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To cite this article: TT Veblen, ME González, GH Stewart, T Kitzberger & J Brunet (2016): Tectonic ecology of the temperate forests of South America and New Zealand, New Zealand Journal of Botany

To link to this article: <http://dx.doi.org/10.1080/0028825X.2015.1130726>



Published online: 07 Jun 2016.



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REVIEW ARTICLE

Tectonic ecology of the temperate forests of South America and New Zealand

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ABSTRACT

Ecological disturbances triggered by earthquakes and volcanic eruptions are of fundamental importance in structuring the temperate forests of southwestern South America and New Zealand. We review studies of the ecological effects of these tectonic phenomena and how they have been central to progress in the modern development of forest ecology in both regions. Studies of tectonic influences on the dynamics of southern temperate rainforests of Chile and New Zealand published in the 1970s and early 1980s contributed prominently to the shift away from the equilibrium paradigms dominant globally in the 1960s and towards modern non-equilibrium frameworks of forest dynamics. Empirical studies of tectonic ecology in these temperate forests in combination with critical evaluations of earlier successional theory have significantly advanced understanding of the roles of coarse-scale disturbance in the dynamics of forests in southwestern South America and New Zealand. Recognition that cohort forest structures triggered by exogenous disturbances such as wind storms and tectonic events are the norm rather than all-aged structures has been of fundamental importance to understanding the dynamics of these forests. The non-equilibrium patch dynamics framework for interpreting forest structure and dynamics bolstered by tectonic ecology studies in southern South America and New Zealand was of key importance in refining older views of these forests as being out of equilibrium with contemporary climate, revising understanding of the effects of introduced browsing animals on forest structure, and guiding the development of appropriate forest management practices.

ARTICLE HISTORY

Received 6 September 2015
Accepted 29 October 2015

KEYWORDS

Argentina; Chile; disturbance; earthquakes; forest dynamics; landslides; New Zealand; volcanism

Introduction

The locations of southwestern South America (SSA) and New Zealand along boundaries of colliding tectonic plates mean that earthquakes and volcanic eruptions are major sources of ecological disturbances affecting the structure and function of the southern temperate forest ecosystems of these landmasses. Although the ecological importance of the

destruction of vegetation on the flanks of erupting volcanoes has long been apparent, it was not until the late twentieth century that ecologists began to appreciate the effects of regionally widespread but diffuse earthquake-triggered mass movements on the structures of southern temperate forests in SSA and New Zealand (Veblén & Ashton 1978; Stewart & Veblén 1982a). Strong parallels exist between SSA and New Zealand as tectonically active zones with rapidly uplifting mountains and rugged topography. Coarse-scale disturbances directly or indirectly related to tectonism play a fundamental role in shaping the structure and function of these forests. Studies of the ecological effects of these tectonic phenomena have been central to progress in modern forest ecology research in both regions and have contributed significantly to the conceptual development of modern non-equilibrium frameworks in ecology globally. We argue that the study of the ecological effects of tectonism in SSA and in New Zealand played a role equivalent to the importance of studies of fire ecology in the development of modern forest ecology in many other parts of the world.

This synthesis focuses on the role of tectonic phenomena as triggers of ecological disturbance affecting the structure and dynamics of temperate forests in SSA and New Zealand. An over-arching theme of this synthesis is the fruitful interplay between ecological theory and the empirical field evidence of vegetation dynamics (e.g. Clarkson 1990). Modern ecological theory was developed primarily from early twentieth century studies conducted in northern temperate ecosystems of North America and Europe (Glenn-Lewin et al. 1992), which naturally raises questions about how observations in southern temperate forests may or may not be consistent with some of the generalities of ecological theory (e.g. González et al. 2014; Lara et al. 2014a). While fundamental ecological processes are expected to have universal applicability, differences in biota and environments between northern and southern temperate forests potentially may result in differences in the relative roles played by various types of disturbance, successional mechanisms, and plant traits shaped by those disturbances (e.g. Lusk et al. 2015). Hence, to provide context for the synthesis of tectonic ecology in SSA and New Zealand temperate forest ecosystems we first briefly describe how shifting paradigms have influenced interpretations of the dynamics of these forests.

Shifting paradigms in vegetation dynamics

During the last several decades of the twentieth century, appreciation of the roles of natural disturbances in vegetation dynamics shifted from viewing coarse-scale disturbances as relatively rare events interrupting otherwise stable vegetation configurations to a modern framework in which repeated disturbance and continuing change are emphasized (White 1979; Sousa 1984). This recognition of the role of natural disturbance in vegetation dynamics was the key driver of the shift from equilibrium to non-equilibrium paradigms in ecology that matured in the 1980s (Sousa 1984; Glenn-Lewin et al. 1992). This paradigmatic shift emphasized the volatility of environmental change and challenged the traditional views of natural systems trending toward stability or some sort of stasis. Research conducted largely during the 1970s and early 1980s in the southern temperate forests of SSA and New Zealand contributed significantly to this paradigm shift (Veblén & Stewart 1982a; Ogden 1985; Burrows 1990; Enright et al. 1995).

Clements' (1916) classic successional theory emphasized predictable changes in species composition culminating in self-perpetuating climax vegetation, the characteristics of

which were largely controlled by a stable regional climate (Glenn-Lewin et al. 1992). The prevailing views in ecology through the 1960s stressed the predictability of vegetation change and the self-regulation of undisturbed ecosystems (White 1979; Sousa 1984). Conceptual frameworks of vegetation change in the 1960s and 1970s were termed developmental models of vegetation change by Drury and Nisbet (1971) because they stressed the development of a predetermined, relatively stable plant community in a stable physical habitat. As an alternative to developmental models, Drury and Nisbet (1971) proposed a kinetic model that does not assume a stable end point for succession and instead emphasizes continuous change. Hence, a kinetic framework accepts the fundamental instability of the physical site, in contrast to the assumption of long-term site and climatic stability in developmental models of vegetation change.

Although the term 'kinetic' did not persist in the ecological literature (but see Burrows 1990), emphasis on repeated disturbance is a key component of the modern non-equilibrium framework for studying vegetation dynamics (White 1979; Sousa 1984). In a non-equilibrium framework, repeated disturbance as a driver of change is given equal weight to plant-controlled changes of the micro-environment typically emphasized in traditional developmental models. Modern ecologists continue to examine the types and relative importance of plant-centred mechanisms of succession stressed by early twentieth century ecologists, but today equal attention is devoted to understanding plant population responses to disturbances and to quantifying disturbance regimens (Pickett et al. 1987; White & Jentsch 2001).

Disturbances influence plant communities through their direct effects on plant biomass by killing entire plants or removing parts of plants, which in turn affects competition, environmental conditions, and the availability of substrate and resources to other plants (White 1979; Pickett et al. 1987). Disturbance is a primary cause of fine-scale as well as coarse-scale spatial heterogeneity in ecosystems (White & Jentsch 2001). Tectonic disturbances are often sources of coarse-scale patchiness (lava flows, ash falls) but also can result in moderate- to fine-scale patchiness (landslides, tree-falls).

A *disturbance regimen* is a description of all the disturbances affecting an ecosystem, landscape, or even a larger region, and must be explicitly linked to a real place in the landscape (i.e. not generalized to an abstract biome type) and to a defined time period. The key descriptors of a disturbance regimen are the type of disturbance, spatial attributes and temporal characteristics (Sousa 1984). In the context of tectonic ecology, examples of spatial characteristics include extent and depth of volcanic ash fall (Swanson & Major 2005) or extent and location of earthquake-triggered mass movements relative to distance to epicentres, slope steepness and substrate (Wright & Mella 1963). Important temporal characteristics include not only frequency of events but also duration (e.g. of ash falls) and timing (e.g. coincidence of earthquakes with drought or high precipitation). *Linked disturbances* (sensu Simard et al. 2011) are disturbances that interact by altering the extent, severity, or probability of occurrence of a subsequent disturbance. Examples relevant to tectonic ecology include the effects of ash fall on susceptibility to wind-caused tree-falls or to foliar herbivory by insects. *Compound disturbances* (sensu Paine et al. 1998) refer to the occurrence of two disturbances at relatively short intervals that have a synergistic effect greater than the effect predicted from the sum of their individual impacts. Examples of compound disturbances relevant to tectonic ecology include ash fall on a post-fire stand too young to have reproductively mature trees, occurrence of

high winds in a forest severely shaken by an earthquake, or torrential rainfall immediately following earthquake-triggered landslides.

Earthquake-related disturbances and forest dynamics in southwestern South America

A conspicuous feature of old stands of the Valdivian rainforests of south-central Chile is the scarcity of understorey trees of the same species that dominate the canopy of old forests, implying a lack of continuous tree regeneration of the regionally extensive dominant species. Specifically, for the Andean forests in the Province of Valdivia in unlogged old forests there is a scarcity of small diameters of *Nothofagus dombeyi*, *Nothofagus alpina*, and *Nothofagus obliqua* in mixed-species rainforests dominated by large trees of these species (Brun 1975). In contrast, the associated shade-tolerant tree species such as *Laureliopsis philippiana*, *Aextoxicon punctatum* and *Saxegothaea conspicua* are abundantly represented in all size classes from juveniles in the understorey through subcanopy and main canopy trees (Brun 1975). Hence, the size structure of these forests is indicative of a successional trend from shade-intolerant *Nothofagus* spp. towards dominance by the shade-tolerant species. The dominance of *Nothofagus* spp. throughout the Valdivian Andes raises the question of why there are apparently no extensive stands representing a compositional equilibrium (or *climax*) dominated exclusively or primarily by the shade-tolerant tree species. Observations in the 1970s of the effects of mass movements and other disturbances triggered by the giant 1960 Chile earthquake (at magnitude 9.5 M_w the most powerful recorded; Cisternas et al. 2005) were pivotal in unravelling this apparent paradox (Veblen & Ashton 1978).

A series of studies conducted in the late 1970s developed and tested the hypothesis that the importance of *Nothofagus* spp. in the old-growth forests of the mid-montane Valdivian Andes depends on their periodic regeneration after severe coarse-scale disturbances (Veblen & Ashton 1978). The evidence in support of this hypothesis included: (i) the abundance and vigorous growth of *Nothofagus* seedlings on surfaces recently disturbed by mass movements; (ii) the absence or scarcity of *Nothofagus* regeneration in the understoreys of the mixed-species old-growth stands; and (iii) the historical frequency of coarse-scale earthquake-triggered mass movements and other associated disturbances such as flooding (Veblen et al. 1980, 1981). Although the hypothesis was developed specifically for the Valdivian Andes (c. 40°S), it provided a conceptual framework for subsequent investigation of the roles of disturbance in the dynamics of temperate forests generally in Chile and Argentina (Gutiérrez et al. 2004; Lara et al. 2014a).

On the wet western side of the Andes, strong earthquakes periodically trigger thousands of mass movements (e.g. landslides, rock falls, debris flows and mudflows; Wright & Mella 1963). Thick volcanic ash layers on glacially over-steepened slopes are highly prone to mass movements triggered by earthquakes or by intense rain storms (Wright & Mella 1963). Bare surfaces exposed by mass movements are rapidly colonized (often within 1 to 5 yr) by tree species including *Nothofagus* spp., *Aristotelia chilensis*, *Caldcluvia paniculata*, *Drimys winteri*, *Embothrium coccineum*, *Eucryphia cordifolia*, *Lomatia ferruginea* and *Weinmannia trichosperma* (Veblen & Ashton 1978; Veblen et al. 1989; Rosas 1991; Larraín 1997). Successful establishment and growth of these trees on bare surfaces is probably facilitated by the ectomycorrhizae of the *Nothofagus* spp. and by the presence of

nitrogen fixers such as the cyanobacterial genus *Nostoc* in symbiotic association with the giant herb *Gunnera chilensis* (Figure 1) (Veblen et al. 1996b).

Over extensive areas in the Valdivian rainforest district, relatively old (> 300 yr old) stands are dominated by emergent trees of shade-intolerant species such as *Nothofagus* spp. and *Eucryphia cordifolia* (Veblen & Ashton 1978; Veblen et al. 1980, 1981; Donoso et al. 1984; Donoso et al. 1985; Veblen 1985; Armesto & Figueroa 1987). In undisturbed stands, young or small trees of these species are absent or scarce. In contrast, shade-tolerant tree species (such as *Laurelia sempervirens*, *Laureliopsis philippiana*, *Saxegothaea conspicua*, *Persea lingue*, *Aextoxicon punctatum* and numerous myrtaceous trees) are typically abundant and occur as all-aged populations (Donoso et al. 1984, 1985; Veblen 1985; Armesto & Figueroa 1987; Lusk 1996b; Pollmann & Veblen 2004). In the absence of disturbance, there is a gradual successional trend towards dominance by these shade-tolerant species. In landscapes with a high frequency of coarse-scale disturbances, this successional trend is not completed and the shade-intolerant trees (especially *Nothofagus*) remain dominant in the oldest stands (Veblen & Ashton 1978, Veblen et al. 1981).

Written records and tree-ring reconstructions document high-magnitude earthquakes affecting south-central Chile and the adjacent eastern slopes of the Andes, which triggered widespread mass movements and floods in 1575, 1737, 1751, 1837 and 1960 (Veblen & Ashton 1978; Kitzberger et al. 1995). Along the coast of Chile these earthquakes caused extensive forest mortality due to subsidence, tsunamis and flooding as revealed by stratigraphy of soils buried by flood deposits (Cisternas et al. 2005). On the islands and the coast south of Chiloé Island, stands of dead-standing trees lacking evidence of fire were attributed to effects of tidal waves and tectonic subsidence associated with the 1837 earthquake (Rothkugel 1916). Dead stands of inundated coastal forests occur throughout the southern Chilean Archipelago from just south of Chiloé Island to Tierra del Fuego and have been linked to earthquake-triggered subsidence (Goodall 1979).

Studies of the effects of large-scale mass movements and associated flooding whether triggered by earthquakes or by torrential rain storms (Lara 1991), supported development of a general model of forest dynamics in the Andean region of the mid-latitudes of South America (Veblen et al. 1996a, 1996b; Pollmann & Veblen 2004). The focus of the model originally was on *Nothofagus* spp. but with modifications to account for differences in distribution and habitats, it also applies to other long-lived shade-intolerant pioneer species for which regeneration is dependent to a large degree on canopy opening by disturbances (e.g. *Eucryphia cordifolia*, *Weinmannia trichosperma*) (Veblen et al. 1981; Veblen 1985; Donoso et al. 1984, 1985; Lusk 1999). The ubiquitous distribution of *Nothofagus* in the Andes at these latitudes can be explained by two processes: (i) At climatically and edaphically favourable sites where there is intense competition from shade-tolerant rainforest species, coarse-scale disturbances create establishment opportunities for *Nothofagus* and other shade-intolerant long-lived pioneer species. (ii) At climatically unfavourable sites (i.e. cooler or drier sites) and on edaphically suboptimal sites, the rainforest species are absent or rare, and consequently *Nothofagus* is able to regenerate even in the absence of coarse-scale disturbance. The interpretation that disturbance favours *Nothofagus* persistence is also supported by life history traits expected for long-lived pioneer species, including rapid tree growth rates under open conditions, longevity of at least several centuries, and effective seed dispersal into canopy openings (Veblen et al. 1996b; Lusk & del Pozo 2002; Pollmann 2004). In species-rich lowland forests intense competition from abundant

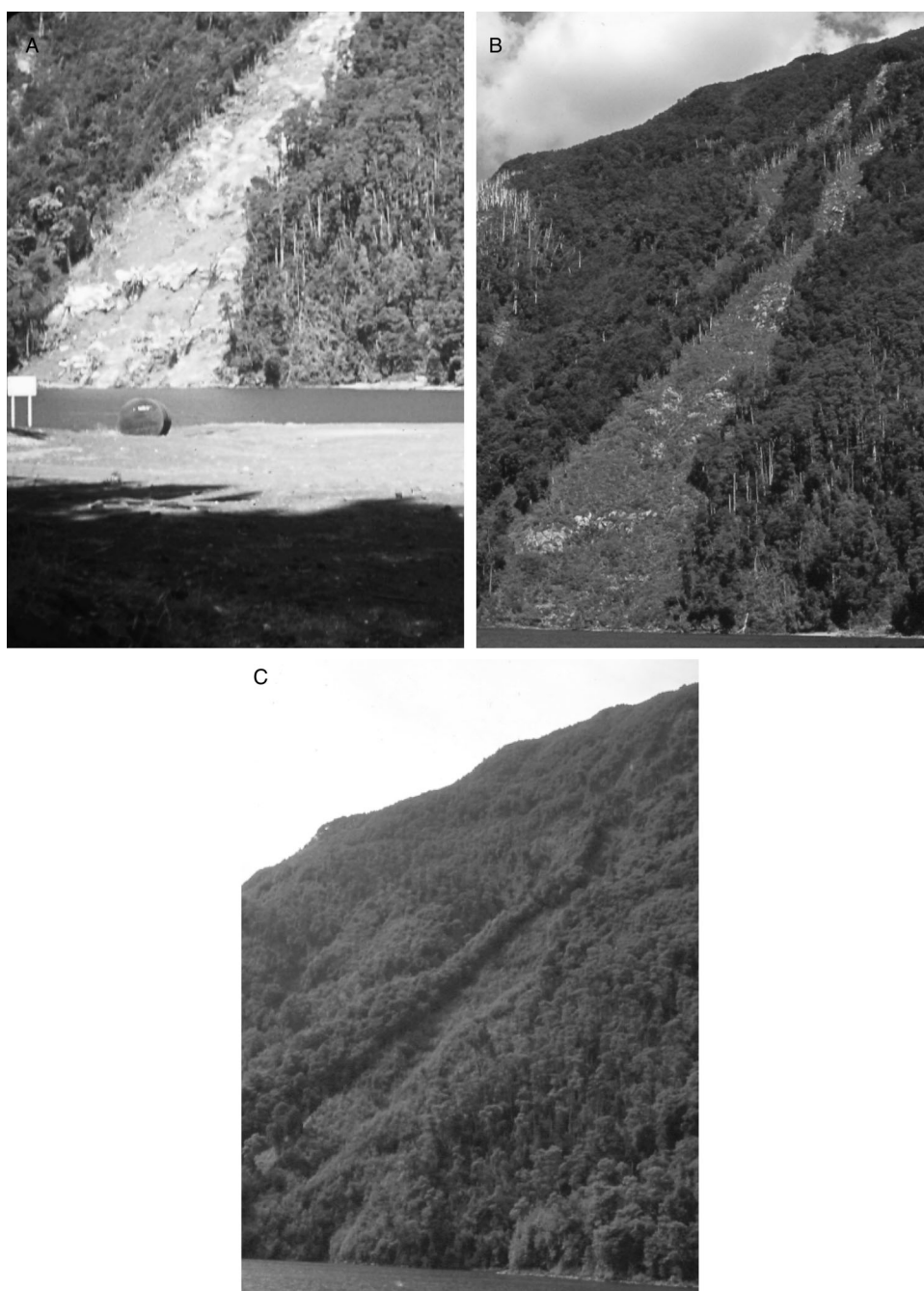


Figure 1. Photographs of landslides at Lago Todos Los Santos, Chile triggered by the 1960 giant earthquake. **A**, January 1966 showing the site completely denuded by the sliding of soil, vegetation and volcanic ash. **B**, The site dominated by the giant perennial herb *Gunnera chilensis* and shrubs in March 1979. **C**, December 1993, showing that trees (primarily *Nothofagus dombeyi*) that were present as seedlings beneath the herb and shrub cover in 1979 have grown into a closed canopy forest. Photographs: A, Carlos Vargas; B and C, Thomas Veblen.

shade-tolerant species precludes regeneration of *Nothofagus* beneath tree-fall gaps (Veblen et al. 1979; Veblen 1985), but at higher elevations or drier sites with fewer tree species the same size gap may result in successful regeneration of *Nothofagus* (Veblen 1989a, 1989b; Pollmann & Veblen 2004).

The general model of *Nothofagus* forest dynamics described above pertains primarily to the Andes where volcanism and earthquake-caused mass movements are common but not to the non-volcanic coastal mountains of southern Chile where these tectonic disturbances are relatively unimportant. In the coastal mountains the relative dominance of shade-tolerant tree species is greater; shade-intolerant pioneer species are less abundant and even locally absent (Veblen et al. 1996b). For example, *Nothofagus* spp. are largely absent at elevations below 400 m between 41°S and 43°S in the coastal mountains (Veblen et al. 1981; Armesto & Figueroa 1987). In the absence of large-scale tectonic disturbances, fine-scale gap processes predominate in the low- to mid-elevation coastal ranges (Veblen et al. 1981; Armesto & Fuentes 1988; Lusk 1996b). In addition, coarse-scale disturbance by stand-scale blowdowns and pre-Hispanic fires have also been documented in the coastal forests (Lusk 1996a, 1996b).

Recognition of the importance of coarse-scale natural disturbances, triggered by tectonic events as well as others such as severe storms, has informed the development of science-based forest management in SSA. Management prescriptions for forests dominated by long-lived pioneer species (primarily *Nothofagus* spp.) are based on a sound understanding of their responses to coarse-scale disturbances (Donoso et al. 2014). As recently as the 1970s the most valuable timber trees, such as *N. alpina*, were selectively logged from these forests, resulting in no or little regeneration of the valuable timber species and a degradation of the resource. Recognition of the role of infrequent coarse-scale disturbance in creating regeneration opportunities for threatened species such as *Fitzroya cupressoides*, formerly regarded as a relict not adapted to the current climate, similarly has been important in restoration and species preservation projects (Lara et al. 2014b).

Earthquake-related disturbance and forest dynamics in New Zealand

New Zealand is prone to earthquakes because it sits on the boundary between the Australian and Pacific crustal plates, a boundary marked in part by the Alpine Fault, which stretches along the entire length of the South Island (Wells et al. 2001). Explorers in the late nineteenth century in Westland noted that much of the forest appeared to be dominated by similarly sized trees and suggested that widespread forest destruction had occurred in the past, possibly caused by earthquakes (Charles Douglas in Holloway 1957). A team of governmental scientists investigating potential causes of forest mortality in the 1950s in Westland also noted what appeared to be even-aged patches of forest and also ascribed their origin to major earthquakes (Chavasse 1955). These patterns were later described by Wardle (1966, 1971) who further suggested that a major earthquake occurred between AD 1730 and 1740 (Wardle 1980). The first in-depth studies of the dynamics of these forests documented that indeed many of the forests were dominated by even-aged stands of trees as a consequence of earthquake-triggered mass movements (Stewart & Veblen 1982a; Veblen & Stewart 1982a; Stewart & Rose 1989).

Regional compilation of forest structure data for Westland indicated episodes of widespread forest regeneration around 250–350 and 550–600 years before present (yr BP) that appeared to have been initiated by catastrophic disturbances (Wells et al. 1998). Tree-ring reconstruction of forest disturbances in south Westland in conifer–hardwood forests documented catchment-wide episodes of cohort-initiating disturbances around AD 1820–30, 1710–1720, 1610–1620 and 1460 (Wells et al. 2001). These episodes coincide with the three most recent Alpine Fault earthquakes (c. AD 1717, 1630 and 1460) and with earthquakes recorded to the south of the study area in AD 1826. Eighty-six per cent of the study area had experienced erosion and sedimentation events over the last 650 yr (Wells et al. 2001).

The impacts of earthquakes on forest structure and composition vary widely with topographic setting, magnitude of the earthquake, and time since the previous strong earthquake. In Westland, even-aged cohorts initiated by the AD 1717 earthquake are located near the Alpine Fault line and in the frontal ranges of the Southern Alps, whereas even-aged stands triggered by the AD 1630 earthquake occur on floodplains all the way to the coast (Cullen et al. 2003). The AD 1630 earthquake followed a relatively long period since the previous strong earthquake in AD 1460, allowing for more sediment build-up in the headwaters of streams for release and deposition downstream in floodplains (Cullen et al. 2003). A combination of fault trenching, ^{14}C dating of landslides and terraces, and tree-ring dating demonstrate that infrequent, strong earthquakes, through triggering erosion and flooding events, are the dominant forest disturbance agents in Westland (Adams 1980; Wells et al. 1999). Tree regeneration opportunities created by earthquakes for different groups of tree species depend on topography and edaphic conditions. The 1968 Inangahua earthquake (magnitude 7.1 M_w) triggered landslides in the Buller Gorge exposing bare surfaces that have recovered to regenerating stands of *Nothofagus fusca* and *Nothofagus menziesii* (Figure 2). In the mixed conifer/beechn/broadleaved forests of north Westland on a post-glacial terrace in the Grey Valley after an earthquake around 365 yr ago, *N. fusca*, *N. menziesii* and *Weinmannia racemosa* regenerated on well-drained sites while *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* along with *N. menziesii* regenerated on poorly drained soils (Urlich et al. 2005). These differential patterns of regeneration can be further complicated by the availability of suitable establishment sites for seedlings as in these wet forests many tree species preferentially establish on raised surfaces such as upturned trees and logs (Stewart & Veblen 1982a; Stewart 2002).

Although less frequently studied than for the Alpine Fault zone of Westland, earthquake impacts are significant in forests elsewhere on the South Island. In the Matiri Valley in the northwest of the South Island the Murchison earthquake (7.7 M_w) in 1929 resulted in pulses of regeneration of *N. fusca* in large gaps created by landslides whereas smaller gaps with little or no landslide damage were rapidly closed by crown expansion of *N. fusca* and/or *N. menziesii* (Vittoz et al. 2001). Further south and east, in inland Canterbury, permanent plots established around 1970 in *Nothofagus solandri* var. *cliffortioides* forests recorded a 23% decline in stand biomass following a 6.7 M_w earthquake in 1994 (Allen et al. 1999). On average, 74% of the total stem biomass mortality resulted from landslides (Allen et al. 1999).

A little-studied but important influence on coastal forests of the South Island has been from forest disturbance caused by earthquake-triggered tsunami inundation.

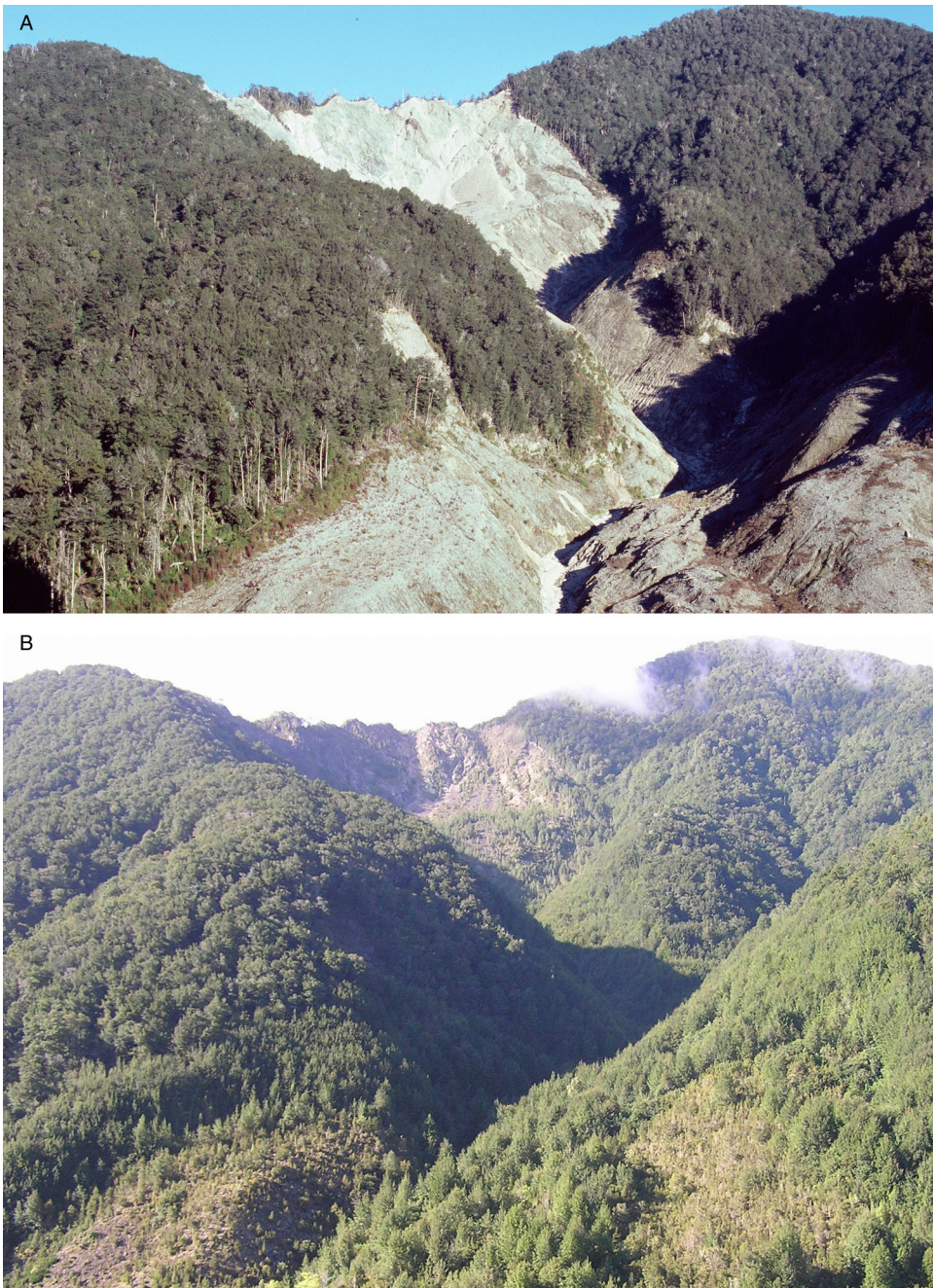


Figure 2. Photographs showing landslides triggered in the Buller Gorge (Westland, New Zealand) by the 1968 Inangahua earthquake (magnitude 7.1 M_w). **A**, Mostly bare surfaces and a narrow band of tree regeneration along the forest edge in 1980. **B**, 2011 showing recovery to young stands of *Nothofagus fusca* and *Nothofagus menziesii*. Photographs: Thomas Veblen.

Sedimentological, geochemical and micro-palaeontological data from the Ōkārīto Lagoon in south Westland indicate that tsunami inundation occurred in 1826, a known date of

earthquake activity reported by early sealers in the area (Goff et al. 2004). Similarly, episodic formation of shore-parallel dune systems at Haast further south has been linked to major ruptures of the Alpine Fault, and the dunes support tree cohorts established soon after major regional earthquakes in c. AD 1460, 1615, 1717 and 1826 (Wells & Goff 2006).

A conspicuous feature of central Westland forests are the extensive, even-sized *Metrosideros umbellata*/*Weinmannia racemosa* stands that are prominent along the steep front ranges and middle valley reaches over at least 250 km (Stewart & Veblen 1982a; Rose et al. 1992). It has been suggested that many of these stands originated following a large Alpine Fault earthquake (Holloway 1957; Wardle 1980; Stewart & Veblen 1982b). The *M. umbellata* and *W. racemosa* sampled in these stands all originated after the last major Alpine Fault earthquake in AD 1717 (Wardle 1980; Wells et al. 2001), and it is likely that stands of this age are widespread. This could help to explain the widespread dieback of these stands at mid-elevations in Westland (Chavassee 1955, Stewart & Veblen 1982b, 1983). Stand dieback has commonly been attributed primarily to browsing by the introduced brushtail possum (*Trichosurus vulpecula*) (e.g. Bachelor 1983). However, trees growing in even-aged cohorts that arose after a region-wide disturbance event would senesce at about the same time, making them more susceptible to widespread synchronous dieback from a trigger factor such as possum browse (Veblen & Stewart 1982b). Location and extent of these even-aged stands helps to explain the variation in the magnitude of canopy dieback observed throughout Westland (Stewart & Veblen 1982b; Stewart & Rose 1988; Rose et al. 1992).

Volcanism and its influence on the forests of the southern Chile and Argentina

Effects on the rainforests of southern Chile

The principal types of disturbances associated with eruptions of the many volcanoes located in the mid-latitude Andean region of temperate rainforests are lava flows, pyroclastic flows, air-borne deposits (tephra or ash falls), mudflows (lahars) and debris avalanches (Swanson & Major 2005). Vast areas in southern Chile are covered in tephra deposits from numerous eruptions throughout the Holocene indicating widespread and severe volcanic disturbances (Casertano 1963; Jara & Moreno 2012). Analogous to the situation described for earthquake-triggered mass movements above, bare or partially bare surfaces created by volcanic disturbances can, under particular circumstances, be colonized by some of the dominant tree species of the region including *Nothofagus* spp. as well as the conifers *Araucaria araucana* and *Fitzroya cupressoides* (Veblen et al. 1977; Veblen & Ashton 1978; Veblen 1982; Lara 1991; González et al. 2014). And, again this is a pattern typical of the Andes but not found in the non-volcanic coastal mountain ranges of south-central Chile and Chiloé Island where non-tectonic disturbances such as fine-scale gap processes are more prevalent (Veblen et al. 1981; Armesto & Fuentes 1988; Lusk 1996b).

Only a few recent volcanic eruptions have been studied in detail to reveal the complexity of their ecological impacts. These include the eruptions of the Hudson, Chaitén and Cordon Caulle volcanoes in 1991, 2008 and 2011, respectively (Swanson et al. 2013;

González et al. 2014). In the 1991 eruption of the Hudson Volcano at c. 46°S, extensive forests of *Nothofagus pumilio*, *N. dombeyi* and *Nothofagus antarctica* were killed by ash fall and by the lahars and floods that affected the Rio Ibañez. The Chaitén eruption affected primarily Valdivian rainforest at c. 43°S, whereas the eruption of Cordón Caulle (c. 40°35'S) deposited ash not only in adjacent areas of Valdivian rainforest but, due to the prevailing westerly winds ash, also affected large areas of drier *Nothofagus* and *Austrocedrus* forests in Argentina east of the Andes (Figure 3). Many woody and rhizoid understorey species survived ash burial of depths of c. 10 cm or more (Vogel et al. 1994; González et al. 2014). The understorey shrubs *Drimys andina* and *Maytenus disticha* survived several months of intermittent ash deposition during Cordón Caulle eruption (Figure 4A; González et al. 2014). Resprouting and production of adventitious roots and shoots facilitated the survival and recovery of the bamboo *Chusquea quila*, the large fern *Lophosoria quadripinnata*, shrubs such as *Ribes magellanicum*, *Ovidia andina*, *Berberis* spp. and *Fuchsia magellanica* and the perennial herb *Gunnera magellanica* (Figure 4B; Vogel et al. 1994; González et al. 2014). *Gunnera magellanica* is abundant at wet sites and due to its symbiotic association with the nitrogen-fixing cyanobacterial genus *Nostoc* is a key species promoting accumulation of C and N in the soil (Fernández-Martínez et al. 2013). Two to three years after the eruption of Cordón Caulle and Hudson volcanoes there was a massive recruitment of *N. pumilio* (Figure 5B), but the long-term survival of these seedling populations is likely to depend on fortuitous

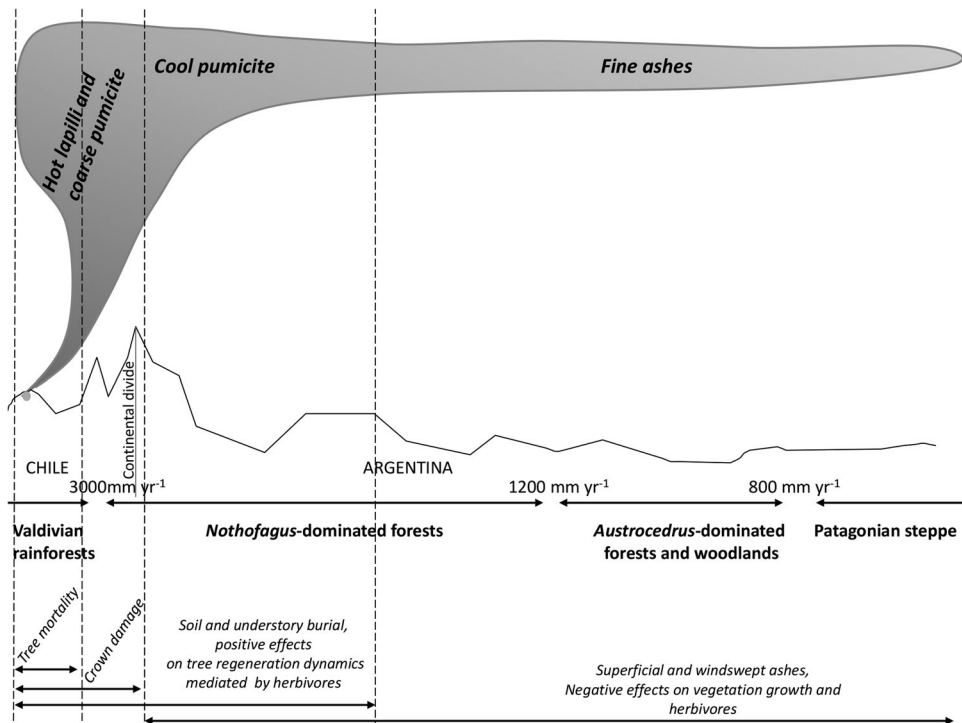


Figure 3. Schematic representation of the typical ash fall patterns and effects on vegetation dynamics along a west-to-east gradient in northwestern Patagonia from eruptions of the Puyehue–Cordón Caulle volcanic complex.



Figure 4. Photographs of the Cordón Caulle ash fall in a *Nothofagus pumilio* forest. **A**, *Drimys andina* survived despite being buried by ash for 6 months. **B**, A fallen tree provided a safe microsite for establishment of the shrub *Ribes magellanicum*, the herbaceous creeper *Acaena ovalifolia*, and the perennial herb *Gunnera magellanica*. Photographs: A, Thomas Veblen; B, Mauro González.

establishment in the limited areas of suitable light and soil nutrient conditions (Vogel et al. 1994). Although the presence of mature trees of species such as *Nothofagus* spp., *Araucaria araucana*, *Fitzroya cupressoides*, *Weinmannia trichosperma* and *Austrocedrus chilensis* on scoria deposited within the last one to a few centuries is commonly observed (Veblen & Ashton 1978; Veblen 1982; González et al. 2014), to date there are no published

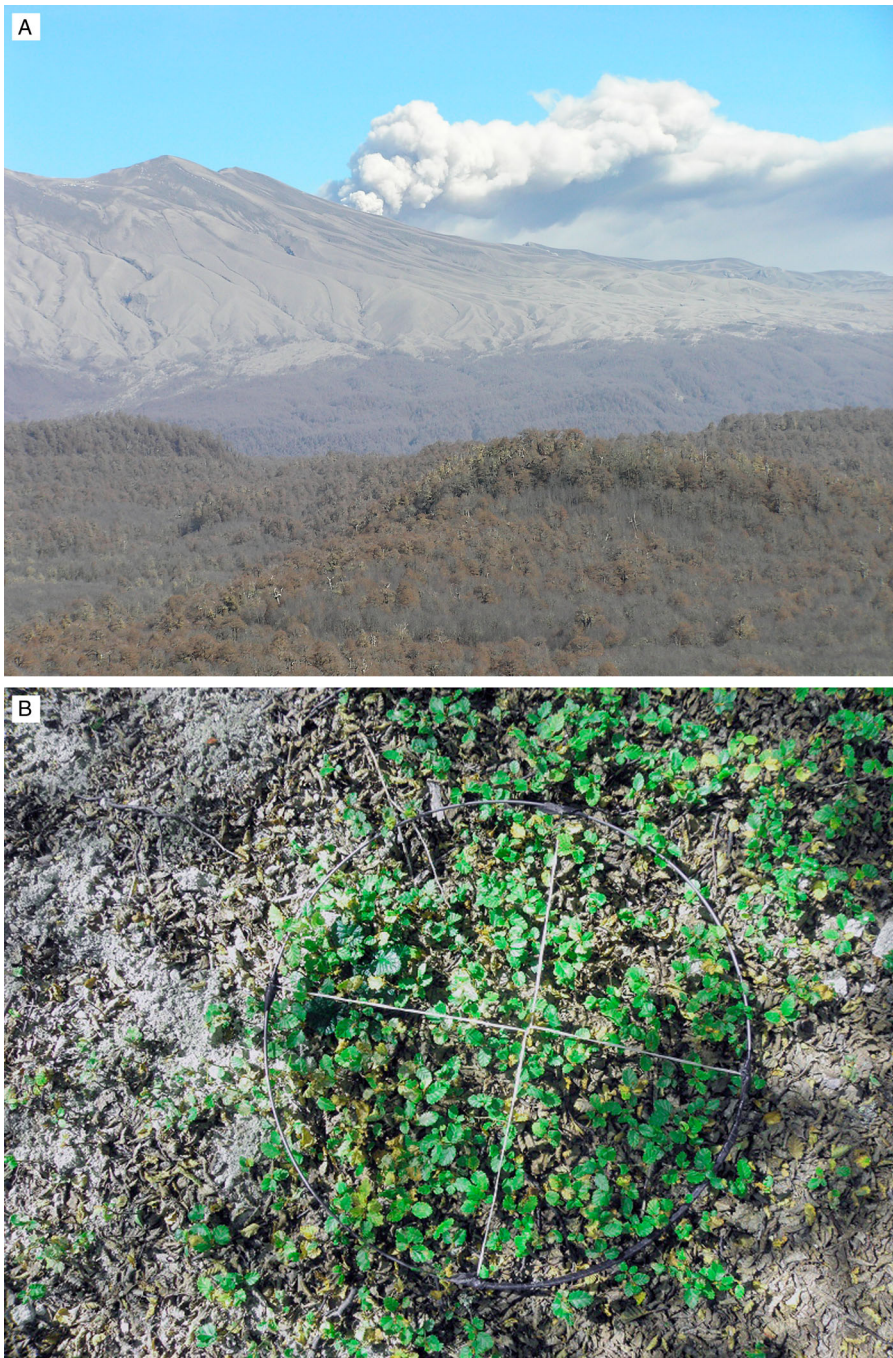


Figure 5. Photographs of volcanic ash from Cordón Caulle. **A**, Cordón Caulle erupting in January 2012 with *Nothofagus pumilio* in the foreground that mostly died; the explosive phase of the eruption lasted from June 2011 to April 2012. **B**, Abundant establishment of *Nothofagus pumilio* seedlings in 2014 c. 40 km west of Cordón Caulle at western Lago Traftal on a c. 5–6 cm thick ash layer. Photographs: A, Thomas Veblen; B, Joaquin Brunet.

studies of the site conditions necessary for such successful tree regeneration on volcanic deposits.

The eruption of the Chaitén Volcano in 2008 sent ash 20 km into the atmosphere, which was transported by the predominantly westerly winds eastwards over an area larger than a 1000 km² (Swanson et al. 2013). During the initial few days of activity, ash up to 10 cm deep was deposited at distances of 30 km from the source. Coarse tephra was deposited on the flanks of the volcano and transported into rivers and forested floodplains. The volcanic and associated hydrological processes resulted in a broad range of mechanisms and severities of ecological disturbance affecting trees, including tree snapping from impact force, defoliation, abrasion, heat damage, canopy loading by ash capture, and stem burial by mudflows and ash. Coarse tephra (gravel size) abraded tree foliage over an area of c. 50 km², and crown weighting due to fine tephra capture broke branches and bent young, flexible trees over an area of 480 km². In the toppled-tree zone, species observed to have sprouted from epicormic buds on trunks and branches included *Weinmannia trichosperma*, *Eucryphia cordifolia*, *Amomyrtus luma* and *Amomyrtus meli*, but in some cases the sprouts subsequently died (Swanson et al. 2013). Flood deposition of > 1 m of re-mobilized tephra buried floodplain forests over many kilometres of the adjacent river valleys (Swanson et al. 2013).

At sites outside the total destruction zone of the Chaitén eruption, the weight of fine-grain volcanic ash stripped branches off large canopy trees and toppled smaller trees (Swanson et al. 2013). The fact that most of the trees in the rainforests of southern Chile are broadleaved evergreen angiosperms makes them particularly vulnerable to damage resulting from the weight of leaf capture of volcanic ash. Litter fall traps installed in a forest 25 km south of the Villarrica Volcano collected 13.6 tons/ha of sand-size ash over a few days of volcanic activity in 1971 (Veblen et al. 1980). This type of relatively infrequent but spatially extensive canopy disturbance may provide regeneration opportunities for the dominant shade-intolerant species (*Nothofagus* spp., *Eucryphia* and *Weinmannia*), which otherwise would slowly be replaced by more shade-tolerant rainforest species (Veblen et al. 1981). In fact, multi-millennial fossil pollen records from rainforest sites indicate abrupt increases in *Eucryphia* and *Weinmannia* pollen following tephra deposition, even at sites many kilometres distant from the volcanic vents (Jara & Moreno 2012). Both *Eucryphia* and *Weinmannia* are long-lived pioneer species dependent on canopy openings for regeneration (Veblen 1985; Lusk 1999; Gutiérrez et al. 2004), leading to the conclusion that eruptions can enhance regional abundance of early to mid-successional species (Jara & Moreno 2012). In addition to regeneration opportunities resulting from canopy openings due to ash fall, fires ignited by volcanism create regeneration opportunities for the shade-intolerant tree species (Veblen & Ashton 1978; Jara & Moreno 2012).

Tephra fall is the most widespread volcanic disturbance and the repeated re-mobilization of ash as mudflows is particularly important in the alpine treeline zone where vegetation recovery is inherently slow (Veblen et al. 1977). In the treeline zone, *N. antarctica* resprouts adventitiously from its branches, giving it the capacity to withstand at least 30 cm of burial by ash mudflows (Veblen et al. 1977). Similarly, *N. pumilio* can develop a new lateral root system at the new soil surface following burial by mudflows of volcanic ash (Veblen et al. 1977). However, repeated burial of trees by volcanic ash in combination with the limited water-holding capacity of the coarsely textured tephra results in treelines

depressed below the elevations they could potentially reach under climatic limitations alone (Daniels & Veblen 2003; Daniels & Veblen 2004).

Ash fall effects on drier forests east of the Andes in northwestern Patagonia

Given the predominantly westerly winds at mid-latitudes in SSA, eruptions of Andean volcanoes on the western side of the continent deposit large quantities of ash eastwards into Argentina affecting a gradient of vegetation from mesic through dry forests and the Patagonian steppe. Thickness of tephra deposits attenuates sharply from west to east and particle size declines from gravel size within a few kilometres of the source to fine tephra (sand and silt) eastwards. Thus, the 2011 eruption of Cordon Caulle deposited thick layers of gravel- and sand-sized tephra in mesic *Nothofagus* forests on the eastern slopes of the Andes and thinner layers of silt-sized ash in the drier *Austrocedrus* forests and woodlands in the foothills near the ecotone with the steppe (Figure 3)

During the June 2011 eruption of Cordon Caulle the westernmost *N. pumilio* forests in Argentina were affected by incandescent volcanic ejecta, which damaged foliage and growth buds on trees in permanent plots at a distance of 22 km from the vent (Chaneton et al. 2014). The result was partial crown mortality but rarely death of the entire tree at that distance from the source. Hot ash damaged winter foliar buds, which reduced leaf area production by nearly 60% during the following season (Chaneton et al. 2014). This is in contrast to more westerly *N. pumilio* stands located within a few kilometres of the volcano, which under hotter ash fall, suffered complete bud mortality and tree death (Figure 5A).

Further east in sub-mesic pure *Nothofagus* forests, the most prominent effect of the eruption of Cordon Caulle is the burial of soils and understorey plants by sandy pumicite layers that create a bare mineral substrate beneath intact forest canopies. Seedling establishment of both *N. dombeyi* and *N. pumilio* is directly and indirectly enhanced by ash deposition (J. Brunet et al. unpubl. data). Dense carpets of new *Nothofagus* seedlings established on the ash (Figure 5B) indicate that germination and early growth are favoured by the shift from a forest litter substrate to an ash substrate from which the pre-existing understorey has been mostly removed. Seedlings of *N. dombeyi* that endured the ash burial form adventitious roots that rapidly proliferate and grow laterally through the new ash layer. Due to the dramatic reduction in available forage (both beneath forest canopies and in open areas), cattle populations declined by c. 50% so that browsing and trampling damage on tree regeneration was sharply reduced. Cattle numbers declined partly due to mortality, but mostly due to the decision of cattle owners to remove animals because of the lack of forage (J. Brunet et al. unpubl. data). Overall, despite some subsequent seedling mortality, burial of soils and understorey had the net effect of increasing *Nothofagus* regeneration; this was particularly the case for stands where large cattle populations had previously impeded tree regeneration (Veblen et al. 1992). Several prominent cohorts of *Nothofagus* (particularly *N. pumilio*) in the Lago Traful area appear to have developed from the release of advance regeneration coincident with the 1920 and 1960 eruptions of the Puyehue–Cordon Caulle complex (J. Brunet et al. unpubl. data).

Further east at the ecotone with the steppe, ash deposition in 2011 grass growth declined by 36–50% due to reduced interception of solar radiation (Oyarzabal et al. 2011; Irisarri et al. 2012). In addition, in the open interspaces among the shrubs and bunchgrasses, ash deposition favoured the recruitment of perennial rhizomatous grasses

or geophytes over annuals (Ghermandi & González 2012). The event had a large impact on livestock dependent on highly productive *mallines* (wetland meadows) composed of short grasses that became buried by ashes resulting in stock losses or relocation to distant pastures.

In addition to direct effects on vegetation, volcanic eruptions have important indirect effects on forest ecosystem functioning mediated by impacts on insect herbivores. Effects of the ash deposition from the 2011 Cordón Caulle eruption on arthropods are highly variable according to feeding habits and habitats of arthropods (Ruggiero & Kitzberger 2014). Ants and ground beetles remained relatively undisturbed by the event. In contrast, arthropod pollinators and canopy foliovores exhibited significant impacts. Ash deposition resulted in a sustained disruption of pollination services by a key bumble bee species (Morales et al. 2014). For insect foliovores, the ash fall acted as a natural insecticide at a regional scale, drastically reducing insect-caused leaf damage in *N. pumilio* forests (Chañeton et al. 2014).

Volcanism and its influence on the forests of New Zealand

Volcanism has strongly shaped the contemporary forest pattern in the North Island of New Zealand. In particular, in the central North Island numerous eruptions of the Taupo supervolcano have occurred over the last 300,000 yr, and its most recent massive pumice eruption in 1718 ± 5 cal yr BP covered 30,000 km² with tephra deposits and c. 20,000 km² with ignimbrite (Hogg et al. 2012). Near Lake Taupo, conifer-broadleaved hardwood forests similar in structure and composition to the contemporary forests were buried by more than 100 m of pyroclastic flows (Clarkson et al. 1992, 1998). Stands of bracken (*Pteridium esculentum*) flourished immediately after the eruption, and fires occurred during and for several decades following the eruption (Wilmshurst & McGlone 1996). Most sites available for plant establishment after an extensive rhyolitic eruption are deficient in nutrients, especially nitrogen and phosphorus, so that often the first establishing plants are species that harbour mycorrhizal associations (Uhe 1972). Several tall forest species (*Weinmannia* and *Metrosideros*) produce abundant, light wind-dispersed seed and also sprout after damage (Wardle 1966, 1971). However, even several centuries following deposition of up to 40 cm of ash over a 150 km² area around Mount Taranaki, the composition of the treeline vegetation reflects this disturbance event and treeline elevation is suppressed below the elevation of unaffected areas (Figure 6A; Efford et al. 2014). Light-demanding, cold-tolerant taxa were able to take advantage of the newly created open sites resulting in establishment of new cohorts of taxa such as *Libocedrus bidwilli* (Figure 6B; Efford et al. 2014).

The relative roles of volcanic disturbance and climatic gradients in determining the spatial pattern of species composition of the current conifer/broadleaved hardwood forests of the Taupo region have been widely debated. McKelvey (1963, 1973) ascribed a dominant role to the eruption, documenting a pattern where conifers were dominant close to the eruption centre, and broadleaved hardwood trees dominated further away. He concluded that the dense conifer stands were a pioneering stage in a somewhat slow centripetal colonization away from the eruption centre. Clarkson et al. (1992) examined macrofossil evidence to evaluate McKelvey's hypothesis. They found that broadleaved forest, notably *Beilschmiedia tawa*, is not the dominant endpoint of the forest succession

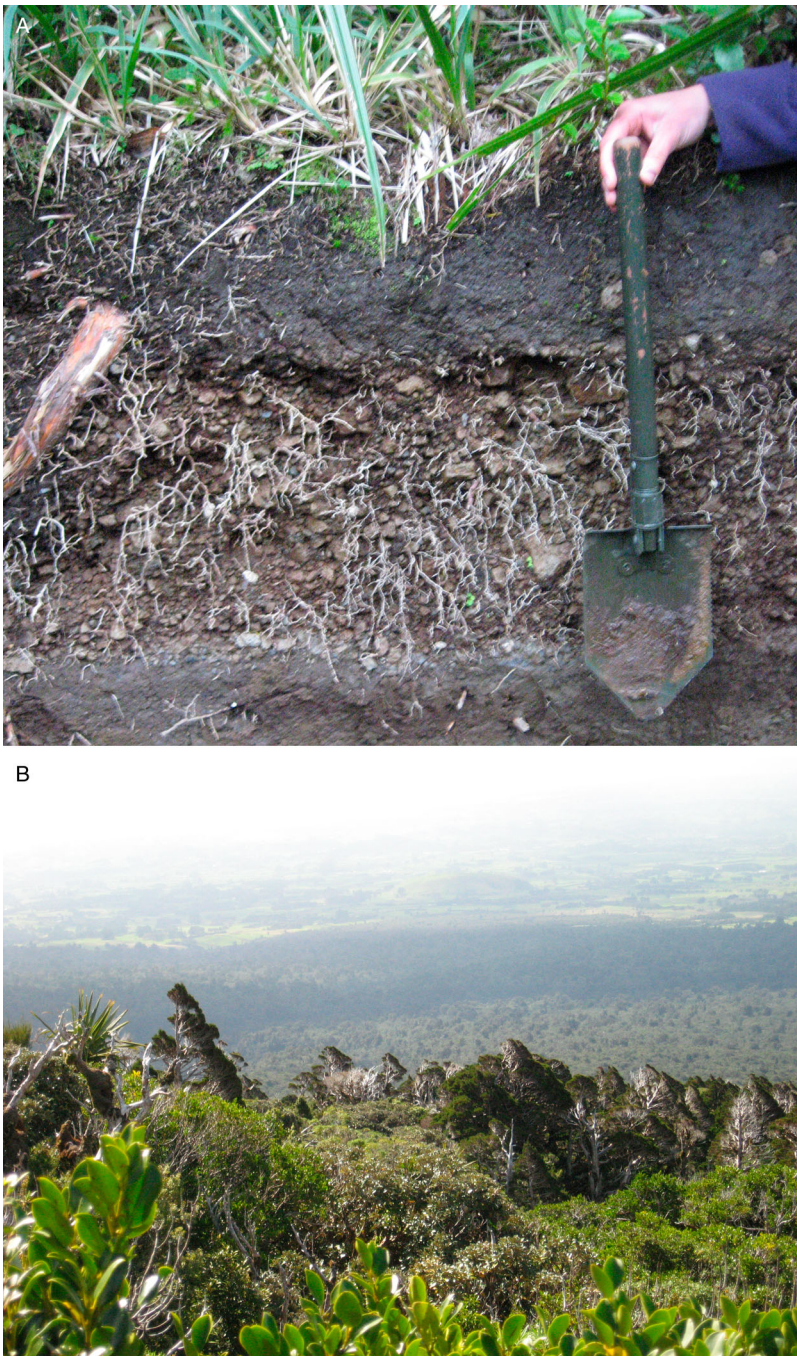


Figure 6. Photographs of treeline vegetation on the North Island of New Zealand. **A**, Tephra deposit (35 cm thick) near Dawson falls. **B**, Treeline vegetation near North Mount Taranaki/Egmont with emergent *Libocedrus bidwillii*. Photographs: Jackson Efford.

on flat to undulating sites. They also showed differences in the species composition of forests buried by the Taupo eruption that were probably due to pre-eruption differences

in local climate and soils. Overall, the fossil record indicates little or no convergence towards broadleaved dominance predicted by McKelvey (1963). Furthermore, it suggests that site differences as well as fertility gradients over time scales of centuries to millennia are likely to be important determinants of forest composition at sites affected by the Taupo eruption. Clarkson et al. (1986) showed that forests can rapidly re-form, especially where forest destruction has been only fragmentary or partial. At least some of the dense conifer stands are of uneven age, suggesting that they may have arisen after a more complex set of circumstances (Herbert 1980). Conifer population age structures in Tongariro National Park exhibit discontinuous age distributions, indicating that establishment had occurred underneath a progressively dying overstorey rather than after a single massive exogenous disturbance (Lusk & Ogden 1992). Leathwick and Mitchell (1992) showed that forest patterns in the volcanically disturbed central North Island are also strongly correlated with spatial patterns of climate, topography and drainage. Although the massive eruption of Taupo in 1718 ± 5 cal yr BP triggered abrupt changes in the vegetation patterns, over time the effects of climate and topographic patterns also have affected post-disturbance vegetation patterns (Leathwick & Mitchell 1992).

Clarkson (1990) systematically evaluated the field evidence of vegetation changes following volcanic disturbance in the context of traditional (Clements 1916) and modern (e.g. Pickett et al. 1987) models of succession. He found that there was no exclusive 'volcanic succession flora'. In fact, the flora of the volcanically disturbed sites has many of the attributes of plants that ensure success after other disturbances, including fire, as can be seen in the greater abundance and range of the same species during periods of Polynesian (and later, European) burning (McGlone 1983). He stressed the importance of variability related to scale and intensity of disturbance, and the type and heterogeneity of the substrate emplaced. Primary succession on large denuded sites exhibited elements of facilitation, autogenic change and relay floristics consistent with classic models of succession. Examples, revealed by subsequent detailed research, include initial establishment of lichens and mosses followed by flowering plants and facilitation by nitrogen-fixers such as *Coriaria* spp. (Clarkson & Clarkson 1995; Walker et al. 2003). An experiment representing post-volcanic succession showed that establishment of *Coriaria arborea* greatly accelerated an underlying trend of gradually increasing numbers and diversity of seeds in the soil (Clarkson et al. 2002). Overall, changes in species compositions involved a range of successional mechanisms including facilitation and inhibition, patterns explained by time gradients of resource availability, and disturbance regimens producing shifting-mosaic steady-states. Clarkson (1990) stressed the need for long-term studies of processes of vegetation change and the importance of chance events that make predictions probabilistic rather than deterministic.

Conclusion

Studies conducted largely in the 1970s and early 1980s of the effects of tectonic disturbances, specifically disturbances associated with strong earthquakes, revealed that in extensive areas of southern Chile and New Zealand these relatively infrequent coarse-scale disturbances are key determinants of forest structure and composition (Veblen & Ashton 1978; Stewart & Veblen 1982a). These studies of the long-lasting effects of tectonic events pioneered systematic investigation of coarse-scale disturbance processes in the context of the non-equilibrium

frameworks that became increasingly accepted during the 1980s and 1990s in both regions. This conceptual framework emphasizing repeated coarse-scale disturbances, including disturbances triggered by tectonism, has strongly influenced subsequent development of ecological research on southern temperate forests (Ogden 1985; Read & Hill 1988; Enright et al. 1995; Ogden et al. 1996; Adie & Lawes 2009; Lara et al. 2014a; Lusk et al. 2015).

Studies of the dynamics of temperate rainforests in the 1970s and 1980s in widely separated areas in temperate forests of SSA and the southwest Pacific yielded a general model of how long-lived pioneer tree species that are shade-intolerant can dominate extensive areas of forest following coarse-scale tectonically related disturbances (Veblen & Ashton 1978; Veblen et al. 1980, 1981; Read & Hill 1988; Read et al. 1990; Veblen et al. 1996a). During long periods lacking coarse-scale disturbance by tectonism or wind storms, these long-lived pioneer species are gradually replaced by more shade-tolerant species but in some regions, coarse-scale disturbances are frequent enough to maintain dominance by the shade-intolerant trees. The role of tectonic disturbances in shaping forest structures and selecting disturbance-related traits in rainforests of southern Chile and New Zealand may be comparable to the ecological and evolutionary influences of fire in some other temperate forest biomes.

Studies of tectonic influences on the dynamics of southern temperate rainforests of Chile and New Zealand published in the 1970s and early 1980s contributed prominently to the shift away from Clements' climax theory and towards modern non-equilibrium frameworks of forest dynamics (Sousa 1984; Attiwill 1994). The recognition that in temperate forests in SSA and New Zealand cohort structures, triggered by exogenous disturbances such as wind storms and tectonic events, are the norm rather than all-aged structures has been of fundamental importance to understanding the dynamics of these forests (Veblen & Ashton 1978; Ogden 1985; Ogden et al. 1996; Ogden et al. 2005; Wells et al. 2001; Lara et al. 2014a). This recognition promoted new interpretations of forest structures that previously had been ascribed to climate-caused regeneration failures, 'relict' status of some tree species, or to impacts of introduced browsing animals (Veblen & Stewart 1982a, 1982b; Ogden 1985; Wilson & Lee 2012). Adoption and refinement of a non-equilibrium patch dynamics framework for interpreting forest structure and dynamics in the 1980s was a fundamental advancement in refining older equilibrium-infused views of southern temperate forest dynamics.

Acknowledgements

We thank CH Lusk, BD Clarkson, and one anonymous reviewer for helpful comments on the draft. Associate Editor: Dr Chris Lusk.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

TTV acknowledges research support from Awards 0956552 and 0966472 from the National Science Foundation of the USA. MEG acknowledges financial support from Award 15110009 from CONICYT/FONDAP.

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