sites results in differences in both the composition of the vegetation states, and the time that they persist during a succession, across geographic and environmental gradients. Although we have tried to capture some of this variation in the descriptions of the states in the following sections, as well as in the timescales stated on the models themselves, as with any model these are generalisations and are provisional. Furthermore, some of the pathways may occur only under certain site conditions or disturbance regimes, and therefore the trajectories of forest change we describe may not all occur at any given site. Conceptual models for beech forests and conifer-angiosperm forests are depicted in Figs 5 and 6, respectively. In these models, the transitions between community states may result from either disturbances of varying types and magnitudes, or a critical period without disturbance (i.e. successional change).

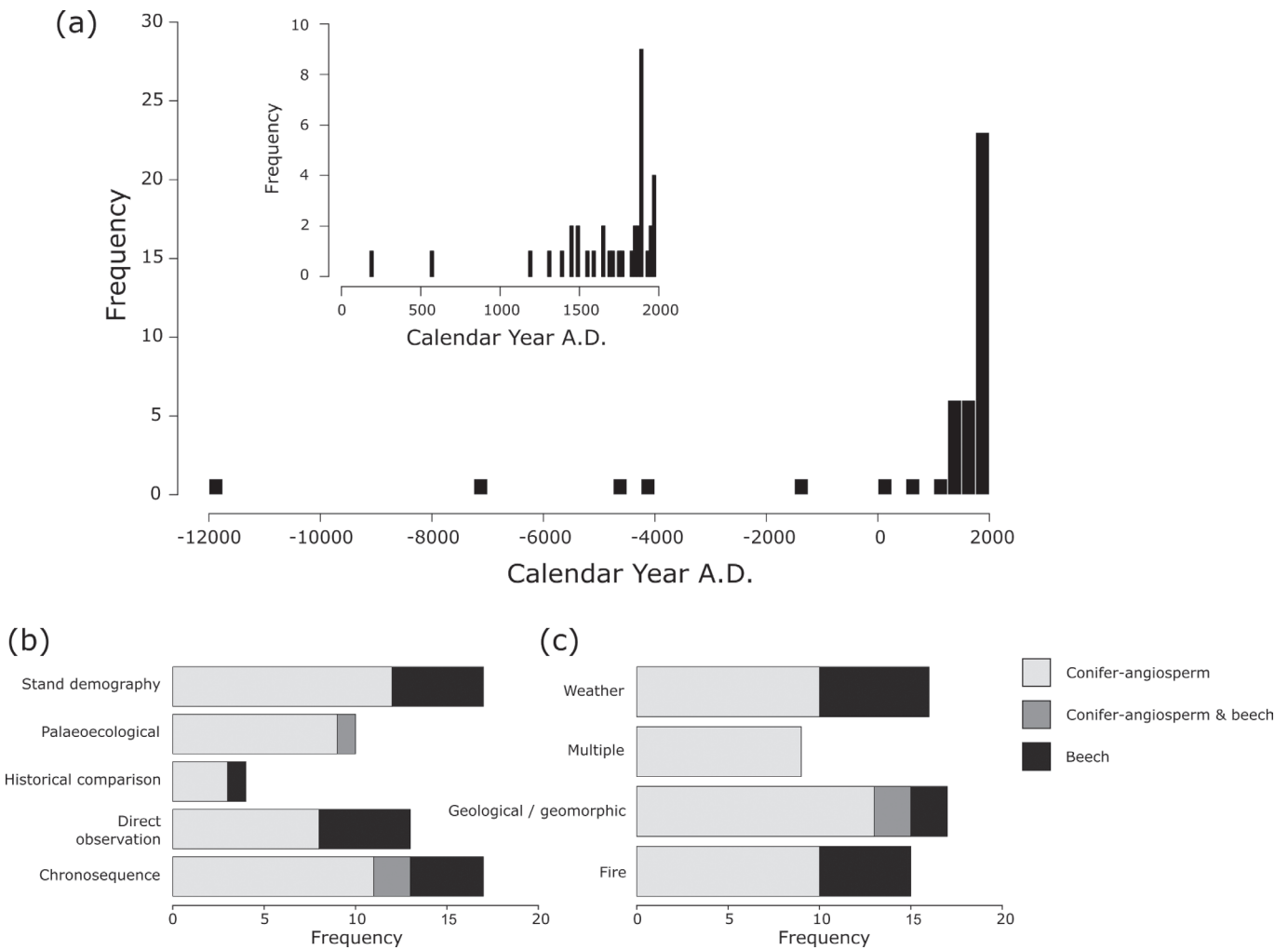


Figure 4. Characteristics of the studies synthesised in our forest models: (a) the timing of the disturbance described (the spike in 1886 relates to the Tarawera eruption), (b) the type of data, and (c) the type of disturbance. There is a clear bias towards conifer-angiosperm forests. See Table S1 in supplementary material for details of specific studies.

Descriptions of forest change for New Zealand beech forests

Beech-dominated forests comprise approximately 68% by area of New Zealand’s beech forests, and consist of forest with either *Fuscospora cliffortioides*, *F. fusca*, *F. solandri*, or *Lophozonia menziesii* as the dominant canopy species (Wardle 1984). *Fuscospora truncata*, the other New Zealand member of the Nothofagaceae, can occur in almost pure stands, but, unlike the other species, these stands are not extensive (Ogden et al. 1996). In beech-dominated forests, the understory may be sparse, or may include *Chionochloa* spp., *Coprosma* spp., *Dracophyllum* spp., *Griselinia littoralis*, *Olearia* spp., *Pseudopanax* spp., or *Pseudowintera colorata*. *Aristotelia serrata* and *Fuchsia excorticata* commonly occupy canopy gaps (Wardle 1984).

In the absence of exogenous stand-destroying disturbance, synchronous stand dieback is an important component of forest change in pure stands of *Fuscospora* spp., initiated by snow break, wind damage, drought, and insect attack, for example (Wardle & Allen 1983; Hosking & Hutcheson 1988; Ogden 1988; Ogden et al. 1996). Either one or a combination of these stressors can initiate dieback, and initial mortality from one stressor may lead to further mortality from another (Ogden et al. 1996). Mature or ‘over-mature’ even-aged stands of

F. cliffortioides and *F. solandri* become vulnerable to dieback at c. 100–200 years of age, whereas stands of the longer-lived *F. fusca* become vulnerable at c. 300–500 years (Ogden et al. 1996). These dieback events trigger the release of a suppressed and light-demanding *Fuscospora* seedling pool, and the cycle begins anew (Fig. 5). As a result, pure *Fuscospora* forests typically have an even-aged cohort, rather than a mixed-age stand structure.

Lophozonia menziesii is more shade-tolerant than the four NZ *Fuscospora* species, and can regenerate under a partially closed canopy (Ogden et al. 1996). As such, *L. menziesii* tends to form mixed-aged stands, even where regeneration was triggered initially by a large-scale disturbance event (Wardle and Allen 1983). *Lophozonia menziesii* is less likely to be disturbed by synchronous dieback events, and is more reliant on gap-phase regeneration than landscape-level events (Ogden et al. 1996). Hence, our successional trajectory for pure *L. menziesii* forests does not contain a cycle of regeneration and stand dieback in the absence of other disturbance factors; rather, we depict mature pure *L. menziesii* forest as maintained by gap-phase regeneration, and regeneration beneath its canopy, between large exogenous disturbances. For both pure *Fuscospora* and *L. menziesii* forest types, the initial ‘state’ following a large

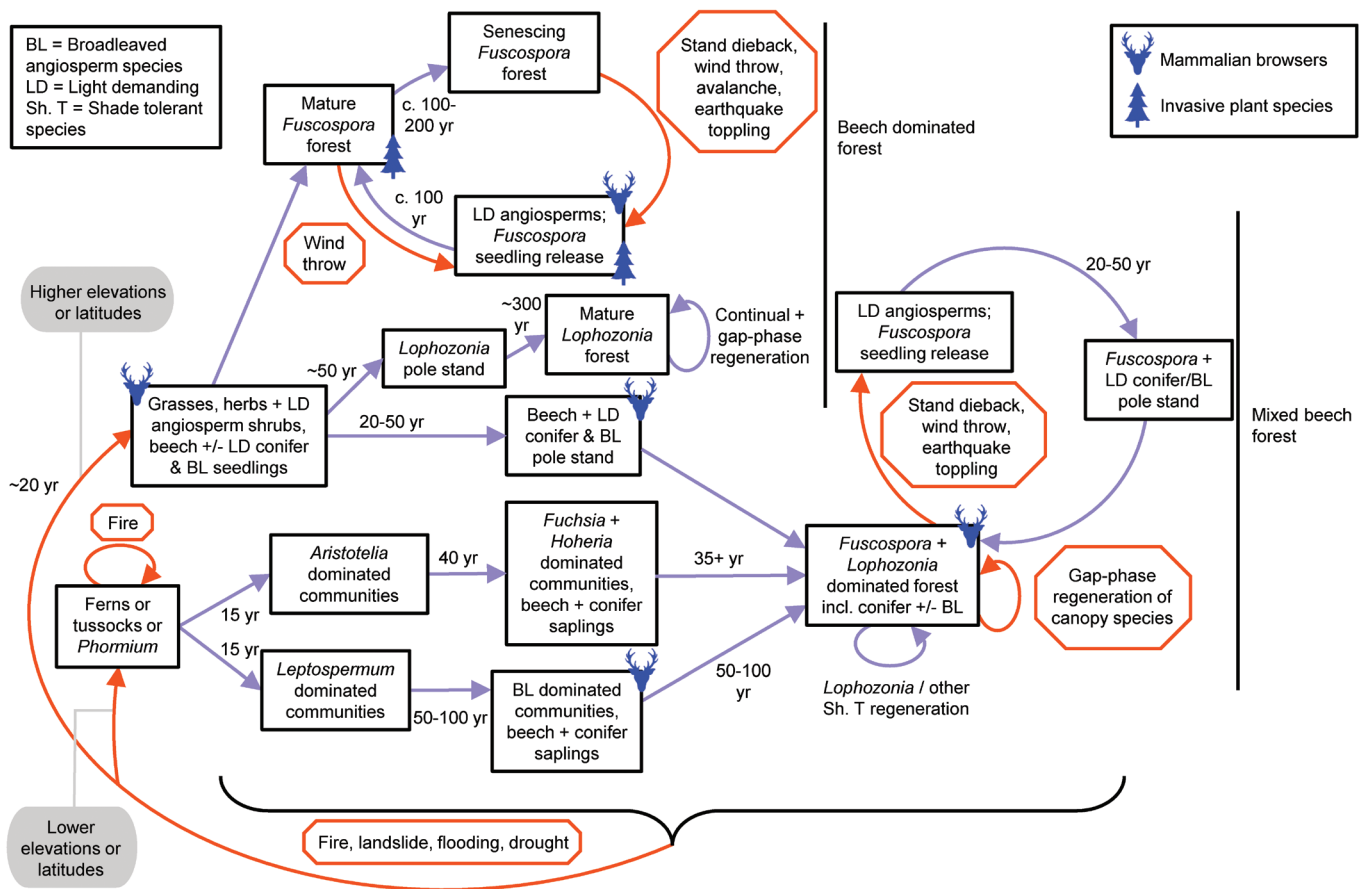


Figure 5. Conceptual model detailing the generalised dynamics of New Zealand beech forests. Orange arrows indicate transitions between states caused by disturbances (named in octagons), purple arrows indicate transitions due to the passage of time in the absence of disturbance. Blue symbols indicate community states that may often have well-documented structural changes as a result of the modern influences of introduced mammalian browsers and invasive plant species. Time estimates are means of the values recorded in the literature. Species composition of states varies geographically; see text for details.

disturbance contains pioneering light-demanding species, typically grasses (e.g. *Chionochloa* and *Poa*), sedges (e.g. *Carex* and *Uncinia*), herbs (e.g. *Epilobium*, *Ranunculus*, and *Wahlenbergia*), and light-demanding, angiosperm shrubs (e.g. *Aristotelia serrata*, *Coprosma* spp., *Discaria toumatou*, and *Dracophyllum* spp.) (Wardle 1972; Wardle 1984; Ogden et al. 1996; Wiser et al. 1997). Early in the succession, seedlings of conifer (e.g. *Libocedrus bidwillii*, *Phyllocladus alpinus*, and *Podocarpus laetus*) and broadleaved-angiosperm tree species (e.g. *Carpodetus serratus*, *Griselinia littoralis*, and *Weinmannia racemosa*) can be present, with the exact species composition varying among localities.

Where *L. menziesii* and *Fuscospora* co-occur, a cycle of *Fuscospora* stand dieback and seedling release takes place in the absence of landscape-level disturbances, with *L. menziesii* recruiting under the canopy or in small gaps (Ogden 1988). Ogden (1988) describes these canopy species as coexisting in a dynamic equilibrium in which *Fuscospora* is favoured following large disturbances or stand collapse but *L. menziesii* is favoured in the absence of these events. As such, the relative density of *L. menziesii* is related positively to the mean size (trunk diameter) of the *Fuscospora* trees (Wardle 1983). However, Stewart and Rose (1990) indicate that although the regeneration of *L. menziesii* is more continuous than that of *Fuscospora* spp., it too requires some disturbance to reach

the main canopy. The differing life-history strategies of these species may also help to explain their co-existence; while *L. menziesii* has lower juvenile mortality, *Fuscospora* has higher longevity and adult survival (Stewart 1995). Mixed stands of *L. menziesii* and *Fuscospora* can also include conifer and broadleaved-angiosperm species, such as *P. laetus*, *C. serratus*, *G. littoralis*, *Pseudopanax crassifolius*, and *W. racemosa* (Wardle 1984; Ogden et al. 1996). *Dacrydium cupressinum* is also common at lower elevations.

The Nothofagaceae species also occur as dominant forest elements alongside other canopy angiosperm trees and emergent conifers. Wardle (1984) and Ogden et al. (1996) describe forest associations throughout the country; with common co-dominant broadleaved angiosperms including *Beilschmiedia tawa*, *Ixerba brexioides*, *Metrosideros robusta*, *M. umbellata*, *Quintinia serrata*, and *W. racemosa*. *Libocedrus bidwillii* and *P. laetus* are common associated conifer species throughout much of the South Island and higher elevations in the North Island, while *D. cupressinum* and *P. ferruginea* are common at low elevations (Lusk & Smith 1998). *Fuscospora truncata*, *A. australis*, and *Phyllocladus trichomanoides* also share associations but only in the north of the North Island (Wardle 1984; Collins & Burns 2001).

The main structural changes to beech forests resulting from modern influences relate to the invasions of exotic

conifer species (Fig. 5), particularly *Pseudotsuga menziesii*. This shade-tolerant conifer can invade intact native forests (Moeller et al. 2015), but is most likely to establish following disturbance (Ledgard 2002). Introduced mammalian browsers have not been found to cause major changes in the recruitment of beech species; however, they do inhibit the regeneration of palatable broadleaved species in these forests, such as *Griselinia littoralis* and *Weinmannia racemosa*, thereby causing increases in the abundance of unpalatable sub-canopy species such as *Pseudowintera colorata* and *Leucopogon fasciculatus* through seedling release (Bellingham et al. 1999; Husheer et al. 2003; Wilson et al. 2003; Husheer & Frampton 2005).

Descriptions of change for New Zealand conifer-angiosperm forests

Although not restricted to conifer-angiosperm forests, the fern *Pteridium esculentum* (bracken) is one of the commonest early colonisers of disturbed openings in these forests; particularly after fire and volcanic-related disturbances (McGlone et al. 2005). While dominant immediately after disturbance, *P. esculentum* is soon over-topped by light-demanding, stress-tolerant angiosperms such as the myrtaceous species *Leptospermum scoparium* and *Kunzea ericoides* agg. (de Lange 2014), that can tolerate the higher temperatures and water-deficits characteristic of early successional environments. Species in the genera *Aristotelia*, *Coprosma*, *Coriaria*, *Gaultheria*, *Geniostoma*, *Melicytus*, *Myrsine*, and *Pseudopanax* can also occur in such settings (Ure 1950; Croker 1953; McKelvey 1955; Leathwick & Rogers 1996; Wilmshurst et al. 1997). Early colonising communities from which *P. esculentum* is absent have also been described, such as those observed after volcanic activity on Mt Tarawera (Timmins 1983) and landslides in central Westland (Stewart & Veblen 1982). On Mt Tarawera, early-successional communities included *Coriaria arborea*, *Gaultheria* spp., *Muehlenbeckia axillaris*, *Olearia furfuracea* and *Raoulia* spp., whilst common pioneering species in central Westland included *Aristotelia serrata*, *Coprosma* spp., *Coriaria* spp., *Griselinia littoralis*, *Olearia arborescens*, and *O. avicenniifolia* (Stewart & Veblen 1982; Timmins 1983; Walker et al. 2003).

The 'Myrtaceae-dominated communities' state encompasses a range of assemblages, typically dominated by *Leptospermum scoparium* and/or *K. ericoides* agg. *Leptospermum scoparium* is often one of the initial colonising tree species with *Kunzea* arriving at a similar time or soon thereafter (e.g. Cameron 1960; Burrows 1973; Wassilieff 1986; Bray 1989; Bray et al. 1999). In these instances, the longer-lived *Kunzea* outlives *L. scoparium* and forms a senescing canopy under which conifer and broadleaved angiosperm species become established (Wardle 1991). In other situations, either *L. scoparium* or *Kunzea* is absent (Leathwick & Rogers 1996). *Leptospermum scoparium* typically occurs in the absence of *Kunzea* on higher elevation North Island sites such as on Mt Tarawera (e.g. Burke 1974; Clarkson & Clarkson 1983), and in localities beyond the environmental range of *Kunzea*, including Southland, South Westland, and Stewart Island (Burrows 1973; Wardle 1974, 1991). By contrast, *Kunzea* occupies the Myrtaceae stage in the absence of *L. scoparium* in some areas such as Te Urewera (Payton et al. 1984; Richardson et al. 2014), Uretara Island in the Bay of Plenty (Smale 1993), and coastal sand dunes (Smale 1994; Smale et al. 1996). From the Bay of Plenty northwards *L. scoparium* and *Kunzea* may be replaced by, or co-occur with, *Metrosideros excelsa* on cliffs (Nicholls 1959), raw volcanic substrates (e.g. lava, scoria)

(Clarkson 1990; Newnham & Lowe 1991; Clarkson et al. 2015), or in coastal areas (Smale 1993; Atkinson 2004). A similar role is played by *M. umbellata* on the subantarctic Auckland Islands, where neither *L. scoparium* nor *Kunzea* occur (Wardle 1971, 1991).

Weinmannia racemosa is a dominant component of many forests throughout the North, South and Stewart Islands, with a northern range limit in the Waikato region (Wardle & MacRae 1966). It is present as a light-demanding broadleaved angiosperm in most forested states in the conceptual model (Fig. 4). In harsher environments, *W. racemosa* is often one of the first post-disturbance colonists. In central Westland *W. racemosa*, alongside *Metrosideros umbellata*, colonises sites recently devastated by landslides (Stewart & Veblen 1982), and in south Westland *W. racemosa* is one of the first tree species to establish following flooding, alongside *Pennantia corymbosa* (Wardle 1974). Near the elevational treeline in the central North Island *W. racemosa* is an initial colonist after volcanic activity, sometimes with *L. scoparium* (Nicholls 1959; Burke 1974; Clarkson & Clarkson 1983). At these sites, as well as montane conifer-angiosperm forest in areas such as Pureora (Smale & Kimberley 1993), *W. racemosa* is a dominant canopy species in mature forest (Ogden et al. 2005). In other regions, such as Te Urewera (e.g. Payton et al. 1984), *W. racemosa* enters a site under a Myrtaceous canopy following disturbances such as fire, often with *Knightia excelsa* as a co-dominant (Richardson et al. 2014). In these successions, *W. racemosa* also persists in mature forest by colonising smaller gaps and root-plate mounds following tree falls, through epiphytic establishment on tree fern trunks, and via resprouting (Adams & Norton 1991; Smale et al. 1997; Ogden et al. 2005; Gaxiola et al. 2008). In Northland and the Coromandel Peninsula *Weinmannia sylvicola* performs a similar ecological role to that of *W. racemosa* elsewhere (Leathwick & Rogers 1996), also establishing following disturbances, in canopy gaps, and through epiphytic establishment on tree fern trunks.

Tree fern communities (dominated by *Cyathea medullaris* and/or *Dicksonia squarrosa*) form an important pioneering community and successional pathway throughout NZ (Bystrakova et al. 2011; Brock et al. 2016). However, there is surprisingly sparse coverage of the dynamics of such communities in the literature. One notable exception is the demonstration by Coomes et al. (2005) that dense tree ferns and ground ferns can affect forest composition by influencing the regeneration success of other taxa, resulting in an advantage for angiosperm canopy tree species over their coniferous counterparts. In addition, recent work by Brock et al. (2018) demonstrates that, in northern NZ forests, *C. medullaris*-dominated early successions are associated with trajectories towards podocarp-broadleaved forests, while those dominated by *Kunzea robusta* are associated with trajectories towards *Agathis australis* forest; although there may also be potential effects of edaphic conditions and initiating disturbance that are difficult to disentangle. The pathway we present here is derived primarily from descriptions by Blaschke (1988) and Blaschke et al. (1992), along with anecdotal evidence (Croker 1953; Silvester 1964; Leathwick & Rogers 1996) and our own observations. Our hypothesised pathway through tree fern communities should be treated as provisional and understanding succession through these communities is an important avenue for future research. This pathway appears to be most common in gullies and on moist slopes, while Myrtaceae dominated communities tend to occur on flat, dry sites, and particularly those that have experienced fire (Croker 1953; Brock et al.

2018). These two pathways are not mutually exclusive, however, and *C. medullaris* can form a sub-canopy beneath *Kunzea*, typically in moist areas (e.g. Smale & Kimberley 1993; Atkinson 2004).

Throughout NZ, conifer pole stands are initiated by landscape-level disturbances. In northern regions such as the Waitākere Ranges (near Auckland) these stands typically also include light-demanding broadleaved angiosperm species such as *Coprosma arborea*, *Knightia excelsa*, *Pseudopanax crassifolius* and *Quintinia serrata* (Esler & Astridge 1974). South of the Waikato region *W. racemosa* is also an important component of young conifer stands (e.g. Wardle 1974; Payton et al. 1984; Six Dijkstra et al. 1985), but can exclude conifers from some sites (Ogden et al. 2005). The species composition of the conifer component of this vegetation state varies with latitude, elevation, and local microsite conditions. In lowland forests north of approximately 38°07' S (Ecroyd 1982), *A. australis* is typically a dominant conifer component, although other conifer species, commonly *Dacrydium cupressinum*, *Phyllocladus trichomanoides* and *Prumnopitys ferruginea*, also occur. *Dacrydium cupressinum* is one of the most widely distributed trees in New Zealand and is a common component of this vegetation state in lowland forests throughout the South Island, and in forests from sea level up to 900 m in the North Island (Norton et al. 1988). *Dacrycarpus dacrydioides* has a similar range to *D. cupressinum*, although *D. dacrydioides* is typically the dominant conifer component on poorly drained alluvial soils following flooding. This species is characteristic of lowland swamp forests, the remnants of which are now mostly restricted to the West Coast of the South Island (Wardle 1974, 1977) and to alluvial plains such as those in the Waikato region of the North Island (Burns et al. 1999; Burns et al. 2000; Burns & Smale 2002). *Prumnopitys taxifolia* is also often associated with such stands (Wardle 1977). *Libocedrus bidwillii* is a dominant conifer component of montane and sub-alpine forests in both the North and South Islands, where it regenerates to form even-aged stands following disturbances such as wind-throws or landslides (Stewart & Rose 1989; Ogden & Stewart 1995). Other conifers such as *Halocarpus biformis*, *Phyllocladus alpinus* and *Podocarpus laetus* also occur in these areas and in cold, dry climates in the inter-montane basins of the South Island (Wardle 1977; Ogden & Stewart 1995; Horrocks & Ogden 1998). These species are sensitive to fire, and prior to the forest loss that accompanied human arrival it is likely *H. biformis*, *P. alpinus*, and *P. laetus* may have been the dominant elements of forests covering what are now frost flats in the central North Island (Burns & Smale 2014), and tussock grasslands in central Otago (Wardle 1984; McGlone 2001).

After long periods without disturbance, a broadleaved angiosperm canopy with emergent conifers and hemi-epiphytic *Metrosideros* typically develops (Smale et al. 2016). In this state shade-tolerant broadleaved canopy species may regenerate beneath the canopy or on the margins of tree-fall gaps. The most common genera forming the canopy in these forests are *Beilschmiedia*, *Metrosideros*, and *Weinmannia* (Ogden & Stewart 1995). *Beilschmiedia tarairi* is dominant north of Auckland in the North Island, while *Beilschmiedia tawa* occurs throughout the North Island and the north of the South Island. In these forests light-demanding species, including conifers such as *D. cupressinum*, persist over generations by colonising areas after small disturbances, such as tree-falls (Adams & Norton 1991). Such gaps are initially colonised by tree ferns, particularly *Dicksonia squarrosa*, followed by

light-demanding broadleaved species such as *W. racemosa*, under which conifers may establish (Beveridge 1973; Smale et al. 1997). Ogden (1985) suggested that with increasing time since landscape-level disturbance cohort regeneration of long-lived, light-demanding conifers such as *A. australis* and *D. cupressinum* becomes less synchronous and there is a compositional shift towards more shade-tolerant species, such as *P. ferruginea* (see also Lusk & Ogden 1992; Smale et al. 2016).

Although the dynamics of the light-demanding podocarp species and *A. australis* can be described as following broadly the same trajectories (Ogden & Stewart 1995) as described above, we have illustrated the *A. australis* vegetation states and pathways as separate to those of the other light-demanding conifers (Fig. 6). We make this distinction because the composition of plant communities associated with *A. australis* differs considerably from other conifer-angiosperm forests (Wyse et al. 2014). Unlike podocarp species such as *D. cupressinum*, *A. australis* can act as a foundation species or ecosystem engineer, producing a specific suite of soil conditions (including a deep, acidic organic layer; Wyse 2012; Wyse & Burns 2013) that in turn leads to the formation of distinct, stress-tolerant plant communities that differ structurally and compositionally from the surrounding conifer-angiosperm forest community (Wyse et al. 2013; Wyse 2014). Species typically associated with *A. australis* forests include *Astelia trinervia*, *Coprosma lucida*, *Dracophyllum latifolium*, *Leucopogon fasciculatus*, and *Myrsine australis* in the understory, and *Beilschmiedia tarairi*, *Knightia excelsa*, *Phyllocladus trichomanoides*, *Quintinia serrata*, and *Toronia toru* in the main or sub canopy (Wardle 1991; Wyse et al. 2013).

In conifer-angiosperm forests, introduced mammalian browsers can exert a considerable influence on forest structure and successional dynamics (Fig. 6). Ungulates including goats (*Capra hircus*) and multiple deer species (*Cervus elaphus scoticus* is the most widespread and well-researched, but others include *C. nippon*, *C. unicolor*, *Dama dama*, and *Odocoileus virginianus*; Coomes et al. 2003) browse on palatable angiosperm seedlings, inhibiting these species regeneration (Allen et al. 1984; Allen et al. 2002; Husheer 2007) and potentially leading to arrested successions in some systems, such as *Weinmannia*-dominated forests (Allen et al. 2002; Richardson et al. 2014). Australian brushtail possums (*Trichosurus vulpecula*) can cause extensive damage in the canopies of conifer-angiosperm forests (Gormley et al. 2012), often leading to deaths of palatable species such as the emergent tree *Metrosideros robusta* (Allen et al. 2002), and resulting in changes to forest structure. Exotic plants tend to affect the early successional stages of conifer-angiosperm forests, where invaders such as *Ulex europaeus* can reach high densities. While early studies noted a successional role for this species in encouraging the re-establishment of native forest on cleared sites (Druce 1957; Healy 1961), more recent research suggests that successional trajectories of *U. europaeus*-dominated native forest communities differ from those of native Myrtaceae-dominated communities (Sullivan et al. 2007). Additionally, *Ulex europaeus* and other introduced species such as *Hakea* spp. are examples of invasive weeds that are highly flammable (Wyse et al. 2016) and can rapidly recolonise recently burned areas, replacing native pioneers (Perry et al. 2014, 2015). Their combined effects may increase ecosystem flammability (Wyse et al. 2017), fire frequency, and lead to arrested successions (Perry et al. 2014).

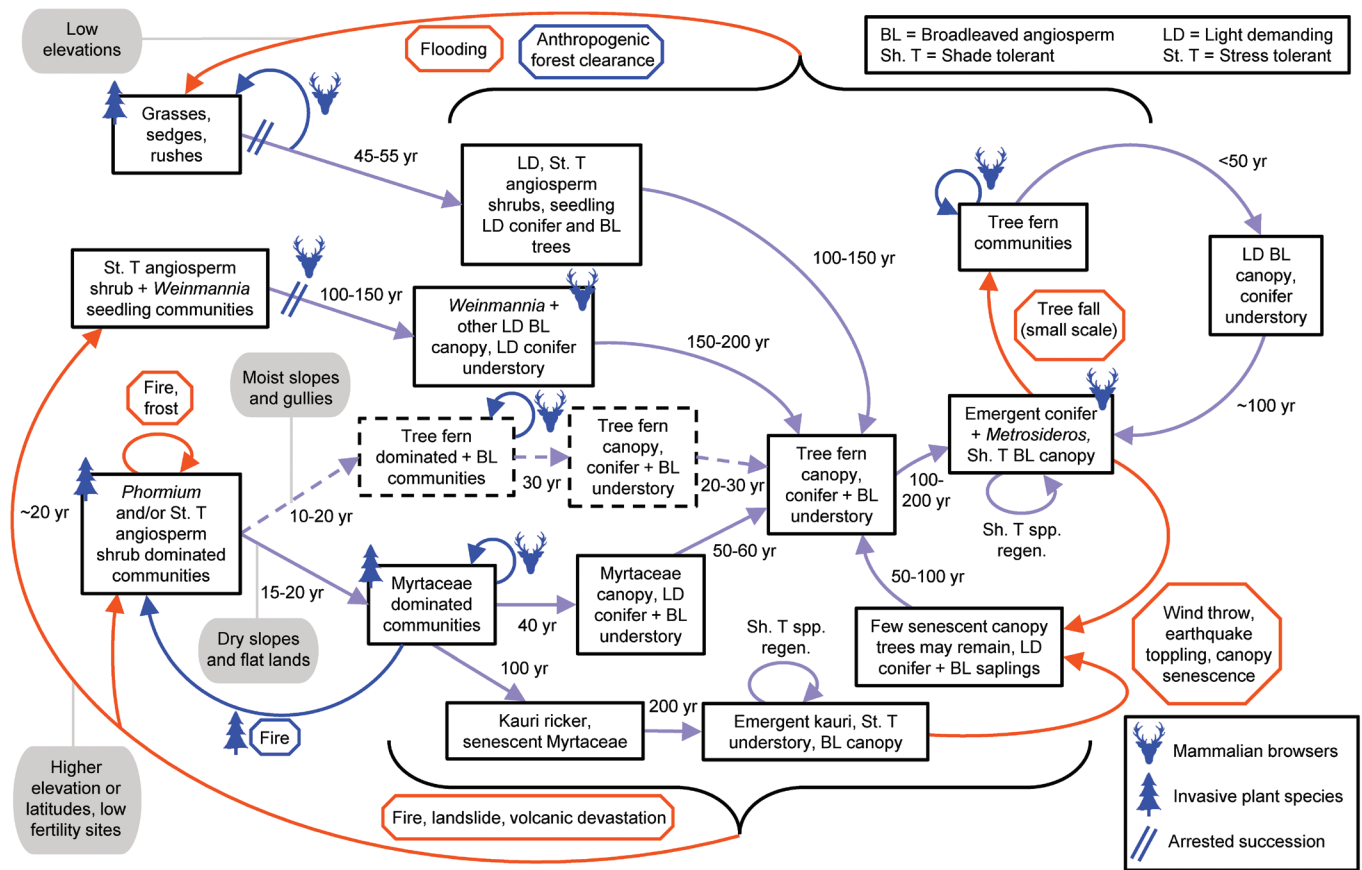


Figure 6. Conceptual model detailing the generalised dynamics of New Zealand conifer-angiosperm forests. Orange arrows indicate transitions between states caused by disturbances (named in octagons), purple arrows indicate transitions due to the passage of time in the absence of disturbance. Blue symbols indicate community states that may often have well-documented structural changes as a result of the modern influences of introduced mammalian browsers and invasive plant species. Blue symbols also signify human induced disturbances, increased disturbance as a result of introduced mammalian browsers and invasive plants, and where the effects of mammalian browsers may lead to arrested successions. Dashed lines indicate a poorly studied pathway (which we therefore have less confidence in), but which is included here as is it may nevertheless be important in some NZ forests. Time estimates are means of the values recorded in the literature. Species composition of states varies geographically; see text for details.

Uncertainties in model pathways

As with all models, those we present here are only as robust as the data used to inform them, and the confidence we have in the different pathways and states reflects the biases in the availability of data and our interpretations. As is evident from Fig. 4, descriptions of post-disturbance forest dynamics are strongly skewed towards pyric successions despite fire’s rarity in pre-human New Zealand forests. We can, therefore, have relatively high confidence in the post-fire trajectories we depict, but less confidence in trajectories following, for example, stand-collapse or flooding (Fig. 4c). As a result, spatio-temporal variation in forest response to such disturbances cannot be represented adequately, and hence the pathways as we depict them may not represent the disturbance or forest type as a whole. Likewise, despite beech forests dominating indigenous NZ forest by area, the data are skewed toward studies of succession in conifer-angiosperm forests (Fig. 4b, 4c).

One potentially key, and yet understudied, pathway that we have included in our conifer-angiosperm model is the pathway from pioneering bracken communities to conifer pole stands via tree fern dominated communities (depicted by dashed rather than solid lines in Fig. 6). The pathway we present is derived primarily from the descriptions of Blaschke

(1988) and Blaschke et al. (1992), anecdotal evidence from Croker (1953), and our own observations. This pathway is likely to be important in some NZ forests, yet the paucity of formal descriptions means we are somewhat uncertain in how to depict both the pathway itself, and the conditions (edaphic and disturbance) under which it occurs (see Brock et al. 2016, 2018).

Discussion

Relation to ecological theory

Our conceptual models of NZ forest dynamics detail the key stages in both primary successions following catastrophic disturbance, and secondary successions that result from disturbances such as wind-throw or earthquake-toppling. These types of successions occur over different spatial and temporal grains and extents, as a consequence of the scales of the different disturbance types they are triggered by. Although disturbances have previously been viewed as moving forests away from an ideal ‘climax’ state (e.g. Cockayne 1928), we follow authors such as Ogden (1985), Bray (1989), and Ogden and Stewart (1995), and see disturbance as having a central

role in structuring both NZ conifer-angiosperm and beech forests, and in maintaining forest diversity at the landscape level. Large disturbances and their associated primary successions are individually major events, yet are spatially and temporally infrequent, as previously discussed. By contrast, the small disturbances we include, such as tree falls, may be separately small but are numerous within a given area and so collectively have important influences on the structural and species composition of the forest (Ogden et al. 1991; Espirito-Santo et al. 2014).

Our conifer-angiosperm forest model (Fig. 6) follows the temporal stand replacement ('lozenge') model of Ogden (1985). Ogden's model sees an initial cohort of *A. australis* or other light-demanding conifers establish following landscape-level disturbance. Once the cohort reaches maturity, falling senescent individuals create gaps of sufficient size for the establishment of further light-demanding conifer seedlings, although the gaps may also be appropriated by broadleaved species and thus successive conifer cohorts decrease in density (Smale et al. 2016). As explained by Ogden and Stewart (1995) and Ogden et al. (1996), regeneration of the conifer and angiosperm components in these forests can be understood to respond to disturbances of opposing spatial and temporal extents and frequencies; this dynamic highlights the importance of Grubb's (1977) 'regeneration niche' in community dynamics, while also removing the problem of the perceived 'conifer regeneration gap' that received much attention in the literature (e.g. Holloway 1954; Wardle 1978, 1985). The role of species' regeneration niches is also evident at smaller extents, such as in the dynamics of the forests where *L. menziesii* and *Fuscospora* co-occur (Hurst et al. 2012). The coexistence of these canopy components in dynamic equilibrium (Ogden 1988) can be seen to relate, in part, to the regeneration requirements and characteristics of the different taxa.

The challenges of scale in forest models

Qualitative descriptions such as those we present here are caricatures of the systems they seek to represent, as with any model, and they are by design high-level, aiming to capture generalities in successional trajectories. Additionally, the data and understanding typically used to develop such models tend to be of regional extent, meaning that this is the spatial domain that they are best equipped to capture (e.g. Bestelmeyer 2015). The cost of such generality is that our models cannot capture the idiosyncrasies of individual successions (we trade-off precision for generality, Levins 1966), and do not represent context-specific historical, contingent, and priority effects (e.g. the unusual succession through *Coprosma* described by Croker, 1953). Deng et al. (2006) provide a palaeoecologically-focussed example of this type of path-dependence in their analysis of different successions relating to multiple sediment contexts from infilled (terrestrialised) estuarine environments on Aotea Great Barrier Island, northern NZ. In all of the records that Deng et al. (2006) describe, the initial stages of succession following estuarine infill were linear and predictable. Beyond a certain point in the succession, however, the individual sites diverged in their trajectories, probably as a function of the magnitude of local terrigenous inputs at individual sites. Models representing fine spatial grains may allow such variation to be portrayed: localised dynamics are extremely difficult to capture in a high-level description of ecosystem change, but are undoubtedly important if site-specific vegetation shifts are to be predicted. However, one of the strengths of well-conceived models is the abstraction that they carry; developing individual models for every site of interest voids this benefit.

Ecologists struggle to describe the dynamics of ecosystems across extended spatio-temporal extents. Recently there has been a growing recognition that understanding and narrating such dynamics requires some degree of methodological pluralism (Willis & Birks 2006). If models are overly dependent on short-term and local data then there is a risk that they will not adequately depict the systems they target. The vegetation history of Tawhiti Rahi (Poor Knights Islands, offshore northern NZ) provides a good example of why multi-scale data are required (Wilmshurst et al. 2014). Currently, as is the case in many other similar settings in NZ, the forest on this island is dominated by *Metrosideros excelsa* and other broadleaved angiosperm forest species. Māori occupied Tawhiti Rahi from the late 13th Century to the early 1800s, and it was assumed that the pre-human forest condition was similar to that to which it 'returned' after occupation ceased. However, fossil pollen and ancient DNA indicate that prior to human settlement the forests of Tawhiti Rahi were dominated by palms (*Rhopalostylis sapida*) and members of the Podocarpaceae; this assemblage is not seen on northern NZ offshore islands today. Human impacts, coupled with dispersal limitations of *R. sapida* and Podocarpaceae species, exceeded a threshold (Anderson et al. 2009) of community change. As this example shows, without long-term data it is difficult to set targets and time-frames for restoration or to develop qualitative models to support such activities.

An additional and subtler challenge relating to scale is that successive disturbances and changes in the disturbance regime obscure the past. The landscape can be thought of as a palimpsest, in which the effects of successive events are superimposed upon the previous state. As we have described (and see Fig. 3), New Zealand's landscapes and ecosystems have been shaped by climatic, geologic, and tectonic disturbances. The infrequency of these disturbance events is reflected in the life history characteristics of the dominant tree taxa (Wardle 1991). However, over the last 750 years, fire has been the dominant disturbance, as is evident in the disproportionate number of post-fire successions among the studies that we assessed, especially those relying on contemporary evidence. This imbalance, relative to other disturbance types, reflects the transformative role that fire has played in the NZ landscape since human arrival (Perry et al. 2014), but means that we are reliant on short-term studies from limited geographic areas or palaeoecological data to reconstruct 'natural' forest dynamics (i.e. dynamics in the absence of human intervention).

Towards the future

As a result of recent (geologically-speaking) anthropogenic effects and species introductions, NZ forests (and indeed ecosystems globally) are likely to be facing no-analogue futures (Shulmeister et al. 2017). Looking into the past, even when considering an appropriately broad range of spatio-temporal scales, may not enable us to anticipate the dynamics of future ecosystems shaped by such novel forces. However, by doing so we are better equipped to comprehend the impacts human pressures are having on our ecosystems; as the example of Tawhiti Rahi demonstrates (Wilmshurst et al. 2014), it is essential to turn to long-term data to derive baselines before we can understand current impacts.

New Zealand's ecosystems are being greatly impacted by the consequences of human action, including habitat loss and fragmentation, faunal extinctions, and the introduction of exotic plants and animals (especially mammals) (Wood et al. 2017). Such impacts may mean that some aspects of

pre-human forest dynamics are no longer possible in the current landscape. For example, seabirds have an important role as ecosystem engineers in island ecosystems, where they input marine nutrients and influence vegetation disturbance (Bellingham et al. 2010). There is now growing appreciation that seabirds also had a wider role on the larger main islands of NZ prior to human arrival, as evidenced by fossil remains and a legacy of nutrient inputs (Bellingham et al. 2010). However, human activities and introduced mammalian predators have decimated seabird populations on offshore islands and in preferred habitats on the main islands, altering disturbance regimes, patterns of species abundance (Norton et al. 1997), vegetation composition (Bellingham et al. 2010), and therefore probably forest dynamics and trajectories (Fukami et al. 2006). Ecological effects of the loss of seabirds owing to the introduction of mammalian predators may therefore have crossed a threshold of forest change.

Other changes that have resulted from human activities, directly or indirectly, have been well documented and experimentally assessed, and can therefore be depicted in our forest models (Figs. 5, 6). These better documented changes are largely the result of introduced mammalian browsers (ungulates and brushtail possums), as well as invasive plant species. Introduced browsers alter forest structure and composition by limiting the regeneration of palatable broadleaved species and causing the loss of certain canopy or emergent species in conifer-angiosperm forests (Allen et al. 2002), as well as negatively affecting the regeneration of broadleaved species in beech forests, although beech species themselves seem largely unaffected (Bellingham et al. 1999; Husheer et al. 2003; Husheer & Frampton 2005). Additionally, invasive plants cause notable forest changes in both beech and conifer-angiosperm forests. Exotic invasive conifers, particularly *Pseudotsuga menziesii*, are causing structural change in beech forests, where their invasions are also facilitated by the spread of ectomycorrhizal inoculum in the faecal pellets of European red deer (*Cervus elaphus scoticus*) and brushtail possums (Wood et al. 2015). In conifer-angiosperm forests, invasions of exotic pyrophilic species such as *U. europaeus* and *Hakea* spp. into early successional communities are of particular concern. These species may also affect disturbance regimes by encouraging increased fire frequencies, thereby facilitating further invasions and novel ecosystems (Hobbs et al. 2009; Perry et al. 2014; Wyse et al. 2017).

Disturbance types, their magnitudes and frequencies, and the resulting vegetation responses are also likely to be altered by future changes, such as increasing frequencies of droughts, fires, and extreme weather events expected under global climate change scenarios (Renwick et al. 2016). As a result of these impacts, current and future successional trajectories may differ from those of the past or present. The rise of novel ecosystems (Hobbs et al. 2009) also challenges our ability to define the states that an ecosystem may occupy. Because of the high-level nature of our models, these challenges are particularly acute where species-level effects propagate through the whole system. For example, the pathogen *Phytophthora agathidicida* causes dieback in *Agathis australis* individuals of all ages (Scott & Williams 2014; Weir et al. 2015). Given that *A. australis* is considered an ecosystem engineer that influences soil conditions (Verkaik & Braakhekke 2007; Verkaik et al. 2007) and community composition (Wyse & Burns 2011, 2013; Wyse et al. 2014), shifts in abundance of this species has the potential to change forest trajectories in surprising ways that may have cascading effects on community composition

and function. In our models, we depict *A. australis* (kauri) forests as an alternative pathway and alternative community states to those of other conifer-angiosperm forests (Fig. 6), highlighting that the consequences of the loss of this single species to forest dynamics could include the loss of unique species assemblages. Additionally, loss of this species from northern NZ forests could cause changes in fundamental ecosystem processes such as decomposition rates, nutrient fluxes and carbon sequestration (van der Westhuizen 2014). *Agathis australis* litter has extremely slow decomposition rates (Enright & Ogden 1987), in turn influencing nitrogen cycling and the storage of carbon: extremely high levels of both carbon and nitrogen accumulate in the organic soil layers beneath *A. australis* (Silvester & Orchard 1999; Silvester 2000). Ellison et al. (2005) have described the consequences of the loss of ‘foundation’ tree species from forest ecosystems, citing numerous examples from North American forests. They show that the loss of such species (e.g. *Castanea dentata*, *Pinus albicaulis*, and *Tsuga canadensis*) from their respective forests can have cascading effects on both terrestrial and aquatic habitats, potentially shifting ecosystems to alternative stable states.

Another example of a possible future tipping-point, and one which would have wider ranging consequences, is the potential influence that the arrival of the pathogen *Puccinia psidii* (myrtle rust) may have on myrtaceous pioneers throughout New Zealand. *Puccinia psidii* has undergone rapid range expansion in the past decade, and globally has over 450 known myrtaceous host species (Carnegie et al. 2016). The pathogen was detected on Raoul Island in the Kermadec Islands in April 2017, where it was infecting *Metrosideros kermadecensis* (Department of Conservation 2017b), and was first detected in mainland New Zealand in May 2017 (Department of Conservation 2017a). Loss of myrtaceous species from early stages of successions would likely facilitate further invasions of pioneer weeds such as *Cytisus scoparius*, *Ulex europaeus*, and *Hakea* spp., and could have long-term consequences for successional trajectories. Invasions of the pyrophilic species *U. europaeus* and *Hakea* spp. may, in turn, result in changes to fire regimes, thereby altering ecosystem dynamics and the pathways of successions in ways that are unpredictable and deviate from pre-human baselines (Perry et al. 2015).

Conclusions

The models that we have developed synthesise a broad range of literature to derive successional trajectories and expected timeframes for NZ’s major forest types in response to disturbances of different types, frequencies and magnitudes. They also highlight some pathways that seem widespread across NZ’s forest ecosystems, but which are poorly understood (e.g. the role of tree-ferns in early successional dynamics). We show that NZ forest dynamics are driven by the interplay of species with differing life-history and regeneration strategies, in a landscape containing a mosaic of disturbances varying in type and spatio-temporal scales. It is therefore evident that alterations to disturbance regimes or to species interactions could have wide-ranging consequences for NZ forest ecosystems, trajectories of community change, and species diversity. Current and future threats faced by NZ’s forest ecosystems, such as invasive species, climate change, and introduced plant pests and diseases, have the potential to cause potentially dramatic alterations to NZ forest dynamics; we

illustrate some of the well-documented changes that are known to have already taken place. The models represent baselines to allow us to understand and assess the further impacts of such threats, and potentially predict future consequences. Additionally, our development of models for the major NZ forest types emphasises the importance of incorporating data spanning a full range of space-time domains in order to capture all relevant disturbance types and pathways governing NZ forest dynamics, and highlights the valuable role of disciplines such as palaeoecology to inform ecosystem dynamics. Our models are high-level and there is scope for more textured development of such frameworks in NZ to support modelling and restoration planning.

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Supplementary Material

Additional supporting information may be found in the online version of this article:

Appendix S1. Key references detailing forest succession following large-scale disturbances in New Zealand.

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