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REVIEW ARTICLE

Fire–vegetation feedbacks and alternative states: common mechanisms of temperate forest vulnerability to fire in southern South America and New Zealand

T Kitzberger^{a,b} , GLW Perry^c, J Paritsis^b, JH Gowda^b, AJ Tepley^d, A Holz^e and TT Veblen^f

^aDepartamento de Ecología, Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina;

^bLaboratorio Ecotono, INIBIOMA, CONICET-Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina; ^cSchool of Environment, University of Auckland, Auckland, New Zealand; ^dSmithsonian

Conservation Biology Institute, Front Royal, VA, USA; ^eDepartment of Geography, Portland State University, Portland, OR, USA; ^fDepartment of Geography, University of Colorado, Boulder, CO, USA

ABSTRACT

In the context of global warming and increasing impacts of invasive plants and animals, we examine how positive fire–vegetation feedbacks are increasing the vulnerability of pyrophobic temperate forests to conversion to pyrophytic non-forest vegetation in southern South America and New Zealand. We extensively review the relevant literature to reveal how these temperate southern hemisphere floras have generated similar positive fire–vegetation feedback mechanisms resulting in increased vulnerability to anthropogenically altered fire regimens. For the two regions, we address the following questions. 1. What are the major plant species, physiognomic types and functional types characteristic of pyrophytic versus pyrophobic vegetation types and how do their traits affect flammability, resistance to fire and recovery after fire? 2. What are the roles of herbivory and microclimate in enhancing fire–vegetation feedbacks? 3. Are there similarities in trends of cover type transitions in relation to altered fire regimens? 4. How are climate change, land-use trends and the effects of introduced plants and animals affecting the vulnerability of these ecosystems to fire-induced transitions to alternative stable states? Most temperate forests of New Zealand and southern South America evolved under conditions of low fire frequencies so few taxa became adapted to recurrent fire. Current dichotomous landscapes consisting of juxtaposed pyrophobic and pyrophytic vegetation types are the outcome of the expansion of fire-resilient and fire-promoting species associated with the arrival of humans. Despite considerable differences in human history and biogeographic history, the case studies presented here show remarkable parallels in life-history traits of the key pyrophobic taxa, fire–vegetation feedback mechanisms, overall ecosystem responses to anthropogenic alteration of fire regimens, and likely vulnerability to expected global change influences on future fire regimens.

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Introduction

Contemporary ecological views conceive fire not as an external agent constantly resetting vegetation succession but as a strongly interlinked process whereby fire (or lack thereof) acts as a strong ecological filter on plant traits. Dominant plant traits in turn change community properties (e.g. productivity, flammability) that feedback into the fire regimen (spread, frequency, severity). Because of this strong filtering effect, biogeographically distinct species pools subject to fire play will influence how vegetation properties will feedback into subsequent fire regimes with important consequences for the resilience of the system to fire.

Bond and Midgley (2012) proposed that biotas dominated by angiosperms develop into two radically different states: (1) a *pyrophytic* state dominated by relatively short-statured, highly productive, flammable vegetation with rapid fuel and litter accumulation and therefore shorter fire return times; and (2) a *pyrophobic* state where trees quickly grow tall enough that their crowns are unaffected by surface fires, and they cast sufficient shade to suppress understorey fuels and create mesic microclimates. Hence there is a strong contrast in flammability between pyrophytic open ecosystems dominated by shade-intolerant resprouting shrubs and herbaceous plants compared with pyrophobic tall, closed-canopy, broad-leaved mesic forests dominated by obligate seeders. Each state could either exclusively dominate a landscape, or alternative states could coexist as a mosaic of intermingled, open flammable and closed-canopy, fire-excluding vegetation patches (Odion et al. 2010; Paritsis et al. 2015). Landscapes converted into one dominant state (pyrophytic or pyrophobic) by fire or lack of fire, respectively, may become ‘trapped’ in that state. Hence, positive vegetation–fire feedback mechanisms may prevent a return to the alternative state through a simple reversal of the forcing factors, so that the return to the previous state may require a totally different path.

Humans play critical roles in shifting vegetation from pyrophobic to pyrophytic (or vice versa) alternative states. Anthropogenic burning is believed to have a greater impact where fire is naturally rare, vegetation is poorly adapted to fire, and fuel biomass is not limiting (McWethy et al. 2013). Indigenous human activities are implicated in rapid forest transitions in some biomass-rich ecosystems of the southern temperate zone (e.g. New Zealand and Tasmania), and these transitions appear to depend on increased landscape flammability through fire–vegetation feedbacks (Perry et al. 2012a; Fletcher et al. 2014). In southern South America, the roles of indigenous peoples in changing landscape-level vegetation patterns are less clear, more variable across biomass-rich vegetation types, and generally interpreted to be of secondary importance to climate as a driver of fire-induced vegetation changes (Holz & Veblen 2012a; Whitlock et al. 2015). In contrast, the efficacy of European settlers in using fire to drive major forest transitions during European colonisation and expansion especially from the mid-nineteenth century onwards is well documented for southern South America (see numerous citations below). Regardless of differences in timing and the roles played by indigenous and European settlers, we suggest that some southern temperate ecosystems exhibit similar vulnerability to rapid forest transitions mediated by positive fire–vegetation feedbacks.

Despite a wealth of recent empirical, retrospective and modelling research from New Zealand and southern South America, a systematic and comparative review of the common drivers leading to fire–vegetation feedbacks and vulnerability to altered fire regimes in temperate southern hemispheres forest ecosystems is still lacking.

Comparative reviews such as this are needed to identify research gaps and develop a common agenda for future research.

Here we propose that some temperate southern hemisphere ecosystems harbour similar positive fire–vegetation feedback mechanisms inducing similar vulnerabilities to anthropogenically altered fire regimens. In order to evaluate this proposition we compare dominant vegetation types of southern South America and New Zealand ecosystems in terms of past and potential transitions from pyrophobic to pyrophytic vegetation types. We specifically address the following questions. 1. What are the major plant species, physiognomic types, and functional types characteristic of pyrophytic versus pyrophobic vegetation types, and how do their traits affect flammability, resistance to fire, and recovery after fire? 2. What are the roles of herbivory and microclimate in enhancing fire–vegetation feedbacks? 3. Are there similarities between the two regions in trends of cover type transitions in relation to altered fire regimens? 4. How are climate change as well as land-use trends and the effects of introduced plants and animals affecting the vulnerability of these ecosystems to fire-induced transitions to alternative stable states?

Southern South America

The Nothofagus forest/dry shrubland system of northwestern Patagonia, Argentina

Broadscale patterns of climate, vegetation and wildfire activity

Air masses coming from the Pacific that carry moist air across the Andean Divide dominate western Patagonia's climate. The Andean range causes abundant orographic precipitation that increases with elevation and sharply declines to the east because of a rain-shadow effect. In central and northwestern Patagonia (c. 37–47°S) this precipitation pattern is largely responsible for the abrupt transition from the humid Valdivian and North-Patagonian rainforests near the Pacific coast to dry shrublands dominated by *Nothofagus antarctica* and Patagonian steppe on the eastern foothills of the Andes (Veblen et al. 1996). Two plant communities dominate the easternmost woody vegetation of the Patagonian Andes, determining the structure and dynamics of most forested landscapes of the region: the deciduous *Nothofagus* forest dominated by the obligate seeder *Nothofagus pumilio*, and shrublands composed of resprouting woody species.

Understorey in the deciduous *Nothofagus* forest is variable depending on elevation and location along the west–east gradient of precipitation. In more mesic environments and in mid- to low-elevation deciduous *Nothofagus* forests, the bamboo (*Chusquea culeou*) is a common and dominant understorey species that grows 3–6 m high, but towards the xeric portion of the gradient, the understorey typically consists of short shrubs (e.g. *Berberis serratodentata*), herbs and grasses. At its eastern limit, where annual precipitation is < 2000 mm, deciduous *Nothofagus* forest typically borders highly diverse shrublands dominated by small trees and shrubs, such as *Nothofagus antarctica*, *Maytenus boaria*, *Lomatia hirsuta*, *Embothrium coccineum*, *Schinus patagonicus*, *Diostea juncea* and *Aristotelia chilensis* (Quinteros et al. 2010; Blackhall et al. 2015), and a rich flora of climbers, bamboo (*C. culeou*), herbs and grasses.

In northern Patagonia, sharp and persistent boundaries between these two communities with no corresponding variation in the underlying abiotic environment are

commonly observed (Figure 1; Veblen & Lorenz 1988). Growing evidence indicates that these boundaries are maintained by differences in flammability between the two communities (Kitzberger et al. 2012; Paritsis et al. 2013, 2015; Morales et al. 2015). The first line of evidence supporting the idea of differential flammability between communities is the reconstruction of fire history across an extensive landscape mosaic at c. 40°S, which revealed higher levels of fire activity in tall *N. antarctica* shrublands compared with adjacent *N. pumilio* forests (Veblen et al. 1992). Empirical fire spread assessments based on

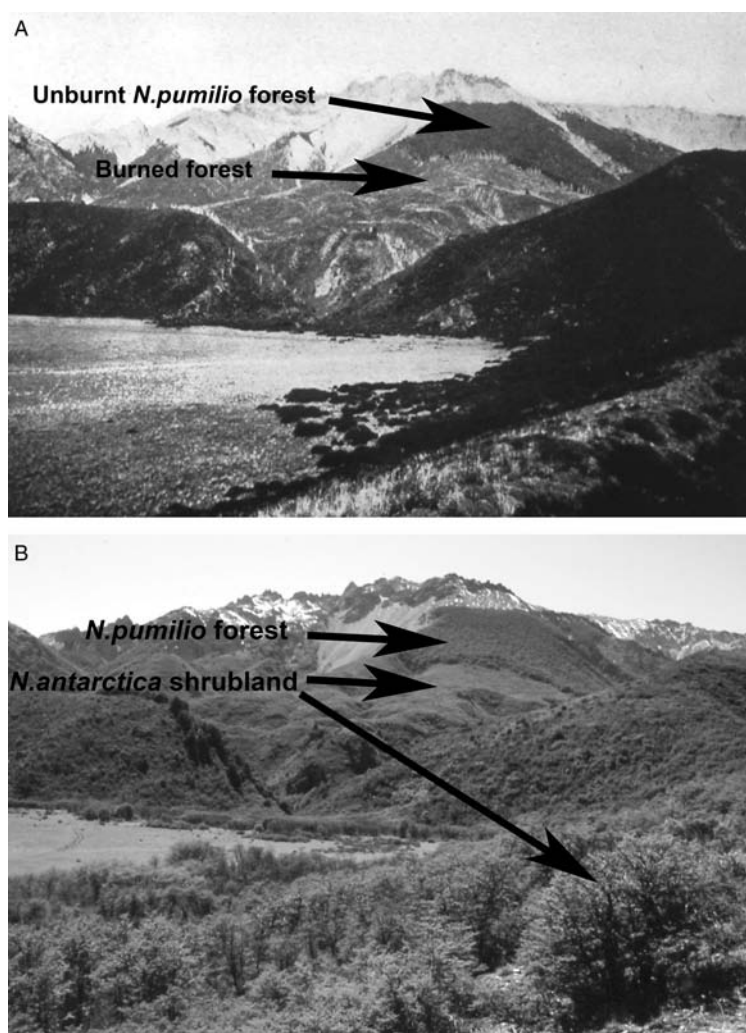


Figure 1. Repeat photography of the slopes facing southeast Lago Guillermo, Nahuel Huapi National Park showing long-term stability of historic fire-generated boundaries between subalpine *Nothofagus pumilio* forests and mid-slope resprouting *Nothofagus antarctica*/*Chusquea culeou*-dominated shrublands. The sharp vegetation boundary on the mid-slope in the background reflects a severe forest fire event in c. 1912 associated with extreme drought (Willis 1914); the post-fire vegetation is a pyrophytic tall shrubland in which subsequent fires have occurred but none have burned into the pyrophobic higher elevation forest of *N. pumilio*. The foreground is anthropogenic grassland. Photo credits: **A**, B. Willis; **B**, T.T. Veblen.

boundaries of fires that occurred over large areas also have shown that fires are less likely to ignite in or spread into *N. pumilio* forests than the neighbouring tall shrublands (Mermoz et al. 2005; Paritsis et al. 2013). Additionally, modelling suggests that in average climate years, fire spreads readily in shrublands whereas mature *Nothofagus* forests act more as firebreaks (Kitzberger et al. 2012; Morales et al. 2015).

Dominant traits

Nothofagus pumilio is a shade-intolerant, tall tree (12–25 m height) that regenerates exclusively through wind-dispersed seeds. Recruitment of *N. pumilio* is triggered by small gaps in otherwise closed-canopy forests and is very sensitive to high radiation and dry conditions (Heinemann et al. 2000), which constrain its capacity to colonise burned areas and shrublands to periods of high precipitation and sites protected from desiccating insolation (Tercero-Bucardo et al. 2007). The closed canopies of deciduous *Nothofagus* forest create shady, cool and mesic microclimates that maintain suppressed shrubs/bamboos (*C. culeou*). Forest understoreys are species poor and typically do not exceed 1.5 m in height, and consequently do not provide vertical fine fuel continuity in mature forests, with the tree canopy starting at heights of c. 7–8 m (Paritsis et al. 2015).

Conversely, shrublands are characterised by the lack of a closed canopy, and a species-rich community of light-demanding shrubs, small trees, herbs and climbers. The multi-stemmed growth form and shorter stature of the shrubs create an open upper canopy beneath which temperatures are high and relative humidity is low, and the understorey intermingles with the low canopy resulting in vertically continuous fine fuels that dry out more easily than in tall, closed-canopy forests (Blackhall et al. 2015; Paritsis et al. 2015). Additionally, shrublands host a variety of species that maintain high amounts of dead fine fuels, such as the climbers *Mutisia* spp., the shrub *Dioslea juncea* and the bamboo *C. culeou*, which facilitates ignition and fire spread by reducing water content and hence the heat sink role of moist live fuels (Blackhall et al. 2015). Finally, shrublands in northwestern Patagonia are dominated by plant species with high foliar flammability (Blackhall et al. 2012). Despite the scarcity or complete absence of the bamboo and other highly flammable species such as *D. juncea* in southern Patagonia (south of 45°S), the pattern of pyrophobic *N. pumilio* forests and fire-prone, shorter-statured shrublands persists (Paritsis et al. 2013).

Fire history

The earliest records of human occupation on the eastern slopes of Patagonia date to c. 13,000 yr BP and for grasslands c. 11,000 yr BP for forests coincident with the timing of gradually increasing Late Glacial temperatures (Mancini et al. 2013). Sedimentary records of fire based on high-resolution charcoal show that Late Glacial conditions (c. 13,250 yr BP) provided enough fuels to support fires along the northern Patagonian forest–steppe ecotone (Whitlock et al. 2006). The formation of mosaics of *Nothofagus* forests and shrublands during a trend towards drier conditions in the early to mid-Holocene corresponded with more frequent fires at dry sites and lower fire frequency in wet sites. Increases in grass/total charcoal ratios at 7500–4400 yr BP (Whitlock et al. 2006) is probably evidence of increases in pyrophytic vegetation (shrublands, grasslands, bamboo thickets) in the landscape. Increased short-term climate variability (onset of the El Niño Southern Oscillation) during the last six millennia generated high variation

in grass/tree charcoal ratios, implying periods of forest closure and periods of frequent burning of pyrophytic vegetation.

Both natural and anthropogenic fires shaped the forest–steppe landscape. Summer lightning strike rates in northern Patagonia decrease from north–south and east–west in relation to the incursion of unstable subtropical air masses of Atlantic origin. On the eastern flanks of the Andes across the Argentinean Lake region estimates of summer (Dec–Mar) lightning strike rates are c. 0.38 lightning km⁻² yr⁻¹.

Tehuelche hunter/gatherer cultures used fire widely for hunting large grazing herbivores, warfare and communication (Veblen & Lorenz 1988). On the arrival of Europeans during the mid- to late 1800s fire frequency along the forest–steppe reverted: fire frequency declined in grasslands due to the demise of aboriginals, whereas in forest areas, fire frequency sharply increased due to deliberate fires set by settlers for the opening of grazing and agricultural land, some of which escaped and burned vast tracts of forest (Willis 1914; Veblen et al. 1999). During this short period (c. 1880–1920s), extensive areas of fire-sensitive *Nothofagus* forests retracted while resprouting shrublands expanded (Veblen & Lorenz 1988, Gowda et al. 2012). A combination of active fire suppression and cooler/wetter conditions during the mid-twentieth century, triggered a pulse of expansion of pyrophobic forests (Kitzberger & Veblen 1999; Veblen et al. 1999), this expansion was restricted to southern slopes and mesic sites, whereas shrublands remained stable at more xeric sites (Figure 1; Gowda et al. 2012). Current trends show increases in the occurrence of large/severe fires related to strong droughts and warmer summers. These fires spread over pyrophytic shrubland types and often continue to burn extensively across adjacent tracts of pyrophobic vegetation (Veblen et al. 2011).

Vegetation dynamics and feedback mechanisms

Potential mechanisms responsible for the existence of alternative states in deciduous *Nothofagus* forest have been long suggested (Willis 1914; Veblen & Lorenz 1988) but only recently assessed in the field (Raffaele et al. 2011; Blackhall et al. 2012, 2015; Paritsis et al. 2015). The process through which the alternative state for deciduous *Nothofagus* forest emerges starts with the burning of this pyrophobic forest community, which normally burns only during extreme drought years (Mermoz et al. 2005). High severity fires typically eliminate all seed sources for *N. pumilio* within the burn perimeter. In addition, even if seed sources are available, regeneration may often fail due to a combination of fire-induced edaphic changes (Kitzberger et al. 2005), unfavourable climatic conditions (Tercero-Bucardo et al. 2007), and browsing and trampling by livestock and other introduced herbivores such as the European hare, *Lepus europaeus* (Kitzberger et al. 2005; Raffaele et al. 2011).

Post-fire regeneration of *N. pumilio* is limited to a narrow belt extending only a few tens of metres from the forest edge and is temporally limited by masting (Veblen et al. 1996). In xeric conditions (i.e. north-facing slopes and areas with low and intermediate precipitation), burned forests are rapidly colonised by shrubland species, many of which are dispersed by birds (Cavallero et al. 2013) as well as resprouting bamboos, turning into shrublands or even into grasslands if livestock pressure is high. Higher fire frequency in the shrublands promotes the persistence of flammable shrubs, all of which vigorously resprout, whereas the juveniles of *N. pumilio*, if present, are eliminated by repeated burning. Therefore, shrublands are maintained through positive feedbacks between fire

and shrubland vegetation, reinforced by xeric and warmer conditions, whereas succession to deciduous *Nothofagus* forest is favoured by mesic site conditions, cooler climate and long intervals between fires. The transition from deciduous *Nothofagus* forest to shrublands is further enhanced by the selective browsing of domestic and wild herbivores, which effectively eliminate seedlings and reduce the growth rates of *N. pumilio* in newly burned areas (Kitzberger et al. 2005; Raffaele et al. 2011). In addition, browsing by livestock may increase flammability traits of some common shrubland species, increasing the overall flammability of post-fire shrublands (Blackhall et al. 2015).

Recent and projected future trends towards a warmer climate, with continued increases in lightning, as well as the growth of urban and ex-urban human settlements in Patagonia are increasing the potential for wildfire activity in this region (Holz & Veblen 2011; Veblen et al. 2011). The fire-induced transformation from initial burning of *N. pumilio* forest to non-forest assemblages will probably be enhanced by a higher frequency of droughts and human- and lightning-ignited fires. Once the forest has been transformed to the alternative state of shrublands, forest recovery is likely to be impeded by both increased probability of burning in shrublands and unfavourable effects of warmer, drier conditions and browsing on tree establishment (e.g. Tercero-Bucardo et al. 2007).

The temperate rainforest–bamboo system of southwestern South America

Broad-scale patterns of climate, vegetation and wildfire activity

Temperate rain forests occur in the Andes and along the coast of southwestern South America south of c. 37°S to the end of the land mass at c. 55°S on Tierra del Fuego (Veblen et al. 1996). Mean annual precipitation is generally > 2500 mm throughout this region of marine west-coast climate. The Valdivian rainforest occurs from c. 37°45' to 43°20'S, the North-Patagonian rainforest from c. 43°20' to 47°30'S, and the Magellanic rainforest south of c. 47°30'S (Veblen et al. 1996). The rainforest region north of c. 43°S has warm dry summers whereas the rainforests south of c. 44°S have precipitation more evenly distributed throughout the year. There is significant latitudinal overlap of these broad forest formations along elevational gradients. For example, at mid-latitudes (e.g. c. 41°S) on the western side of the Andes low elevations are characterised by the Valdivian rainforest, mid-elevations by the Patagonian rainforest, and subalpine forests by first a transition of evergreen *Nothofagus dombeyi* and *Nothofagus betuloides* mixed with the deciduous *N. pumilio* and then by pure stands of *N. pumilio* near the treeline (Pollman & Veblen 2004).

The dominant life forms of the rainforests of southern South America are evergreen broadleaved and conifer species most of which are easily killed by fire due to their thin bark with the exception of the thick-barked conifer *Fitzroya cupressoides*, which can withstand even high-severity fire (Veblen et al. 2003). None of the other dominant tree species are thick barked or are serotinous, implying a lack of traits selected by fire. On the other hand, many of the rainforest species resprout from roots, root crowns or trunks after mechanical damage (e.g. damage by treefalls, flooding, ash deposition and logging) but it cannot be assumed that resprouting would have been selected by fire as opposed to being an exaptation to fire. Nevertheless, several rainforest species (*Eucryphia cordifolia*, *Gevuina avellana* and *Weinmannia trichosperma*; Figure 2C), have been observed to vigorously resprout after burning of forests dominated by the evergreen *Nothofagus*

nitida, *N. dombeyi* or *N. betuloides* all of which are obligate seeders that do not resprout after fire. These evergreen *Nothofagus* species are prolific (but masting) seeders, capable of rapid growth on open sites, and more so than any other canopy dominants are likely to form dense post-fire stands (*renovales*) at upland rainforest sites. North of c. 48°S understory *Chusquea* bamboos typically dominate the rainforest understoreys (Veblen 1982). They are keystone species because of their ability to constrain tree regeneration and their synchronous flowering and death at multi-decadal intervals over large areas, which may have profound, cascading effects on other trophic levels (Veblen 1982; Gonzalez et al. 2014). Wetlands are locally prominent within the rainforest regions, and south of c. 44° S they are represented by extensive bog forests of *Pilgerodendron uviferum*, which—due to its moderately thick bark—can withstand low-to-moderate severity fire in stands where fires kill the associated species (Holz & Veblen 2012b).

Fire history

Fire in southern South America has often been misperceived as being exclusively of human origin, even to the extent that charcoal in Holocene sedimentary records has been interpreted as unequivocal evidence of human activity (Heusser 1994). In fact, however, lightning detection networks (2010–2014) for Andean Chile (c. 40–43°S) for the summer period (Dec–Mar) indicate c. 0.13 lightning strikes km⁻² yr⁻¹ (detection-corrected World Wide Lightning Location Network data). Nevertheless, due to the lack of even medium-term (i.e. multi-decadal) records quantifying burn areas by fire origin, there is much uncertainty about the relative importance of lightning in igniting large fires throughout the rainforest region of Chile. Sedimentary charcoal records document fire activity during periods in the early Holocene of no known local human presence, which implies ignition by lightning (Holz et al. 2012a). Modern observations in the North-Patagonian rainforest record presence of lightning scars on trees, which, according to local informants, sometimes result in large fires (Holz & Veblen 2012a). Ignition by volcanism is indicated by the association of tephra with macroscopic charcoal in sedimentary palaeorecords even at sites that are distant from the flanks of volcanoes (Jara & Moreno 2012; Montade et al. 2013). Despite uncertainty about the magnitude of burning by aboriginal peoples and its broad-scale impact, there is no doubt that when access and weather permitted it, indigenous populations intentionally set fires for hunting, opening of travel routes, extraction of fuel, and clearing for horticulture (Veblen & Lorenz 1988; Holz & Veblen 2012a). Sedimentary records of charcoal and pollen indicate that periods of warmer and drier climate have been the primary driver of occurrence of widespread fires at millennial time scales (Huber et al. 2004; Whitlock et al. 2007; Abarzua & Moreno 2008; Jara & Moreno 2012). All fire history records, both sedimentary and tree-ring records, document marked increases in burning associated with European settlement and forest clearing in the Valdivian rainforest and the Magellanic rainforest (mid-eighteenth to late-nineteenth centuries, Figure 2A) and in the North-Patagonian rainforest (mostly early to mid-twentieth century) (Veblen et al. 2003; Holz & Veblen 2012a).

Vegetation dynamics and potential positive fire feedbacks

We propose two working hypotheses involving positive feedback mechanisms by which initial burning of tall, closed-canopy rainforest leads to a subsequent increase in stand-

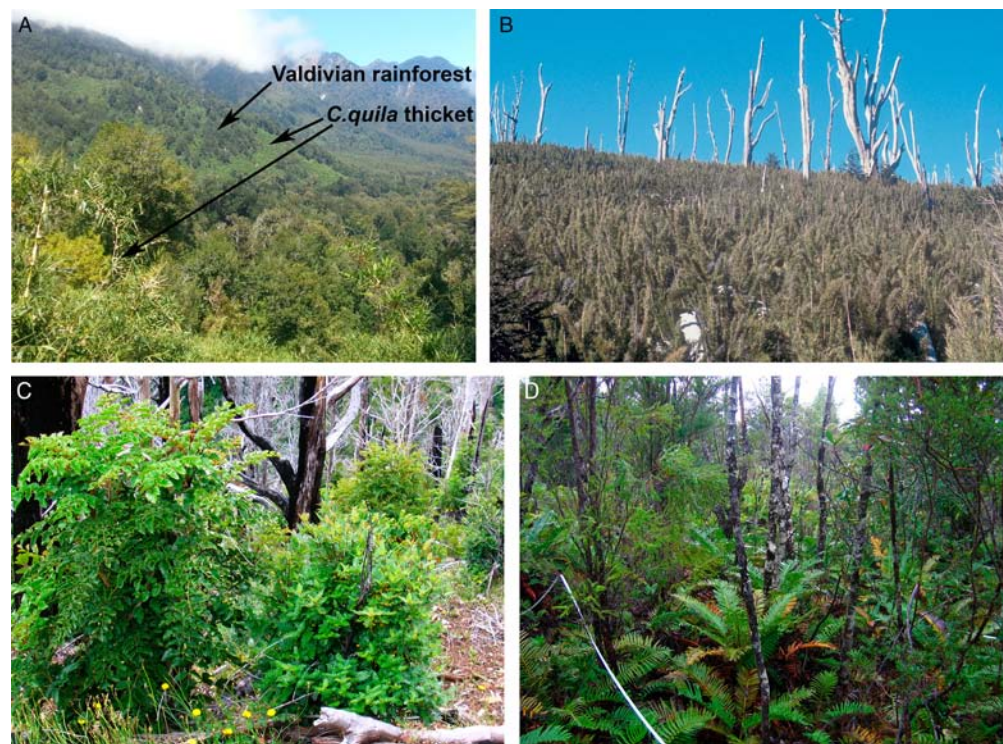


Figure 2. **A**, Pyrophytic patches of *Chusquea quila* originated from human set fires during mid-1800s settlement fires in a matrix of pyrophobic Valdivian rainforest near Puyehue National Park. **B**, Proliferation of *Chusquea culeou* about 15 years after this *Nothofagus dombeyi* forest was burned in the Valdivian Andes. Note the scarcity of any tree regeneration due to the inhibitory effect of the quickly resprouting bamboo. **C**, *Weinmannia trichosperma* and *Gevuina avellana* resprouting after fire near Lago Yelcho, Chile. **D**, Post-fire North-Patagonian rainforest stand dominated by *Blechnum* and Myrtaceae in southern Chiloe.

level flammability that potentially could lead to alternative, more fire-prone stable states: (1) the bamboo understorey-mediated model and (2) the soil-waterlogging model.

The *bamboo understorey-mediated model* applies to upland sites with adequate soil water drainage in forests with understoreys dominated by *Chusquea* bamboos north of c. 48°S. The most widespread *Chusquea* species occurring on well-drained sites in the Valdivian rainforest and North-Patagonian rainforest are the multiple-branching, climbing bamboos *Chusquea quila* and *Chusquea macrostachya* at low elevations and the clump-forming *C. culeou* at mid-elevations. When tall, closed-canopy rainforest is initially burned it is replaced by post-fire *Chusquea*-dominated vegetation, which is inherently more flammable. This model applies to pyrophobic rainforests of variable composition but the most typical canopy dominants are *N. dombeyi*, *N. nitida*, *N. betuloides*, *Eucryphia cordifolia*, *Podocarpus nubigenus*, *Saxegothaea conspicua* and *Weinmannia trichosperma*; subdominant tree species often include *Drimys winteri*, *Raukaua laetevirens*, *Gevuina avellana*, *Embothrium coccineum*, *Caldcluvia paniculata* and *Amomyrtus luma*.

The bamboo-mediated model of positive feedbacks in the Valdivian rainforest and the North-Patagonian rainforest is supported by the following rationale: (1) Microclimates of closed-canopy, tall forests are less conducive to initiation and spread of fire because of higher fuel moistures in the understorey as a result of cooler temperatures and higher relative humidity. (2) Fuel profiles of tall, closed-canopy forests reduce the probability of fire spread from the understorey into the forest canopy because of the > 15 m vertical discontinuity between fine fuels in the *Chusquea*-dominated understorey up to a height of 6–8 m and the fine foliage of the tree canopy beginning at heights of c. 30 m. (3) *Chusquea* biomass consists of small diameter fuel with a high surface-area-to-volume ratio that readily dries and easily combusts both as live and dead fuels. (4) Post-fire tree regeneration is often constrained by competition from vigorously resprouting *Chusquea* spp. (Figure 2B) so that recovery of a forest canopy may require many decades. Overall, the first two mechanisms make forests more resistant to burning (pyrophobic) and the latter two mechanisms increase the likelihood that *Chusquea*-dominated (pyrophytic) vegetation will burn again before the return to tall forest cover.

Following fire, *Chusquea* vigorously resprouts producing dense thickets of fine fuels, often with patch sizes of tens to hundreds of hectares, culm densities > 150,000 per hectare, and total biomass > 150 tonnes per hectare (Figure 2B; Veblen et al. 1980). Approximately 15% of the *C. culeou* biomass is in a very fine fuel size (grass leaves), most of it is in a < 24 mm size class, and none of it exceeds 36 mm in thickness. The amount of small diameter fuel in post-fire *Chusquea* thickets in combination with both tall erect culms (up to 8 m tall) or climbing culms of *C. quila* (c. 20 m long) results in ladders of highly flammable fine fuels from the soil surface to the top of shrub canopies and well into the canopies of secondary forests. In addition, at multi-decadal intervals high proportions (often more than half) of a regional population of *Chusquea* synchronously flowers and dies over 2–3 year periods, producing massive amounts of dry dead fuels over tens to hundreds of thousands of hectares (Veblen 1982; Gonzalez et al. 2014).

Chusquea spp. vigorously resprout following fire, producing abundant new culms that can attain lengths of c. 8 m in a single growing season (Figure 2B), far exceeding height growth rates of any tree species (Veblen 1982). Inhibition of tree regeneration by *Chusquea* greatly extends the period of high flammability associated with early post-fire

successional stages, providing a mechanism for a potential shift to a pyrophytic alternative dominated by *Chusquea* (Figure 2A). Even when post-fire regeneration of *Nothofagus* spp. is successful (i.e. in *renovales*), the crown–base heights of post-fire stands < 50 years old are short (e.g. 6–15 m) so that there are fine fuels extending from the *Chusquea*-dominated understorey continuously into the tree canopy (Veblen et al. 1996).

South of 44°S the abundance of *Chusquea* spp. declines, but even in the absence of understorey bamboos, post-fire vegetation is more flammable than tall, closed-canopy forest (Paritsis et al. 2013). Post-fire vegetation is typically dominated by resprouting shrubs, trees and ferns, and it is inherently more flammable than tall forest because of its shorter stature, warmer–drier microclimate, and shrubby plant architectures. Post-fire stands include abundant shrubs or shrubby small trees that are densely branched from the base and woody climbers with fine fuels continuously distributed from the soil surface to the top of the shrub canopy. Examples include trees and shrubs such as *Embothrium coccineum*, *Weinmannia trichosperma*, *Gevuina avellana*, *Aristotelia chilensis*, *Amomyrtus* spp., *Luma apiculata*, *Azara* spp., *Gaultheria* spp., *Baccharis* spp., *Ovidia* spp., numerous myrtaceous shrubs (e.g. *Myrceugenia* spp.) (Figure 2D) and woody or semi-woody climbers such as *Griselinia*, *Campsidium*, *Lapageria*, *Luzuriaga*, *Mitraria*, *Muehlenbeckia* and *Philesia* spp. (Albornoz et al. 2013; Romero-Meires et al. 2014). In addition, abundant fine fuel is present in the form of graminoids (*Juncus*, *Scirpus*, *Uncinia*, *Carex* and *Poaceae*) and large ferns (*Lophosoria quadripinnata*, *Blechnum* spp. and *Gleichenia* spp.) (Figure 2D; Romero-Meires et al. 2014). Ferns often form dense patches of shade, which delays tree regeneration and prolongs the more flammable stage of an open-canopy vegetation.

The second working hypothesis is based on the *soil-waterlogging model*, which applies to rainforest areas in topographic and edaphic settings with high water tables. Following removal of most canopy trees by blowdowns, logging or fire, soils at these sites often become waterlogged due to reduced canopy interception and transpiration by large trees (Diaz et al. 2007). Post-fire waterlogging of soils hampers regeneration of tree species even if seed sources survive (Holz 2009; Bannister et al. 2012; Albornoz et al. 2013). Consequently, in areas of high water tables, burning of rainforests results in a mosaic of small patches of regenerating forest on well-drained sites surrounded by larger, more poorly drained areas of either woody species tolerant of waterlogging (e.g. *Tepualia*) or bog plants including *Sphagnum*, Cyperaceae and other graminoids (Holz 2009; Albornoz et al. 2013). Fire initiation and spread are more likely in bogs than in forests on better-drained sites because during unusual droughts the fine fuels on the surface of a bog dry out more quickly than the coarse fuels beneath a closed-canopy forest. Local inhabitants take advantage of short-term drying of bogs to ignite intentional burns, and tree-ring fire scars indicate high fire frequencies (yet low-to-mid severities) at forest–bog ecotones (Holz 2009).

Several exacerbating factors are likely to further promote transitions from pyrophobic rainforests to landscape mosaics of more pyrophytic vegetation. These include massive conversion of native forests to plantations of introduced conifers and eucalypts, which provide highly flammable and homogeneous fuels over extensive areas (Veblen et al. 2011). Invasion by pyrophytic exotic species such as *Teline*, *Ulex*, *Pseudotsuga* and *Pinus* spp. is increasing throughout southern South America and is facilitated by fire, logging and livestock grazing (García et al. 2015).

Climate change towards a warmer, drier climate undoubtedly is the most important determinant of rate of burning in rainforests of southern South America and therefore of potential for conversion to more pyrophytic landscapes. Over the past c. 50 years, rainforest ecosystems in the Patagonian–Andean region have experienced pervasive and rapid regional-scale warming as well as a marked reduction in precipitation in the northern rainforest region (c. 40–47°S; Garreaud et al. 2013). In addition, rising sea surface temperatures are expected to increase convective activity, and hence lightning activity, in these temperate rainforests (Garreaud et al. 2014). This multi-decadal pattern of recent and expected continued climate change portends increased wildfire activity in the rainforests of southern South America. As the ecological impacts of this climate change continue to unfold, we expect that the positive feedbacks described above will result in more fire activity than would be predicted from a warming, drying climate alone.

New Zealand

An overview of New Zealand's pre-human fire history and ecology

Before the arrival of humans in the mid-thirteenth century, New Zealand's predominant vegetation cover was evergreen forests, which, depending on location, included various associations of *Agathis australis* (kauri), conifers (including members of the Podocarpaceae, Phyllocladaceae and Cupressaceae), a range of 'hardwood' angiosperms and the southern beech (Wiser et al. 2011; Allen et al. 2013). New Zealand experienced a naturally low fire frequency throughout most of the pre-human Holocene (Ogden et al. 1998, Perry et al. 2014). This is not to say that fire was absent altogether—charcoal records provide evidence for fire activity during the Last Glacial period (e.g. D'Costa et al. 2009) and recurrent if sporadic fire throughout the Holocene in restiad wetlands (low-fertility wetlands dominated by members of the Restionaceae) in northern New Zealand—but it was infrequent (McGlone 2009). Around 3000 yr BP fire activity increased, especially across the drier eastern parts of both islands, as the El Niño Southern Oscillation strengthened and the climate became more conducive to fire (Perry et al. 2014). Nevertheless, fire activity across much of New Zealand, especially in the wetter regions, was extremely low with some sites (e.g. the extremely wet west coast of the South Island; Newnham et al. 2007) probably experiencing no fire at all across the entire pre-settlement Holocene.

So, what explains this absence of fire? In general, the global distribution of fire activity is dependent on the coincidence of sufficient vegetative resources (i.e. fuel) to burn, weather conditions that promote fuel combustion and ignition sources (Krawchuk et al. 2009). Of these three factors, the only one potentially missing or rare across the diversity of climates and forest types in New Zealand was ignition sources. Flammable vegetation can occur in fire-free environments (Bowman et al. 2014) and recent shoot-level flammability assessments suggest that New Zealand's flora—including some tree species dominant in temperate forest—are highly flammable (Wyse et al. 2016). Rates of lightning activity in New Zealand are, however, extremely low, with a median nationwide strike-rate of around 0.10 (5th–95th centiles of 0.02–0.50) strikes $\text{km}^{-2} \text{yr}^{-1}$ (Met Service NZ, data 2000–2014). These numbers are comparable with those in the eastern Andes but contrast strongly with the levels seen over continental land masses, which typically exceed 30 strikes $\text{km}^{-2} \text{yr}^{-1}$ (Cecil et al. 2014). Lightning activity in New Zealand is concentrated

at high elevations on the west coast of the South Island (where densities peak at c. 13 strikes $\text{km}^{-2} \text{yr}^{-1}$) in the Southern Alps and is associated with westerly frontal systems, which typically carry significant rainfall (Ogden et al. 1998; Rogers et al. 2007). Hence, New Zealand's pre-human fire regimen appears to have been largely ignition limited, rather than fuel limited.

An important characteristic of succession in New Zealand is that, at the stand level, flammability declines with time since fire: in other words, earlier successional communities are more flammable than later successional ones. This trend is a result of both the high flammability of some widespread early successional species (e.g. *Leptospermum scoparium*) and the differences in micro-climate and fuel structure between early and late successional communities (Tepley et al. 2016). Such a relationship underpins positive feedbacks between fire and vegetation age in which successive fires cause the landscape to become more flammable, so promoting future fires (Kitzberger et al. 2012). In New Zealand before human settlement, pollen records suggest that after large fires, such as those associated with volcanic eruptions, tall forest re-established within 150–200 years (Wilmshurst & McGlone 1996); presumably the feedback dynamics described above were not entrained because under strong ignition-limitation, fire was not sufficiently frequent. However, because of their limited exposure to fire in the evolutionary past, few indigenous New Zealand woody plant taxa show adaptation to a high-frequency fire regimen, with the notable exceptions of fire-related reproductive traits in *Leptospermum* (serotiny; Bond et al. 2004) and possibly some species of *Pomaderris* (fire-stimulated dormancy breaking; Haines et al. 2007). This limited adaptation to fire meant there was little resilience to changes in the fire regime that accompanied human settlement, to the point that entire dry land forest types all but disappeared once fire activity increased (Rogers et al. 2005, Perry et al. 2014).

Humans settled New Zealand in c. ad 1280 (Wilmshurst et al. 2008) and a number of environmental transformations rapidly ensued. An initially intense period of burning destroyed large areas of lowland podocarp-hardwood forest, especially in the drier eastern lowlands of both islands. In the South Island at least, this wave of anthropic fire was not time-synchronous across multiple sites, but individual sites (catchments) may have been deforested by a few repeated burns in less than a couple of decades (McWethy et al. 2010, 2014). Nationwide, the pattern of deforestation broadly followed moisture and topography gradients, but it does not seem strongly associated with patterns of human occupancy, which is surprising given that fire is anthropic in origin (Perry et al. 2012b). Simulation modelling suggests that the positive feedbacks between fire and vegetation described above may have made it inevitable that large areas burned once an ignition source was added to the landscape (Perry et al. 2012a). Irrespective, by the time of European settlement in the mid-nineteenth century forest cover had been reduced from c. 85% to c. 45% and European logging and fire activity (primarily for land clearance and pastoral activities) have further reduced this to the current-day levels of c. 23% (Ewers et al. 2006; Allen et al., 2013; Perry et al. 2014).

The ecological changes resulting from the introduction of fire to New Zealand's ecosystems must be placed in the context of the other ecological transformations that occurred at that time. Fire operates now in a different ecological context to that which it did when the first humans settled New Zealand. Extinctions and declines in bird populations driven by hunting and predation by exotic mammals have compromised seed dispersal and

pollination functions to the point that some plant taxa are on the verge of functional extinction (Kelly et al. 2010; Anderson et al. 2011). Likewise, invasive mammals now play important roles as seed and seedling predators (e.g. rodents; Wilson et al. 2003; Towns 2009) and herbivores (e.g. deer; Husheer et al. 2003), both of which may reshape the direction and rate of successional trajectories.

The southern beech–*Leptospermum*/Kunzea system of New Zealand

Beech-dominated (*Nothofagus*) forests with few associated tree species are among the most extensive of New Zealand's remaining forest types, comprising about 45% of the 6.25 million ha of forest area (Wardle 1984; Allen et al. 2013). Moving east, toward drier, lower elevations, pure beech forests transition to a mix of beech with podocarp and hardwood trees (c. 20% of the existing forest area); podocarp-hardwood forests lacking beech formerly dominated the lowlands along the eastern sides of both main islands (Ogden et al. 1998). Beech trees occur in association with almost all of the main canopy dominants of New Zealand.

New Zealand has five indigenous beech species: silver beech (*Nothofagus menziesii*), red beech (*Nothofagus fusca*), mountain beech (*Nothofagus cliffortioides*), black beech (*Nothofagus solandri*), and hard beech (*Nothofagus truncata*). All five species are evergreen. They have thin bark, shallow roots and high susceptibility to rot following injury. Together, these traits render the indigenous beech species highly susceptible to mortality by fire. For instance, a late twentieth century fire in a mountain beech forest of the eastern South Island caused nearly 100% mortality even though the fire burned primarily through surface and ground fuels and left the foliage intact (Wiser et al. 1997). New Zealand's beech species are obligate seeders whose post-fire regeneration depends on seed dispersal from unburned patches or populations outside the fire perimeter, which is effective over only short (tens of metres) distances (Figure 3) and is limited temporally by masting (Wardle 1984).

Although beech species are slow to recolonise, except in a narrow zone along the fire perimeter, bracken fern (*Pteridium esculentum*) and a suite of indigenous woody shrub and small tree species can become abundant soon after fire. Two of the most common small-tree genera to establish after fire are *Leptospermum* and *Kunzea*, both of which are myrtaceous (Burrows 1973; Allen et al. 1992). Both genera flower prolifically and produce small, wind-dispersed seeds in woody capsules. Each capsule may contain 50–300 tiny seeds ($> 10,000$ seeds g^{-1}) that are blown long distances and germinate on the mineral soil exposed after fire (Esler & Astridge 1974). Serotiny of these capsules in some populations of *Leptospermum* (Bond et al. 2004) further enhances its ability to persist at sites subject to repeated burning. In southeastern Australia and Tasmania *Leptospermum*, a Pleistocene immigrant to New Zealand, has large lignotubers but these are absent in New Zealand (Bond et al. 2004).

Although beech forests have relatively high biomass (i.e. a heavy fuel loading), the surface fuels rarely dry out in the cool, moist microclimate beneath the dense beech canopy. Hence, fire in beech forests is commonly thought to spread slowly through fallen twigs, mosses, lichens, litter and duff on the forest floor and rarely spread into tree crowns (Wardle 1984; Wiser et al. 1997). Extensive burning of intact beech forests could nevertheless occur under extremely dry, windy conditions (Figure 3A) or where

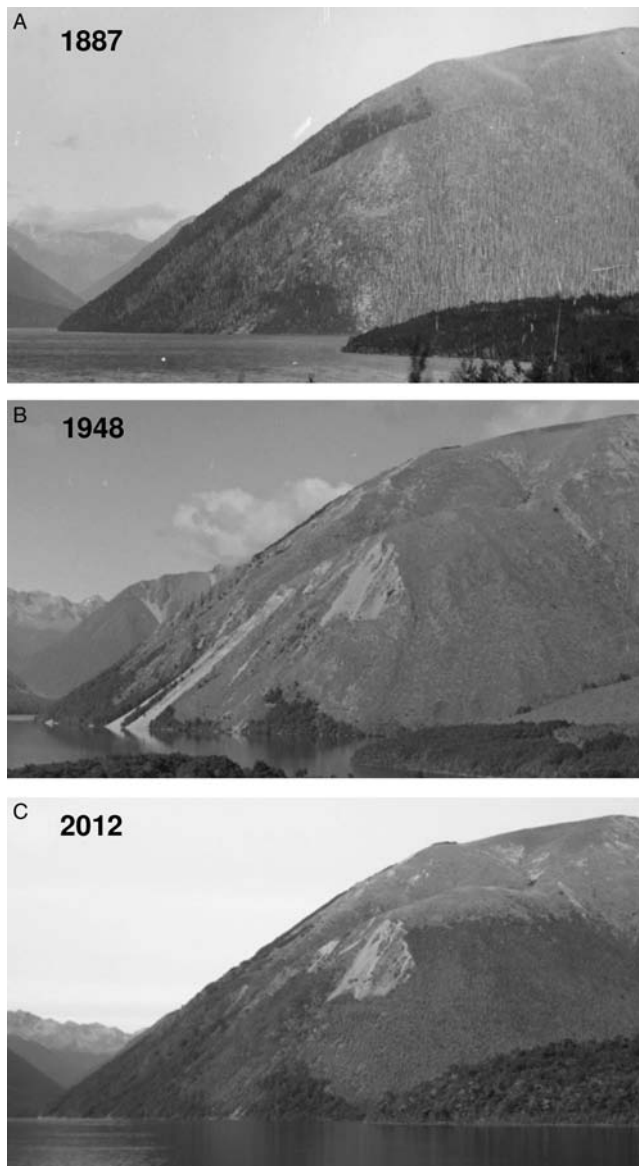


Figure 3. Fire-driven loss of *Nothofagus* forests along the north face of Mount Robert in the Nelson Lakes National Park in the northern South Island of New Zealand. Historical photos show **A**, extensive snags in 1887 shortly after a fire burned nearly the entire mountainside (The Nelson Provincial Museum. Tyree Studio Collection: 182030); **B**, areas of erosion and a lack of forest recovery in 1948 (The Nelson Provincial Museum. Ellis Dudgeon Collection: 212201); and **C**, the present dominance of *Leptospermum* and *Kunzea* across nearly the entire mountain slope with minimal recovery from the remaining forest patches despite an absence of fire at least since the National Park was established in 1956. **D**, Data on tree density and ages from a series of contiguous 20×20 m plots sampled from the forest margin into the burned patch are shown. Tree ages in the lower panel are shown at 20 m intervals corresponding to the 20 m intervals on the x-axis of the upper panel. Dashed horizontal lines represent the time of the initial fire (1887) and the establishment of the National Park (1956).

D Vegetation dynamics along the forest margin

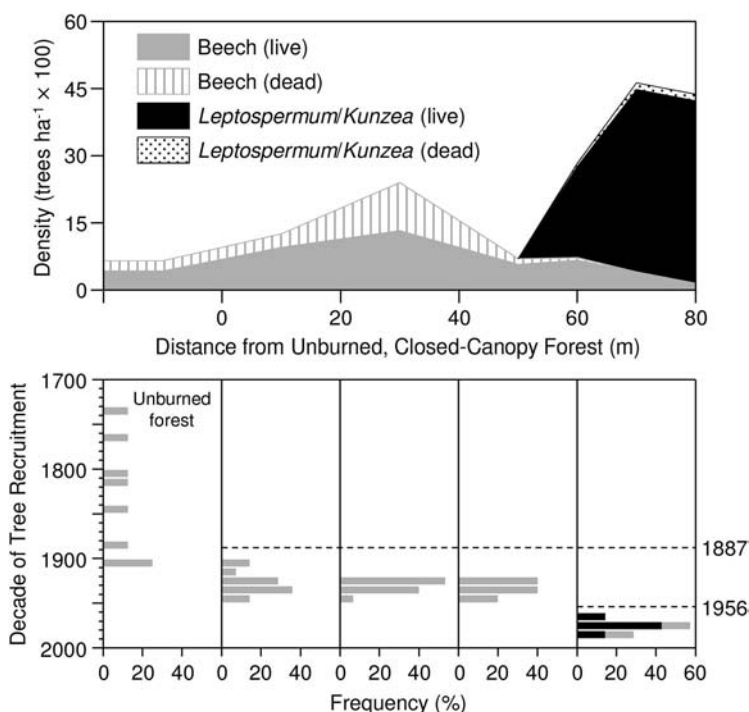


Figure 3. Continued.

previous disturbance by wind, snow, or tectonic activity has opened the canopy and dried out fuels before the fire.

The vegetation that develops after fire is much more fire-prone than the taller, closed-canopy beech forests, and therefore, the burning of beech forests initiates a positive feedback cycle whereby the perpetuation and expansion of fire-prone, shorter-statured vegetation is almost inevitable provided ignitions are available. The *Leptospermum* and *Kunzea* trees that establish after fire have highly flammable exfoliating, papery bark, and their experimentally determined shoot-level flammability is as high as some invasive pyrophyllic species (Wyse et al. 2016). They also have sparse crowns that provide little moderation of sub-canopy microclimate. Light penetration through their sparse crowns enables the persistence of a dense layer of shorter shrub species (e.g. *Coprosma*, *Leucopogon*, *Leptecophylla*, *Myrsine* and *Pseudopanax*), along with grasses, herbs, forbs, mosses and lichens in the lower canopy. The living and dead fuels of this short vegetation along with the papery bark of *Leptospermum* and *Kunzea* are highly conducive to fire spread given an ignition source.

The *Leptospermum* and *Kunzea* stands that commonly develop after the burning of beech forests persist in this fire-prone state until regeneration by beech eventually produces a taller, denser canopy that shades out some of the lower-canopy vegetation and provides cooler, moist conditions near the ground. However, given the short seed dispersal of beech trees, large burned patches may persist in a fire-prone state for decades to well over a century (Figure 3) until forest eventually recovers or subsequent fire resets this

slow development sequence. Furthermore, when recently deforested patches are burned repeatedly, each successive fire may extend farther into the adjacent closed-canopy forest (Perry et al. 2012a), further expanding the area subject to seed-dispersal limitation and delaying forest recovery.

The warm temperate rainforest–shrubland system of New Zealand

Grubb et al. (2013) delimit New Zealand's warm temperate rainforest as lying north of about 38°S (scattered southwards to 41°S) up to elevations of around 800 m. Although the dominant taxa in these forests show a range of shade tolerances and regeneration strategies, none of them are strongly fire-adapted (with the exception of *Leptospermum*). Although New Zealand's indigenous tree species are thin-barked when compared with those in other forest types, they do vary in their bark thickness. However, thick bark is associated with limited soil resources rather than fire frequency (Richardson et al. 2015). All of the potential canopy trees are obligate seeders. Although several species can resprout (e.g. *Beilschmiedia*, *Griselinia*, *Weinmannia*) (Enright & Cameron 1988; Martin & Ogden 2006), this is not necessarily interpretable as a response to fire and relatively little is known about post-fire resprouting responses in the New Zealand flora. Soil seedbanks are relatively unimportant in New Zealand's forest communities and are often decoupled from the canopy vegetation and dominated by exotic plant species (Sem & Enright 1995; Ferguson & Drake 1999). As with most of New Zealand, fire activity in the warm temperate rainforest vegetation type was rare before the arrival of humans, and even following Māori arrival was restricted to coastal lowlands often in association with horticulture (see Appendix 1 of Grubb et al. 2013). In general, before the arrival of Europeans, New Zealand's warm temperate rainforest escaped the intense burning that occurred in other parts of the country (Perry et al. 2012b). In particular, there was comparatively little fire in northern *Agathis* forests (a distinctive type of warm temperate rainforest), although Māori probably used small-scale fire in these forests for hunting (Ogden et al. 2003).

Following European settlement, large expanses of warm temperate rainforest were lost to fire, often in association with logging activity (Beaglehole 2012); in some cases very large areas were burned in single events (e.g. the Puhipuhi fire of 1887 burned in excess of 7000 ha of kauri forest; Thode 1983). Fire activity declined over the latter part of the twentieth century, and over the period 1991–2007 on average 560 ha per year burned across the Northland, Auckland and Waikato fire regions (c. 10% of the national annual average) (Doherty et al. 2008). The outcome of this period of deforestation was, at least on nutrient depleted soils, secondary succession through shrubland dominated by *Leptospermum* and *Kunzea* and vulnerable to invasion by pyrophytic taxa such as *Ulex* spp., *Erica* spp. and *Hakea* spp. The presence of these invasive species may make the community more flammable as a whole (Anderson & Anderson 2010) and hence potentially more vulnerable to further fire. Successions have been slowed by high levels of seed and seedling predation and browsing by exotic mammals, changes in soils, and potential dispersal and pollination failure as bird populations have declined.

Studies of post-fire vegetation dynamics in the Te Urewera region (eastern North Island) have demonstrated how exotic herbivores such as deer can divert the course of post-fire successions and potentially hold plant communities in fire-vulnerable early

successional stages for longer and longer periods (McKelvey 1955; Payton et al. 1984; Richardson et al. 2014). In particular, the small tree *Weinmannia racemosa*, a preferred perch tree of the frugivorous New Zealand wood pigeon (*Hemiphaga novaeseelandiae*), is susceptible to browsing, and a reduction in its abundance can significantly influence successional trajectories (McKelvey 1955). Fire successions have also been studied on New Zealand's northern offshore islands, including Great Barrier Island (Atkinson 2004). The legacy of the two waves of anthropic fire that Great Barrier Island experienced—one Māori and one European—is the early successional *Leptospermum* shrubland that now covers c. 50% of the island (NZ Land-cover Database [<https://lris.scinfo.org.nz/layer/423-lcdb-v41-land-cover-database-version-41-mainland-new-zealand/>] 4.1). In some parts of Great Barrier Island *Leptospermum* shrubland is slowly reverting to forest, but in others, such as dry ridges, the succession appears to be inhibited by interactions between depleted soils, pyrogenic woody weeds and seed/seedling limitation (Perry et al. 2010). The course of post-fire succession can be difficult to predict, however. For example, after Tawhiti Rahi (Poor Knights Islands) was abandoned by Māori in the 1820s, the post-fire and gardening succession back to forest, which occurred in the absence of invasive mammals, has resulted in a community composition unlike that of the pre-human era (Wilmschurst et al. 2014). Before human settlement, the forests on the island were dominated by the indigenous palm *Rhopalostylis sapida* alongside podocarps such as *Dacrydium cupressium* and angiosperms such as *Nestegis*. However the post-abandonment forests are characterised by an absence of *R. sapida* (until seedlings were observed in the late 1990s) and podocarps, and a predominance of angiosperms; Wilmschurst et al. (2014) attribute this shift to a change in the abundance of burrowing sea birds and their effects on soil conditions.

Spatial simulation models suggest that fire frequency and seed predation are the key determinants of the rate of succession from shrubland to forest in northern New Zealand landscapes (Perry et al. 2015). This modelling work suggests that if pyrophytic woody weeds are present, then fire frequency is the dominant control but in their absence seed predation is more important. Perry et al. (2015) isolated abrupt thresholds in the rate of succession as fire frequency and seedling predation increased, but neither the rate of long-distance seed dispersal nor changes in soil conditions with recurrent fire had a strong influence. The model suggests three stable conditions: *Leptospermum* shrubland (dominated by invasives if present) under high fire frequencies, *Kunzea* shrubland under low fire frequencies and high seed predation, and forest under low fire and seed/seedling predation. In very few landscapes did a stable or persistent mosaic of shrubland (flammable) and forest (non-flammable) emerge, suggesting that each represents a feedback-reinforced quasi-stable state.

Future of fire in New Zealand's ecosystems

In some parts of New Zealand, fire shaped distinctive ecosystems before humans arrived. For example, the low-fertility gumland heaths of northern New Zealand probably represent early successional communities where fire is, or has been, recurrent but which may slowly return to closed forest in the absence of fire (Enright 1989). Such 'naturally' fire-induced communities are the rarity in New Zealand, however, and their persistence may require the active use of fire (Allen et al. 1996). In most New Zealand landscapes and ecosystems it is almost impossible to disentangle the deleterious effects of fires

from those of invasive pyrophytic plants and mammals. Observational and modelling studies suggest that recurrent fire, alongside pollination and dispersal failure and high levels of seed predation and/or herbivory by exotic mammals, can arrest successions (Richardson et al. 2014; Perry et al. 2015). These stressors continue to interact to reshape the relationship between fire and vegetation age: slowed successions alongside failed regeneration mean that longer time is spent in the fire-prone early successional stage(s), where invasive plants can readily colonise under the open canopy and potentially increase community-level flammability early in the succession. If these successions are to be kick-started, fire reduction and the removal of exotic mammals (seed/seedling predators and herbivores) need to occur in tandem (Perry et al. 2015).

Globally there is considerable concern as to how fire regimes will respond to climate change. Projections for New Zealand suggest that weather conditions may become more conducive to fire, especially in the drier parts of the country (the east) and that lightning activity and drought may increase (Pearce et al. 2005). On the other hand McGlone and Walker (2011) consider climate-induced shifts in fire regimes to be a relatively small threat to New Zealand's indigenous biodiversity, but they do note the potential effects of ongoing invasion by pyrophytic species and the risks posed to threatened and rare ecosystem types in drier parts of the country.

Conclusions

Despite considerable historical, floristic and biogeographic differences, the case studies presented here show remarkable parallels in life-history traits of the key taxa, fire-vegetation feedback mechanisms, overall ecosystem responses to anthropogenic alteration of fire regimes, and likely vulnerability of temperate forests in New Zealand and southern South America to expected global change influences on future fire regimes. The case studies show that dominant species in the alternative pyrophobic/pyrophytic states have common traits that were moulded in ecologically similar settings (Figure 4). Key species of the pyrophobic community are in all cases fire-sensitive, thin-barked tall trees that cast large amounts of shade in the understorey and produce moist, cool, light-limited understoreys. Despite these conditions, some levels of internal heterogeneity should allow species of the alternative (pyrophytic) state to persist in some way, either within the pyrophobic community (e.g. seed banks, seedling banks, as low vigour plants, or under canopy gaps), or through meta-population dynamics with locally more favourable patches such as portions of the landscape prone to non-fire disturbances. Where the dominant trees of pyrophobic forests are obligate seeders, such as in the case of widespread New Zealand and South American forests dominated by evergreen beeches (as well as by the deciduous *N. pumilio* in South America) seed availability is limited spatially by poor seed dispersal capacity and temporally by masting. New Zealand's conifers potentially have longer seed dispersal by birds, but this has been reduced by population declines or extinctions of some of the most important dispersers. Hence, following severe burning, seed availability becomes limiting except for sites near forest boundaries.

Seedlings and saplings of some of the pyrophobic trees tend to be sensitive to high radiation, which impedes regeneration in the open conditions after fire, and they are easily killed by even low-intensity fires that further perpetuate the pyrophytic state (Figure 4). Seeds of some of the pyrophobic tree species tend to be large and consumed by predators

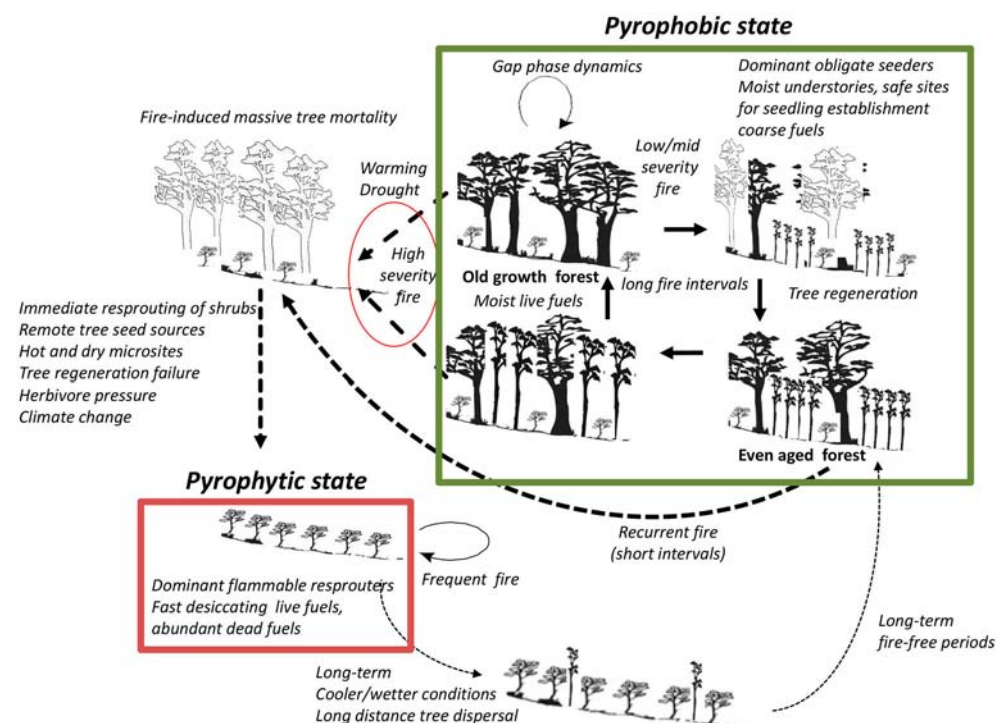


Figure 4. Conceptual model of dynamic stability and critical transitions between fire-driven alternative states. In the absence of fire, tall, closed-canopy forests produce dense shade that either excludes members of the pyrophytic community or limits them to a suppressed state, whereas pyrophobic tree species are able to regenerate through small canopy gaps. Pyrophobic closed-canopy forests are unlikely to burn except during extreme drought or severe fire weather, but when fire does occur, tree mortality is typically high. The resulting high light levels, low soil moisture and long distances from surviving seed sources provide few opportunities for regeneration of hydrophobic tree species. Climatic warming and herbivores may further deter tree regeneration. As long as ignition sources persist, the pyrophytic state that rapidly develops after fire may be perpetuated by repeated fires. In the hypothetical case of a long-term climatic change towards wetter fire-free conditions (and effective fire/herbivore suppression), slow accretion of recruiting trees could eventually overtop and suppress the shrub/bamboo thicket and convert into forests.

and/or reproduction relies on animal mutualisms. Increased granivory or decreased mutualisms may further arrest succession from pyrophytic to pyrophobic states. Live fuels and coarse dead debris in pyrophobic states tend to retain moisture and act as heat sinks during fires. Hence, large severe fires in pyrophobic communities occur infrequently and most commonly associated with extreme El Niño Southern Oscillation-related droughts and possibly disturbances such as windthrow and bamboo flowering that produce abundant dead fuel and/or open the canopy to accelerate the drying of those fuels. Self-reinforcing (i.e. positive) feedbacks of the pyrophobic community include moist understorey microenvironments that promote tree establishment and reduce understorey flammability, and competitive suppression of species of the pyrophytic state. Because trees grow tall, another reinforcing mechanism is the fact that with succession, canopies of old trees tend to separate from understoreys and disrupt the continuity of

fuel ladders that are common in early post-fire situations so that the potential of fire spread into the canopy is reduced. Reduced flammability with successional age is a feedback mechanism that further promotes the pyrophobic state (Kitzberger et al. 2012; Tepley et al. 2016).

Pyrophytic states and fire-promoting mechanisms also show many commonalities among the case studies. Dominant or functional key species tend to be short-statured, heliophyllous, fast growing and with abundant fine fuels distributed from the ground surface to the top of the plant canopy (Figure 4). In some cases, the pyrophytic species are tolerant of waterlogging. All of these traits allow these species to rapidly dominate following stand-replacing burning of the pyrophobic community or persist in open ecosystems subject to more frequent fires (Figure 4). High flammability of these communities is ensured by variable combinations of species with traits such as flammable exfoliating bark, inherently low foliar moisture contents, retention of dead foliage, and open canopies that permit rapid drying of understorey fuels and duff. Persistence of species with more flammable traits is achieved by a variety of different mechanisms such as longer distance seed dispersal (compared with pyrophobic tree species), and in some cases, serotiny or resprouting. Severe fires within this community as well as dry understorey microenvironments prevent successful tree establishment. Pyrophytic communities may also provide favourable habitats to seed/seedling predators of tree species, and compared with pyrophobic forests, their open canopies are more easily colonised by flammable exotic plants, further reinforcing the fire-prone treeless state (Figure 4).

In both southern South America and New Zealand, abrupt shifts from pyrophobic to pyrophytic communities are well documented and are triggered by severe, stand-replacing fires (Figure 4). Landscape level shifts in dominance towards pyrophytic vegetation in all cases occurred over short periods (e.g. a few decades to a century or two) in response to increased anthropogenic ignitions. This commonality suggests that where natural ignitions have been low and the flora has experienced little evolutionary exposure to fire, vulnerability to anthropogenically induced shifts to a pyrophytic landscape is high.

Conversely, conditions that induce shifts from the pyrophytic to pyrophobic state are generally related to slow processes of accretion of trees within the surrounding flammable landscape (e.g. during moist, long fire-free periods) until thresholds of canopy cover start suppressing the species of the pyrophytic community, increasing understorey moisture, reducing fuel ladders, and so reducing overall flammability (Figure 4). Although active fire suppression is a current management objective in all of the areas studied (but with varying effectiveness), at a landscape scale there is no evidence of reversion from the pyrophytic back to the pyrophobic condition. All of the studies suggest that there are additional reinforcing factors (other than fire) that can more or less permanently arrest successions and prevent recovery to pyrophobic forests. These factors include changes in waterlogging conditions (Albornoz et al. 2013), invasions of both exotic herbivores and exotic flammable plants (Richardson et al. 2014; Perry et al. 2015) and climatically altered fire intervals and woody plant demography (Enright et al. 2015). There is a growing consensus based on multiple lines of evidence including both empirical studies of mechanisms of fire-vegetation feedbacks and the exploration of their implications in simulation modelling that reversing these broad-scale strongly directional changes in vegetation is futile or will require ever-increasing efforts.

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ORCID

T Kitzberger  <http://orcid.org/0000-0002-9754-4121>

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