

Past and Present Vulnerability of Closed-Canopy Temperate Forests to Altered Fire Regimes: A Comparison of the Pacific Northwest, New Zealand, and Patagonia

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The relative importance of people and climate in shaping prehistoric fire regimes is debated around the world, and this discussion has helped inform our understanding of past and present ecosystem dynamics. Evidence for extensive anthropogenic burning of temperate closed-canopy forests prior to European settlement is geographically variable, and the factors responsible for this variability are not well resolved. We set out to explain the differences in the influence of prehistoric human-set fires in seasonally dry forest types in the Pacific Northwest, New Zealand, and northern Patagonia by comparing the fire traits of dominant taxa, postfire vegetation recovery, long-term climate trends, and human activities that may have motivated burning. Our analysis suggests that ecological and climatic factors explain much of the differences in how these mesic-dry forests responded to prehistoric anthropogenic burning. Understanding past human-environment interactions at regional scales is an important step for assessing the impact of biomass burning at all scales.

Keywords: fire history, vegetation flammability, prehistoric anthropogenic burning, Pseudotsuga menziesii, Nothofagus forest fire regimes

Although humans have long used fire as a tool to manage their physical surroundings (Bowman et al. 2011), the degree to which anthropogenic burning has reshaped natural patterns of vegetation and their associated fire regimes varies geographically. The reasons for this variation are unclear. Many recent studies have emphasized climate as the primary driver of fire regimes, especially at regional to continental scales (e.g., Krawchuk and Moritz 2011, Marlon et al. 2013). In this context, climate is considered a top-down control that governs the frequency of weather conditions necessary to start and support the spread of individual fires, and it defines the persistence of atmospheric circulation patterns that govern the area burned over decades to centuries. On centennial to millennial scales, climate also shapes the composition and distribution of vegetation, which acts as a bottom-up control of fire regimes,

inasmuch as fuel structure and composition determine fire behavior and trajectories of postfire recovery. At these broad scales, human influences on fire regimes are generally considered secondary to climate and are geographically localized.

Indigenous people alter natural fire regimes directly, by offering a new ignition source, suppressing fires, and modifying vegetation and corresponding fuel patterns. The magnitude of past (and present) human influences on natural fire regimes, however, varies along a broad moisture gradient of vegetation types (Whitlock et al. 2010, Archibald et al. 2013, McWethy et al. 2013). In general, anthropogenic burning has relatively little impact on fire regimes at the extreme wet or dry end of the moisture gradient because of the high fuel moisture in mesic settings and the discontinuous fuel cover in arid regions. Humans can and do exert a

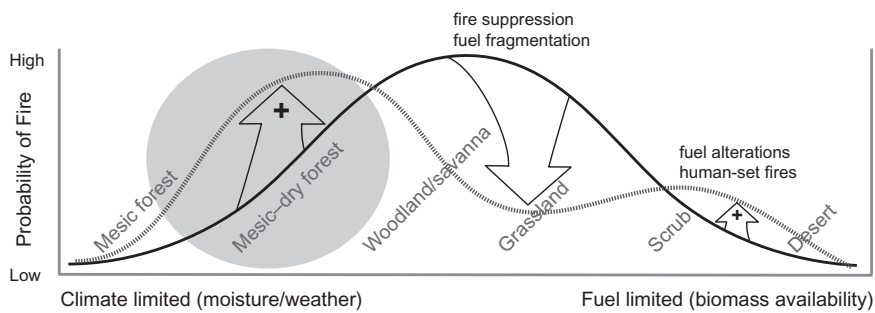


Figure 1. The strength of natural and anthropogenic controls on fire activity in mesic-dry forests. The magnitude of human influences on natural fire regimes varies along a broad moisture gradient of vegetation types. Climate exerts strong controls on fire activity at the extremes of the wet and dry end of the moisture gradient as a result of the low flammability of fuels in mesic settings and the scarcity and disconnected arrangement of fuels in arid regions. Humans have the potential to alter fire regimes through changing ignition frequency, fuel composition and pattern, and fire suppression (dashed line). In the mesic-dry forests of the Pacific Northwest, the South Island of New Zealand, and northern Patagonia (shaded circle), biomass availability is high, but natural ignitions are limited. Humans—past, present, and future—increase the vulnerability of vegetation by adding and targeting ignitions in more-flammable vegetation and synchronizing ignition timing with dry periods. Source: Adapted with permission from Whitlock and colleagues (2010).

strong influence at an intermediate range of moisture and productivity in which biomass availability is high and natural ignitions occur infrequently or not at the timing of fuel desiccation. These intermediate settings include seasonally dry, closed-canopy forests in which human-set fires have potential to markedly increase the area burned over time by increasing the frequency of ignitions, synchronizing ignitions with dry periods, and increasing the amount of flammable early-seral vegetation across the landscape (figure 1; e.g., in New Zealand, Perry et al. 2012a).

In this article, we examine the environmental and human factors that caused prehistoric human-set fires to have widely varying consequences in relatively similar biophysical settings. We focus on seasonally dry temperate regions, which are capable of supporting closed-canopy mesic to dry-mesic forests in the absence of anthropogenic burning. These forests (hereafter, referred to as *mesic-dry*) include the cool-temperate evergreen forests of the Pacific Northwest and the cool-temperate evergreen and broadleaf forests of the South Island of New Zealand and northern Patagonia (figure 2a). They are characterized by intermediate to high productivity and moisture levels, and they represent some of the last forests worldwide to experience large-scale clearing. Mesic-dry forests of the Pacific Northwest, New Zealand, and Patagonia share a common range of climate conditions and biophysical characteristics (table 1, figure 2b). In all three regions, the fire season is limited by high fuel moisture and infrequent lightning-set ignitions, but dry spells create opportunities for large burns. We suggest that the consequences of pre-European anthropogenic burning in these

forests are best understood when fire, climate and human history is coupled with modern studies of vegetation dynamics that elucidate the feedback mechanisms driving those changes.

Study areas

The Pacific Northwest forests of interest are the low- and mid-elevation Cascade Mixed Forest at latitudes from 41 degrees (°) to 52° north that extend from the eastern slopes of the Coast Range to the western slopes of the Cascade Range (200–1200 meters [m] above sea level; McNab et al. 2005). These forests are composed of evergreen conifer species, predominantly *Pseudotsuga menziesii*, but with *Tsuga heterophylla*, *Thuja plicata*, and *Abies* spp. (i.e., *Abies procera*, *Abies amabilis*, and *Abies grandis*) as the main shade-tolerant associates. Forest understories consist of numerous tall shrubs (*Acer circinatum*, *Corylus cornuta*, *Rhododendron macrophyllum*, *Vaccinium parvifolium*), short shrubs (*Gaultheria shallon*, *Berberis nervosa*, *Rubus ursinus*,

Linnaea borealis), ferns (*Polystichum munitum*), and a variety of forbs. Most precipitation falls between November and February, followed by several months in which the available moisture is limited (July to September). Summer maximum temperatures average 24° Celsius (C) but exceed 30°C in some parts of the region (www.prism.oregonstate.edu). Lightning strikes are typically associated with rainfall events, and, currently, most lightning ignitions either extinguish naturally or are suppressed within a few days. In the southern mesic-dry forests, a rate of 0.00005 lightning-ignited fires per square kilometer per year occurred between 1970 and 2007 (these data are for Willamette and Umpqua National Forests; www.fs.usda.gov/goto/r6/gis), and a trend of decreasing lightning ignition occurs toward the coast and northern regions.

Comparable biophysical settings in New Zealand occur at 250–1200 m above sea level in the eastern South Island, where the potential vegetation is closed-canopy evergreen broadleaf forests (McGlone 1989, Leathwick 2001). At low altitudes, under dry climates, and into the intermontane basins of the central Southern Alps, the natural vegetation consists of tall podocarp trees (e.g., *Podocarpus*, *Prumnopitys*, *Dacrycarpus*) that form a canopy above small-leaved angiosperm trees (e.g., *Elaeocarpus*, *Hoheria*, *Pittosporum*, *Sophora*). Mid-elevation forests of *Nothofagus fusca* and *Nothofagus menziesii* extend to the tree line, with increasing *Nothofagus solandri* var. *cliffortioides* and *Phyllocladus alpinus* in the subalpine zone. East of the central portion of the Southern Alps, the areas of natural vegetation feature *Podocarpus*, *Phyllocladus*, and *Libocedrus* forest, with an understory of angiosperm trees and shrubs. The

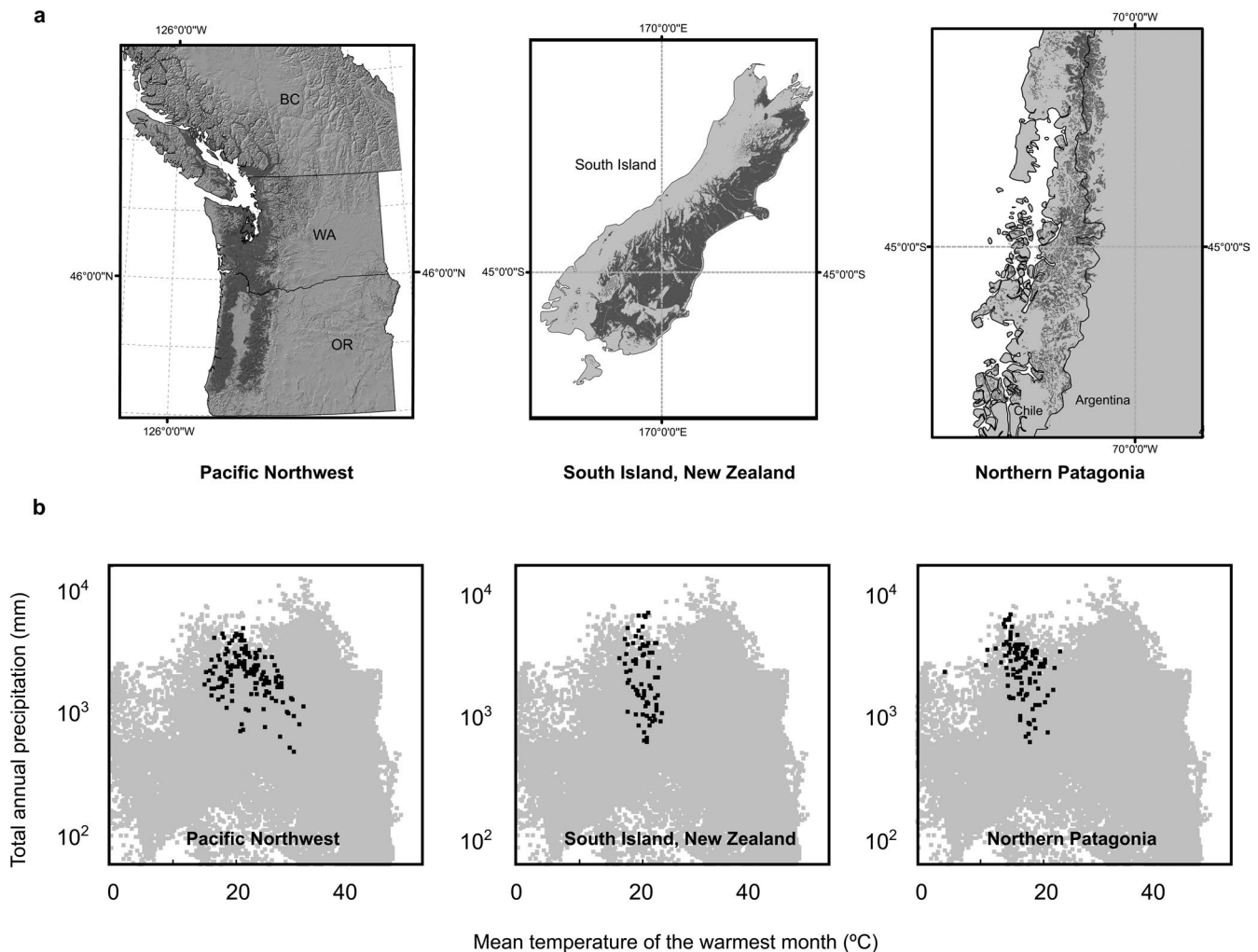


Figure 2. The location of three regions in (a) geographic and (b) climate space. In panel (a), the dark gray shading indicates the distribution of present-day Cascade mixed-conifer forest in the Pacific Northwest (McNab et al. 2005 for the conterminous US; www.landfire.gov) and Canada (www.for.gov.bc.ca/hre/becweb); the former extent of low- to mid-elevation *Nothofagus* and podocarp forests in the South Island of New Zealand (Leathwick et al. 2004); and the present-day cool, temperate *Nothofagus* forest in northern Patagonia (Veblen 1996, Lara et al. 1999). (b) Climate space (the black rectangles) of grid cells containing forests identified in panel (a) within a grid of global climate space (the gray rectangles) for two variables important for fire activity: the mean temperature of the warmest month and mean annual precipitation. The grid cells have a spatial resolution of 0.5°. The climate data are from the Climate Research Unit (similar to those of Marlon et al. 2008, provided by Patrick J. Bartlein). Abbreviations: C, Celsius; E, east; mm, millimeters; N, north; S, south; W, west; °, degrees.

climate features mild winters and moderately warm summers, although summer temperatures occasionally exceed 30°C. Lightning is infrequent; a total of 50 lightning-ignited fires accounted for only 0.1% (90 hectares [ha]) of the area burned between 1991 and 2007 (Anderson et al. 2008).

In southern South America, similar biophysical settings support the cool temperate *Nothofagus* forests of northern Patagonia, which lie along the eastern flank of the Andes in Argentina (40°–45° south; Veblen et al. 1996). At the mesic end of the moisture gradient, we focus on tall forests dominated by evergreen *Nothofagus dombeyi*, which grow

at low- to mid-elevations (500–1000 m above sea level) and which are bordered to the west by seasonally dry Valdivian rainforest. These mesic–dry forests are closed canopy and support a mix of angiosperms and gymnosperms. In the eastern mesic–dry forests, we include transitional forests in drier settings that are codominated by *N. dombeyi* and the evergreen conifer *Austrocedrus chilensis*. *Austrocedrus* forms pure xeric forests and is replaced by Patagonian steppe farther east. The third common tall forest species is the deciduous *Nothofagus pumilio*, which dominates in sub-alpine forests (less than 1000 m above sea level) and drier

Table 1. Geographic, physical, and vegetation characteristics of the three study areas.

Characteristic	Pacific Northwest	South Island New Zealand	Northern Patagonia
Study area location	Eastern Coast Range and western Cascade Range	East of the southern Alps	East of the Andes
Latitude and longitude	41°–52° north, 122–124° west	40°–46° south, 167.5°–172.5° east	40°–45° south, 72°–71° west
Lifeform description	Evergreen (mixed-conifer)	Broadleaf evergreen	Evergreen broadleaf, deciduous broadleaf, and evergreen scale-like leaves
National classification description	Cascade mixed forest–coniferous forest (McNab et al. 2005)	Predominantly podocarp mixed with <i>Nothofagus</i> at mid-elevations (McGlone 1989)	Cool temperate <i>Nothofagus</i> forest (Veblen et al. 1996), mixing with rainforest taxa to the west
Dominant species	<i>Pseudotsuga menziesii</i> with <i>Tsuga heterophylla</i> , <i>Thuja plicata</i> , and <i>Abies</i>	Podocarps (<i>Podocarpus</i> , <i>Prumnopitys</i> , <i>Dacrycarpus</i> , <i>Halocarpus</i> , <i>Phyllocladus</i>), <i>Nothofagus fusca</i> type (= <i>Fuscospora</i>) and <i>Nothofagus menziesii</i> (= <i>Lophozonia</i>)	<i>Nothofagus dombeyi</i> (evergreen), <i>Nothofagus pumilio</i> (deciduous) in subalpine and eastern dry forests, and xeric <i>Austrocedrus chilensis</i>
Elevation range (meters above sea level)	200–1200	250–1200	500–1000
Total annual precipitation (in millimeters [mm]) between 1961 and 1990	1500–3000	500–1600	1500–3000
Mean temperature (in degrees Celsius) of the warmest month between 1961 and 1990	20–31	18–25	12–27
Months with limited water availability (precipitation of less than 150 mm)	3	3	3
Early-seral dominants after stand-replacing fire	Bracken (<i>Pteridium</i>) and shrubs (e.g., <i>Ceanothus</i> , <i>Berberis</i> , <i>Rubus</i> , <i>Gaultheria</i> , <i>Acer</i>)	Tussock grasses (<i>Chinochloa</i>), bracken (<i>Pteridium</i>), shrubs and small trees (<i>Leptospermum</i> and <i>Kunzea</i>)	Tall shrubs and shrub-like trees (<i>Schinus</i> , <i>Nothofagus antarctica</i> , Proteaceae), bamboos (<i>Chusquea</i>) and tussock grasses
Rate of tall forest regeneration	Multiple pathways of initial cohort development; all pathways typically reach canopy closure in about 4 decades	A few decades within tens of meters from the forest edge; several decades in the interior of large burned patches	Decades to centuries without fire
Trajectory of change in flammability with time since fire	High until tree species reach canopy closure, producing a cooler, moister microclimate and shading out flammable early-seral species		
Natural ignition flash rate	Less than two per strike per square kilometers per year	Less than one per strike per square kilometer per year	Less than two per strike per square kilometers per year
Natural adaptations/exaptations to fire	Resistance (thick bark and elevated crown base of <i>Pseudotsuga</i>); rapid regeneration of <i>Pseudotsuga</i> and other species following fire	Resprouting for a few species of tall trees and shrubs; variable serotiny in <i>Leptospermum scoparium</i>	None for dominants of tall forests; resprouting for <i>N. antarctica</i> , bamboos, and tall shrubs
Summer insolation maximum	Early Holocene	Late Holocene	Late Holocene
Magnitude of pre-European human influence	Low	High	Low to moderate
Terrestrial resource availability	High	Moderate then low following avian extinctions around AD 1500	Moderate

Note: The Nothofagaceae have been recently revised; in New Zealand, species previously assigned to the genus *Nothofagus* have been reclassified within the *Fuscospora* and *Lophozonia* (Heenan and Smissen 2013). We have decided to retain the longstanding *Nothofagus* nomenclature in this paper for purposes of comparison.

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forests bordering shrublands and open woodlands transitional to the steppe. Summer temperatures in Patagonia are similar to those of the other regions, and a majority of the precipitation (more than 40%) falls in winter (June to August), followed by several months of limited moisture availability (December to March). Although humans accidentally set most fires in northern Patagonia, a few lightning-ignited fires in recent decades have burned large areas of forest (Veblen et al. 2011). Argentine national park

fire records indicate that a total of 17 lightning-ignited fires accounted for 16.4% of the area burned between 1938 and 2005 (Mermoz et al. 2005).

In contrast to their environmental similarities, the history and duration of indigenous human occupation in these regions differ. On the basis of our current understanding, people have been in the Pacific Northwest and southern South America for at least 14,000 years (Meltzer 2009) but in New Zealand for no more than 750 years (Wilmschurst

et al. 2008). The populations at the time of European arrival were relatively large in the Pacific Northwest (approximately 30,000 people west of the Cascade crest in Oregon and Washington; Boyd 1990), compared with the South Island of New Zealand (approximately 5000 people; McGlone et al. 1994) and northern Patagonia (no specific estimates are available, but see Méndez et al. 2014). The influence of prehistoric peoples on fire regimes is most evident in New Zealand, where 40% of the mesic-dry forests on the North and South Islands was lost within less than 200 years of human arrival (Perry et al. 2014). In contrast, evidence suggests that the effects of anthropogenic burning prior to European arrival was relatively limited and localized in the Pacific Northwest and Patagonia. European arrival in the seventeenth and eighteenth centuries and settlement in the nineteenth and twentieth centuries led to pastoral and agricultural activities and extensive burning in all regions (Weisberg and Swanson 2003, Veblen et al. 2011, Perry et al. 2014).

The consequences of altered fire regimes

In this article, we explore a central question: Why were the effects of pre-European human-set fires limited in extent in the mesic-dry forests of the Pacific Northwest and Patagonia, whereas indigenous burning transformed closed-canopy forests into nonforested vegetation in comparable biophysical settings of New Zealand? We address this question by examining the degree to which the extent of prehistoric vegetation change by fire can be explained by (1) regional differences in the life histories and fire adaptations of the dominant tree species; (2) the strength of positive feedbacks driven by the trajectories of postfire vegetation flammability; (3) late-Holocene climatic controls on fire activity; and (4) human use of fire as influenced by local environment and available resources and technologies. We suggest that no single factor explains the regional differences, but rather, the explanation lies in the interaction of these variables.

Differences in the fire-adapted plant functional traits of the forest dominants. The traits of the dominant species, which developed as part of those species' long-term evolutionary history, are an important influence on the structure and function of biomes and account for regional differences in vegetation sensitivity to fire (Lehmann et al. 2014). *Pseudotsuga menziesii*, the dominant species in Pacific Northwest mesic-dry forests, has evolved with fire and displays several life-history traits that enable it to persist across a wide range of fire frequencies and severities (Tepley et al. 2013). An ability to survive low- and moderate-intensity fires is promoted by its thick bark, its elevated crown base height due to rapid self-pruning of shaded lower branches when trees grow in dense stands, and its resistance to rot if injured by fire (Hermann and Lavender 1990). These traits ensure that seed sources are well represented within fire perimeters, even after very large fires, and seeds are commonly dispersed to distances of about 400 m (Donato et al. 2009). Rapid establishment and growth of seedlings and an ability to establish beneath and overtop

competing shrubs promote redevelopment of *Pseudotsuga* canopy often within decades after fire (Tepley et al. 2014).

The dominant *Nothofagus* and podocarp species of the mesic-dry forests on the South Island of New Zealand, in contrast, are poorly adapted to fire, in that they lack traits that allow them to survive or recolonize after even low- and moderate-intensity fires. Mature trees and seedlings of gymnosperms and angiosperms are easily killed by fire. Their relatively thin bark, extensive roots at or near the soil surface, and poor resistance to rot if they are injured render them susceptible to mortality even after a low-intensity fire (Wiser et al. 1997). Most overstory trees of New Zealand lack the ability to resprout following fire and do not produce a persistent dormant seed bank. Postfire regeneration therefore depends on seed dispersal from surviving trees, which are located primarily outside the fire perimeter. Although propagules of conifer species are well-dispersed by birds, *Nothofagus* has heavy, wind-dispersed seeds with short dispersal distances (tens of meters), strong ectomycorrhizal requirements, and short-lived seed viability, all of which contribute to slow post-fire regeneration of forests (Wardle 1984). Following repeated fires, it can take from several decades to more than a century for the forest to regenerate back to its prefire composition. Similarly, the dominant species of the tall forests in northern Patagonia (*N. dombeyi*, *N. pumilio*, and *A. chilensis*) are easily killed by fire and generally do not resprout after fire. Wind-dispersed seeds mostly fall within tens of meters of the seed source, and juveniles are easily killed by fire, both of which constrain forest regeneration (Veblen et al. 1996).

Regional differences in postfire vegetation dynamics and flammability. Each of the three regions supports closed-canopy forests that provide relatively cool, moist microclimates in which fire is unlikely to spread except under unusually hot, dry, and windy conditions. High-severity fire, when it occurs, removes this microclimatic buffering and results in diverse early-seral communities (figure 3). Grasses, forbs, ferns and shrubs, and varying densities of tree seedlings establish after fire and form a dense layer of fine fuel near the ground, which, together with their generally higher flammability, makes early-seral vegetation in each region more flammable than the corresponding closed-canopy forests (e.g., Agee and Huff 1987, Fogarty 2001, Mermoz et al. 2005). Vegetation changes following recent fires offer clues for inferring past responses, although present-day land use and climate change make them imperfect analogs. In the case of New Zealand, where most of the original *Nothofagus*-podocarp forest is gone, the trajectory of postfire recovery is understood largely from modern observations in *Nothofagus*-dominated forests, which have a greatly reduced gymnosperm component compared with prehistoric mesic-dry forests.

In the Pacific Northwest, a cover of highly flammable shrubs (e.g., *Ceanothus*, *Berberis*, *Rubus*), vigorously sprouting bracken fern (*Pteridium aquilinum*), and less flammable small trees and shrubs (e.g., *Acer circinatum*) develops soon after fire and persists until regenerating trees

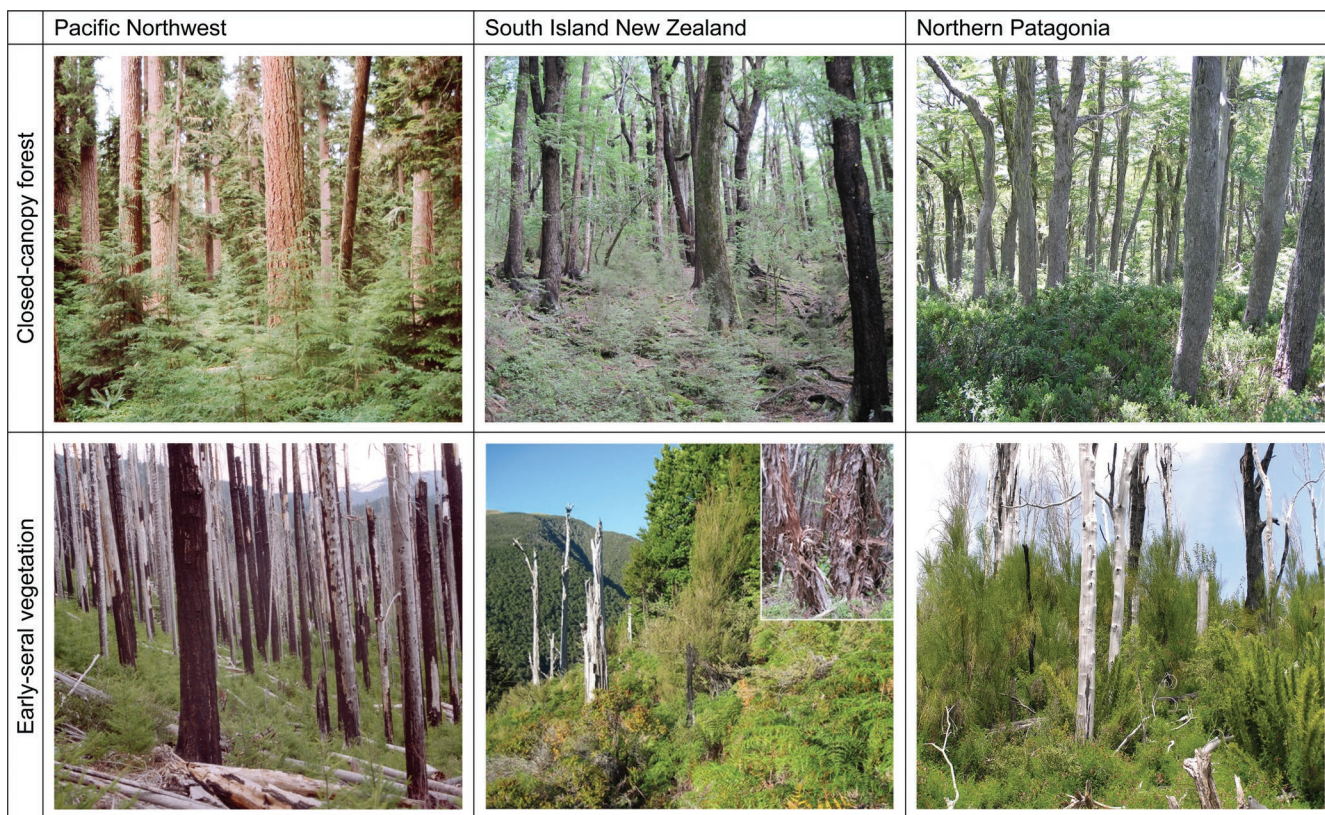


Figure 3. A comparison of the vegetation composition and structure of closed-canopy forests and early-seral vegetation among the three study areas. Pacific Northwest: a 400-year-old forest of *Pseudotsuga menziesii* and *Tsuga heterophylla* (top row) and dense *Pseudotsuga* regeneration 13 years after fire in the central western Cascades of Oregon (the bottom row). South Island New Zealand: old *Nothofagus* forest (*Nothofagus fusca* and *Nothofagus menziesii*; top row) and an adjacent early-seral patch burned several decades ago and currently dominated by *Pteridium esculentum* and *Leptospermum scoparium* (the inset photo shows the exfoliating, papery bark of *Leptospermum*) in the Canterbury High Country of the South Island (bottom row). Patagonia: unburned, mesic *Nothofagus pumilio* forest (top row) and 11 years after fire (bottom row).

reach canopy closure (figure 3). A feedback mechanism that supports repeated burning lies in the time-dependent changes in fuel structure and microclimate, which result in a U-shaped trajectory of flammability after a stand-replacing fire (figure 4a). For example, models of potential surface-fire behavior based on measured fuel characteristics along a 500-year-long chronosequence in western Washington (Agee and Huff 1987) indicate that flammability is highest during the first few decades, corresponding with the maximum biomass of herbs, *Pteridium*, and shrubs. Herb and shrub cover and measures of potential fire behavior decline to minimum values during the stem exclusion stage (110–180 years). Later in the postfire recovery, fine fuels increase and develop continuity with the upper canopy, promoting greater potential flame lengths and higher rates of fire spread. Numerous examples of repeated burning in the Pacific Northwest after European settlement (e.g., following the 1933 Tillamook Fire and the 1902 Yacolt Fire; Gray and Franklin 1997) provide evidence of this feedback mechanism.

In New Zealand, conversion of closed-canopy *Nothofagus*-podocarp forests to highly flammable shrublands dominated by mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea ericoides*), as well as bracken (*Pteridium esculentum*), has been described in many empirical studies (see Perry et al. 2014). The myrtaceous small trees (mānuka and kānuka) have papery, exfoliating bark (figure 3b) and high levels of leaf phenols that make them easily ignited and ranked among the most flammable of native tree and shrub species (Fogarty 2001). They readily colonize burned areas because of their copious production of small, wind-dispersed seeds, and some populations of mānuka produce serotinous capsules (Wardle 1984). Other common small trees and shrubs of the postfire community are also capable of sprouting after disturbance, including *Cordyline*, *Coprosma*, *Pseudopanax*, *Weinmannia*, *Griselinia*, and *Carpodetus* (Burrows 1994, Wiser et al. 1997). Flammability remains high until shrubs and small trees form a closed canopy, a condition which can occur within a few decades for areas within tens of meters of

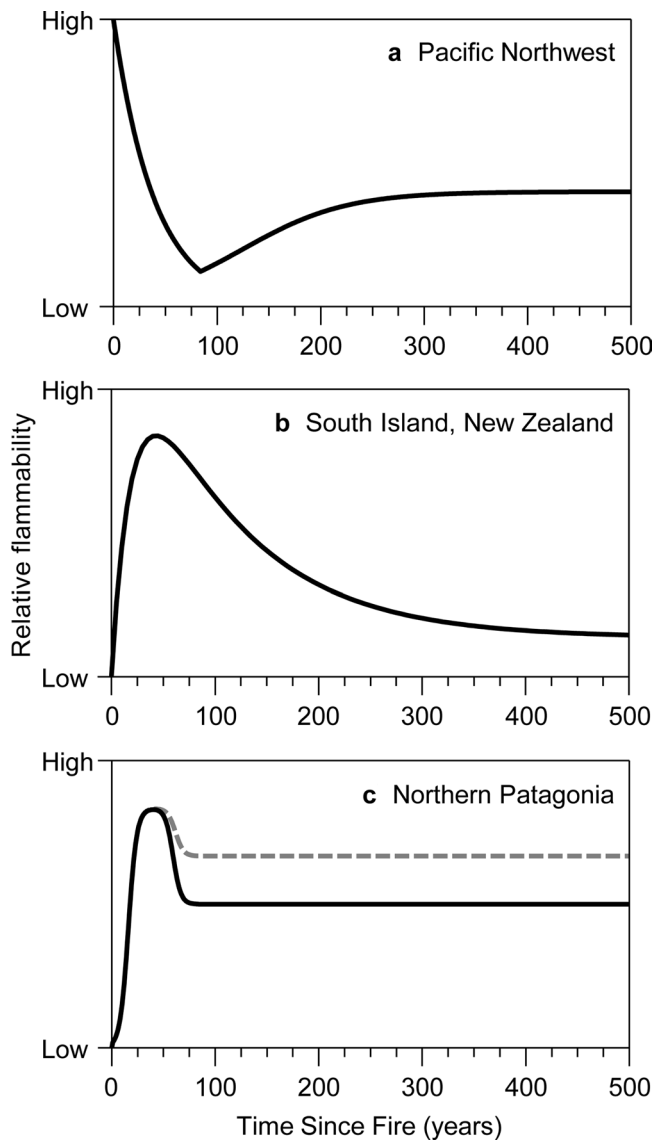


Figure 4. The trajectories of change in the relative flammability of vegetation as a function of time since a high-severity fire in (a) the Pacific Northwest (Wimberly et al. 2000, based on the empirical study of Agee and Huff 1987), (b) New Zealand (Perry et al. 2012b), and (c) Patagonia (Kitzberger et al. 2012, based largely on the empirical study of Mermoz et al. 2005). These curves have been incorporated into fire-spread algorithms of spatial simulation models in which relative flammability is defined as the probability that fire will spread into a focal cell in a particular time step, given that one of the adjacent cells is burning. The solid and dashed lines in panel (b) represent two scenarios with a strong and moderate decrease in flammability following canopy closure, as was explored in the modeling study of Kitzberger and colleagues (2012).

seed sources but which may take more than a century in the interior of large burned patches (figure 4b).

In Patagonia, vegetation flammability also increases substantially following fire, largely as a result of the dense

layer of shrubs (e.g., *Schinus*, *Diostea*, *Nothofagus antarctica*) and bamboo (*Chusquea*) that establish in early-seral stages. Sprouting shrubs and small trees that dominate after fire provide continuous live and dead fine fuels from the ground surface to shrub canopy. Flammability decreases as canopies close with regenerating *Nothofagus* species (figure 4c; Raffaele et al. 2011, Blackhall et al. 2014, Paritsis et al. 2014). High flammability of early-seral vegetation is evidenced in the patterns of recent fires, which often trace the boundaries of previous fires and stop in mature, closed *Nothofagus* stands. Shrublands experience more fire, and *Nothofagus* forests have less fire than would be expected were each vegetation type burning in proportion to its representation on the landscape (Mermoz et al. 2005, Paritsis et al. 2013).

In the largely deforested landscapes of the South Island of New Zealand and northern Patagonia, remnant forest patches show a strong association with cool, moist gullies and areas of cold air drainage. In contrast, where burning has progressed to the edge of extensive forests, the boundary between forest and shrubland tends to be sharp and not delineated by topography. These distinct borders are likely the result of repeated fires following European settlement. Human-set fires spread through young shrubland and were extinguished soon after entering closed-canopy forest (Wiser et al. 1997, Perry et al. 2012a, Paritsis et al. 2014). Such observations may be analogs for the type of burning that was undertaken by prehistoric peoples in both New Zealand and Patagonia.

The potential for positive feedbacks from repeated burning therefore exists in all of these forests, but the long-term replacement of forest by shrubland is and was apparently less common in the Pacific Northwest than in New Zealand and Patagonia. We suggest four related explanations for this difference: First, the difference in flammability between closed-canopy forest and early-seral vegetation may be smaller in Pacific Northwest than in New Zealand and Patagonian mesic-dry forests. The diverse postfire community in the Pacific Northwest includes species that are not particularly flammable (e.g., *A. circinatum*), whereas nearly all of the early-seral species in the mesic-dry forests of the South Island of New Zealand and northern Patagonia are highly flammable (Fogarty 2001, Raffaele et al. 2011, Blackhall et al. 2014), which creates postfire vegetation that is somewhat similar in structure to dense chaparral.

Second, the more continental setting of the Pacific Northwest helps support climate patterns conducive to ignition and fire spread as compared with the other ignition-limited regions in which fuel-driven factors are often more important. The majority of the area burned in the Pacific Northwest occurs at times when the top-down influences of climate and weather override bottom-up fuel feedbacks. More than 90,000 ha of the 160,000-ha Tillamook Fire of 1933 in the Oregon Coast Range was burned in a 48-hour period of strong east (foehn) winds accompanied by very low relative humidity. Under such conditions, the direction

and rate of fire spread are probably insensitive to stand-level differences in microclimate and fuel loading that vary in relation to the time since previous fires. Although the southern hemisphere regions also experience extreme fire weather and large events (e.g., the Falso Granito fire in 1999 in Argentina), the bottom-up influences of fuels and microclimate seem to remain significant across a wider range of fire-weather conditions than do those in the Pacific Northwest. In New Zealand, recent fires have been generally confined to grasslands and shrublands and extinguished shortly after burning into closed-canopy *Nothofagus* forests (e.g., Wiser et al. 1997, Anderson et al. 2008); similar patterns of burning likely occurred in *Nothofagus*-podocarp forests in the past under most climate conditions. In Patagonia, there are also numerous examples of closed-canopy mesic-dry forest suppressing the spread of fires that began in adjacent tall shrubland, as well as a few examples of very large fires in extreme weather years in which even mesic forests burned (e.g., 1943–1944, 1999; Mermoz et al. 2005). Certainly, under extreme weather conditions, ancient *Nothofagus*-gymnosperm forests would have burned more extensively, but large weather-driven conflagrations are better documented and probably more common in the Pacific Northwest.

Third, the duration of the postfire shrub-dominated stage, and therefore, the time of peak flammability are shorter in Pacific Northwest forests than in the mesic-dry forests of the South Island of New Zealand and northern Patagonia (figure 4). Following high-severity fires, *Pseudotsuga* forests tend to reach canopy closure within about four decades (Tepley et al. 2014). The combination of numerous *Pseudotsuga* trees surviving within the fire perimeter and long-distance seed dispersal (up to about 400 m) typically results in high seedling densities of *Pseudotsuga* soon after even very large fires (e.g., Donato et al. 2009). In the New Zealand and Patagonia mesic-dry forests, peak flammability remains high for several decades after fire, according to empirical and model studies of modern and pre-European forests (Kitzberger et al. 2012, Perry et al. 2012a, Paritsis et al. 2014). *Nothofagus* regeneration is typically limited to areas within about 100 m of the fire perimeter, which allows fast recovery of small (tens of hectares) burned patches but very slow recovery following larger fires (Wiser et al. 1997, Mermoz et al. 2005).

Finally, burning at low and moderate severity is a more substantial component of the fire regime in the mesic-dry forests of the Pacific Northwest than those of New Zealand and Patagonia. In the Pacific Northwest, each fire typically produces a mosaic of patches of different burn severities, and a trend toward shorter fire intervals from wetter to drier parts of the region is associated with an increase in the coverage of low- and moderate-severity patches that retain partially or largely intact forest canopy (see appendix F of Tepley et al. 2013). The residual canopy patches buffer against repeated burning by moderating the local microclimate and providing seed sources for adjacent high-severity patches, thereby accelerating the return to closed-canopy conditions. *Pseudotsuga* exhibits multiple pathways

of recovery following fire, including the development of multi-cohort stands in patches burned at moderate severity and single-cohort stands in high-severity patches (Tepley et al. 2013). These pathways, in combination with the long lifespan of *Pseudotsuga* (more than 1000 years), ensure that the most fire-resistant tree species of the region persists as a component of nearly all forest stands.

In summary, the relatively short duration of the flammable early-seral vegetation stage and smaller differences in flammability between shrub stages and closed-canopy forests in the Pacific Northwest contrast with the flammability characteristics of early postfire stages in the mesic-dry forests of the South Island of New Zealand and Patagonia. Also different is the persistence of partially intact forest canopy in portions of most Pacific Northwest burned areas, which enable *Pseudotsuga* to rapidly colonize high-severity patches. Together, tree survival at various patterns and densities within the fire perimeter and the relatively rapid development of canopy closure in high-severity patches (Tepley et al. 2014) weaken any bottom-up feedbacks that might have been instigated by human-induced increases in fire ignitions. It is highly unlikely that a targeted ignition strategy in the Pacific Northwest would have resulted in large-scale forest conversion, because increases in postfire landscape flammability were less pronounced in the Pacific Northwest than in New Zealand and were too brief to initiate the positive feedbacks necessary to facilitate extensive forest loss.

Late-Holocene climatic controls on burning. This explanation posits that late-Holocene climate change functioned as an important driver of the differences in the effects of indigenous burning, and it is based on the idea that long-term trends in climate and climate variability in the three study regions gave rise to different vegetation and fire histories. Climate on millennial time scales is driven directly and indirectly by changes in the seasonal cycle of insolation and the influence of insolation on atmospheric circulation patterns and climate variability (Kutzbach et al. 1998). Persistent components of ocean-atmosphere variation—namely, the El Niño Southern Oscillation (ENSO) and the Southern Annular Mode (SAM)—strongly control fire activity in the southern hemisphere regions by promoting both fire weather and high fuel flammability (Kitzberger et al. 2001, Holz and Veblen 2011). In contrast, ENSO interannual variability is not as strong a predictor of the area burned in mesic-dry Pacific Northwest forests (Gedelov et al. 2005). Therefore, long-term variations in climate influence the links between fire climate and fire weather, as well as between the composition and distribution of vegetation (fuels).

In the Pacific Northwest, summer insolation was 8% higher than that of the early Holocene, and summers were longer (Kutzbach et al. 1998), which intensified and lengthened the fire season in general. Fires were more frequent prior to about 5000 years ago, and pollen data suggest that the forests shifted toward early- and intermediate-seral stages

(with more *Pseudotsuga*, *Alnus*, *Quercus*, and *Pteridium*), and woodland, prairie, and savanna were expanded compared with their present distributions (e.g., Whitlock et al. 2008, Walsh et al. 2010, Gavin et al. 2013). As summer insolation decreased in the late Holocene, summers became cooler and wetter. In the last 4000 years, the mesic-dry forests at the wet end show an increase in *Pseudotsuga*, *Tsuga*, and *Thuja* and a decrease in fire frequency and area burned; at the dry end, areas of woodland, prairie, and savanna were replaced by expanding conifer forests (Walsh et al. 2010). Human-set fires in the early Holocene would have reinforced the climate-driven trends in fire activity, whereas in the late Holocene, when modern mesic-dry forests were established, summer conditions were less conducive for fire, possibly increasing the motivation for burning strategies to maintain open landscapes.

In northern Patagonia, long-term climate variations are related to the strength and position of the Southern Westerlies and interannual variability driven by ENSO and SAM (Fletcher and Moreno 2011). Fires were widespread between 9000 and 12,000 years ago in all vegetation types, at a time when high levels of winter insolation and an attenuated pole-equator temperature gradient (i.e., a persistent La Niña-type pattern) shifted the westerlies south of their present position and weakened them (Whitlock et al. 2007). Unlike in the Pacific Northwest, a second period of high fire activity began approximately 3000 years ago in northern Patagonia on both sides of the Andes (Fletcher and Moreno 2011, Iglesias et al. 2014). The increase is attributed to overall wetter conditions than before, enhanced fuel development, warmer summers, and greater interannual variation in wet and dry conditions. Charcoal records at the dry end of the gradient show fluctuations in forest dominance between *Nothofagus* and *Austrocedrus* that are attributed directly to interannual climate variability and indirectly to the local effects of fire as a result of changing flammability (Iglesias et al. 2012). Tree-ring data also suggest a strong association between fire and ENSO variability and the positive phases of SAM in recent centuries (Kitzberger et al. 2001, Holz and Veblen 2011). Alternating dry and wet conditions in Patagonia apparently increased the severity of fires by shifting the vegetation toward more-flammable types and by increasing the frequency of fire-weather events. These long-term climate conditions were conducive to fires with or without people.

Charcoal records from the South Island of New Zealand indicate few fires in the late Holocene prior to human arrival, and those that occurred were mainly in drier, leeward montane regions or wetlands. A rise in fire activity about 3000 years ago is evident in some regions (e.g., Central Otago) and may have been related to a northward shift in the westerlies, increased interannual variability, and more lightning ignitions than before (Perry et al. 2014). On shorter time scales, fires during the initial burning period have not been associated with episodes of drought thus far (McWethy et al. 2010).

At large scales, climate explains much of the long-term variation in fire activity. In the Pacific Northwest, a late-Holocene trend toward cooler and wetter conditions reduced potential fire activity and led to the development of the current closed-canopy forest, which was less flammable than early-Holocene communities. On the South Island of New Zealand and in northern Patagonia, a contrasting trend toward warmer summers and increased interannual climate variability in the late Holocene enhanced the potential for fire (Whitlock et al. 2007, Fletcher and Moreno 2011). Although the climate was suitable for more fires, the mesic-dry forests of the South Island of New Zealand were ignition limited, and fire frequency remained low (Perry et al. 2014). In northern Patagonia, long-term summer warming and increased climate variability heightened fire activity. Late-Holocene climate trends potentially amplified the impacts of human-set fires in Patagonia and New Zealand, in contrast to the Pacific Northwest, where conditions became less conducive for fire with the onset of a cooler, wetter climate than before.

Differential use of fire in prehistoric time. Indigenous people use fire for a variety of reasons but most often to enhance vital resources and facilitate travel (Bowman et al. 2011). The extent of prehistoric burning is inferred from a variety of data sources: archeological evidence, estimates of population size and inferences of resource needs, changes in past vegetation and fire activity, ethnographic records, and early European accounts. Burning practices must be understood in light of the ecological constraints on fire use, as well as the socioeconomic context and benefit to human well-being. Observations of present-day hunter-gatherer groups (Bliege et al. 2012) suggest that the scale of prehistoric human impact was related to the time required to acquire resources, and deliberate burning strategies would have offered immediate benefit. Nonetheless, the archeological and ethnographic evidence is too sparse in our study regions to comment on subsistence strategies or human-set ignition frequencies.

In the Pacific Northwest, the archeological data indicate that low-density, highly mobile groups occupied the region prior to approximately 3000 years ago, after which settlement became semipermanent (Aiken et al. 2011). Subsistence strategies to support increasing populations and reduced residential mobility would have included greater investment in resources and processing technologies, some of which required the use of fire (e.g., *Camas* processing, berry gathering). Lake-sediment charcoal records with their decade- to century-scale time resolution do a poor job of detecting these types of burning activities and, as a result, general trends in past fire activity often do not match cultural changes inferred from archeological information. The lack of evidence for broadscale burning or synchronous fire events in multiple paleoecological records suggests that anthropogenic fires were small in extent and focused on managing or acquiring local resources. Humans likely

provided an added source of ignition in lightning-limited forests, but the overall fire history closely tracked Holocene climate variations, as was noted above.

Our understanding of prehistoric anthropogenic activities in the mesic-dry forests of northern Patagonia rests on very limited archeological data (e.g., Borrero 2008, Méndez et al. 2014) and a few observations by Europeans (for a summary, see Veblen and Lorenz 1988). An analysis of late-Holocene archeological sites in Chile indicated that hunter-gatherer groups lived in low densities primarily along the steppe margin and accessed mesic-dry forests on a nonpermanent basis to gather resources from lakes and hunt in forest and high grasslands. Zooarcheological studies indicate local rather than broad-ranging foraging strategies (Méndez et al. 2014), and fire may have been a tool for hunting guanaco, rhea, and huemul. Increased fire activity in mesic-dry forests around 3000 years ago may be related to late-Holocene climate change, but it also coincides with increasing populations and semipermanent settlement along the forest-steppe border and the Pacific coast (Borrero 2008). Increased ignitions at the hands of humans, coupled with seasonally drying fuels, would have facilitated fire frequency and spread. European explorers and missionaries reported fires set by indigenous peoples at the lower tree line, and early settler accounts and tree-ring evidence suggest that small forest patches were burned (Veblen and Lorenz 1988). As in the Pacific Northwest, evidence and narratives suggest that the extent and frequency of anthropogenic fires in closed-canopy mesic-dry forests was limited.

In contrast to the other regions, New Zealand experienced an extensive loss of forest soon after human arrival as a result of fire. Archeological evidence from the South Island provides little direct information on the motivation, but modeling experiments suggest that targeted ignitions on dry and flammable vegetation types facilitated the magnitude of the forest transformation that occurred (Perry et al. 2012b). Widespread deforestation was accomplished in the first few centuries after Māori arrival, and this initial burning period (approximately 800–500 calendar years ago) lasted only a few decades at individual sites (McWethy et al. 2014). From the initial burning period into the nineteenth century, Māori used fires for hunting birds, including moa, and to maintain *Pteridium* and other plants (McGlone et al. 2005). European settlers set fire to previously burned successional forests and closed-canopy forests in order to promote pasturelands, thereby enlarging the area of nonforested vegetation (Perry et al. 2014). Although the mesic-dry forests are not inherently unburnable, the addition of human ignitions, especially ones targeting the most flammable vegetation, seems to be crucial in explaining the vegetation transformation.

Conclusions

A long-standing debate in the human-environment literature concerns the extent to which temperate forests were subject to extensive human modification in prehistoric times and the impact that such burning had on

vegetation dynamics (Bowman et al. 2011). Views on this topic shape public values and scientific research, influence fire policy, and guide conservation strategies. Hunter-gatherers, pastoralists, and farmers have used fire differently throughout human history, and their influence on biomes and fire regimes has also differed. The archeological and ethnographic evidence about the indigenous use of fire is limited in mesic-dry forested regions, and this is a major source of uncertainty that requires future research. Extreme views would hold that prehistoric humans exerted no control over the frequency, location, or timing of their ignition practices (i.e., ignitions were random) or that humans tried to exert the maximal amount of effort toward the transformation of particular fire regimes and vegetation (i.e., ignitions were targeted for the specific purpose of deforestation). Neither assertion is congruent with the evidence presented here. On the one hand, human efforts to modify vegetation were at least partially constrained by moisture conditions at the wet end of the gradient (figure 1). On the other hand, the motivation and ability to alter vegetation were shaped by ecological constraints on fire use, the socioeconomic context of costs and benefits, and the ecological sensitivity of the forest to changes in disturbance regime. In other words, human subsistence strategies must be understood in light of the vegetation and natural fire regime, population density, and available resources and technologies, and this suite of variables defines the scale of anthropogenic influence on the landscape at any given time. In the case of New Zealand, deliberate burning by small populations initiated positive feedbacks that resulted in the loss of over 40% of the native mesic-dry forest. In contrast, in the Pacific Northwest, prehistoric human-set fires had only limited impact in mesic-dry forests, even though late-Holocene human populations were relatively large. In Patagonia, the use of fire by small, dispersed populations prior to European arrival also did not result in extensive forest loss.

We suggest that the interaction of ecological, climatic, and human factors explains the different impacts of prehistoric anthropogenic burning in these three settings: First and foremost, the capacity of fires to transform large forested areas into nonforested vegetation varied as a result of differences in the fire sensitivities of the dominant tree species. *Pseudotsuga* is well adapted to persist in fire-prone environments through a set of plant functional traits and adaptations to fire. In essence, the mesic-dry forests in the Pacific Northwest respond to fire through the persistence of forest cover in patches that burned at low and moderate severity and through the relatively rapid recovery of closed-canopy conditions after high-severity fire. Resistance of mature *Pseudotsuga* to even moderate-severity fires and rapid recolonization of seedlings after high-severity fires help create a complex mosaic of age classes and stand structures. In contrast, fire-adaptation traits are largely absent in southern hemisphere mesic-dry forests dominated by *Nothofagus* and gymnosperms. As a result, the forests of the South Island of

New Zealand and those of northern Patagonia were more vulnerable to anthropogenic burning.

Second, because early-seral vegetation in the Pacific Northwest typically returns to closed-canopy forest within a few decades after fire, it would have been difficult to sustain extensive areas in a nonforested condition. In contrast, *Nothofagus*-gymnosperm forests are converted to highly flammable early-seral communities dominated by tall shrubs (and ferns in New Zealand) after fire, and these communities persist for several decades. This longer time interval would have afforded indigenous peoples multiple opportunities to reburn. The initiation and maintenance of a positive feedback loop between fire and flammable communities in New Zealand led to rapid forest loss. In Patagonia, a similar positive feedback loop is evidenced by the rapid transformation of the forest by Europeans—in particular, in association with annual to decadal drought.

Third, the late-Holocene climate conditioned both the development of modern vegetation and fire regimes and the effectiveness of anthropogenic ignitions to alter fire potential and forest dynamics beyond that expected from lightning-ignited fires alone. Late-Holocene climate variables of importance to long-term fire occurrence are the interhemispheric differences in the timing of the seasonal cycle of insolation and the stronger interannual climate variability in the southern hemisphere than in the Pacific Northwest. Rising summer insolation in the southern hemisphere led to a longer fire season, and alternating wet and dry periods created weather and fuel conditions for fire ignition and spread. The concurrent establishment of a cooler, wetter climate than before in the Pacific Northwest reduced the number of natural ignitions and decreased fuel flammability. As a result, the area burned was small in the Pacific Northwest except during dry years and under extreme fire weather conditions. Deliberate burning in that region would have been most effective in stalling forest advancement into more-open landscapes that offered important and diverse resources.

Finally, prehistoric people likely increased ignition frequency in all regions. The ecological impact of added ignitions was shaped by the traits of the key forest taxa and the trajectory of postfire vegetation recovery. In New Zealand, the consequences were particularly striking, because lightning-ignited fires accounted for little of the area burned. In contrast, in the Pacific Northwest and northern Patagonia, the impact of human-ignited fires on the forests was mostly indistinguishable from those driven by natural ignition patterns, and the climate and human drivers of past fire activity are difficult to separate. Prehistoric anthropogenic burning in the Pacific Northwest and Patagonia was either localized and limited or not ecologically significant, at least at the resolution at which paleoecological records can detect environmental change.

It is possible that early humans in Pacific Northwest and Patagonia instigated an initial burning period like that of New Zealand soon after their arrival, but there is no evidence of this, and the cool conditions and sparse vegetation

of the late-glacial period were not conducive to fires or positive fire-vegetation feedbacks. These constraints would have prevented the occurrence of a broadscale short-lived fire episode or a major fire-induced vegetation transformation. The severity of the initial burning period in New Zealand may also have been magnified by the fact that it is a forested island and the Polynesian colonists were familiar with fire (Kirch and Kahn 2007). Strategies for deliberate burning combined with the effects of increased ignition on a highly vulnerable native forest led to dramatic consequences. In contrast, the early human populations in the Pacific Northwest and Patagonia found resources in the adjacent steppe and woodland environments that did not require such burning strategies.

Charcoal-based compilations of biomass burning at a global to regional scale tend to underplay the nonsynchronized activities of local human populations and invariably point to climate as the primary driver of past fire activity, whether in the western United States, Australasia, or southern South America (see Marlon et al. 2013). In global syntheses, climate's role is only attenuated in the mid-eighteenth and early nineteenth century with European settlement and land-cover changes (Marlon et al. 2008). We suggest that an examination of fire history at regional to local scales is an essential component of global analyses of biomass burning, because these finer scales disclose the critical dynamics and feedback mechanisms that lead to vegetation change. In other words, regional to local examinations are needed in order to understand the role of humans and environmental change in altering fire regimes in different biophysical settings, both in the past and present. The three closed-canopy temperate forest ecosystems examined here suggest that the characteristics of *Pseudotsuga* were largely responsible for the weak signal of prehistoric anthropogenic burning in the Pacific Northwest. In contrast, forests in similar biophysical settings but dominated by *Nothofagus* and gymnosperms were vulnerable to changes in fire frequency and severity with the arrival of the Māori in the South Island of New Zealand and Europeans in northern Patagonia. The New Zealand story is particularly compelling, because deforestation of sites was accomplished rapidly by small transient populations employing targeted ignition strategies over broad areas, and the event happened so recently that the ecological consequences are still significant.

Much attention is given to natural and human-driven changes in fire regimes in dry (fuel-limited) forest and grassland (Lehmann et al. 2014), but future climate change will also have a significant influence on wet and transitional forests toward the other end of the moisture spectrum (Krawchuk and Moritz 2011). These forests have abundant fuel, but fire is naturally rare; they are also regions in which human populations are expanding rapidly. Increased burning in these forests is capable of creating multiple stable states that may be difficult to reverse, and restoration may require the exclusion of fire or any process that acts to increase fire frequency or intensity. Understanding the

long-term sensitivity of temperate forests to fire is essential if we are to appreciate the full range of fire conditions and forest responses possible under different climate and land-use scenarios.

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