Global Ecology and Biogeography A Journal of Macroecology

RESEARCH REVIEW

A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes

D. B. McWethy[1]*, P. E. Higuera[2], C. Whitlock[1,3], T. T. Veblen[4], D. M. J. S. Bowman[5], G. J. Cary[6], S. G. Haberle[7], R. E. Keane[8], B. D. Maxwell[9], M. S. McGlone[10], G. L. W. Perry[11,12], J. M. Wilmshurst[13], A. Holz[5] and A. J. Tepley[4]

[1]*Department of Earth Sciences, Montana State University, Bozeman, MT 59717, USA,* [2]*College of Natural Resources, University of Idaho, Moscow, ID 83844-1133, USA,* [3]*Institute on Ecosystems, Montana State University, Bozeman, MT 59717, USA,* [4]*Department of Geography, University of Colorado, Boulder, CO, USA,* [5]*School of Plant Science, University of Tasmania, Hobart, Tas., Australia,* [6]*Fenner School of Environment and Society, The Australian National University, Canberra, ACT, Australia,* [7]*Centre for Archaeological Research, Department of Archaeology and Natural History, College of Asia and the Pacific, The Australian National University, Canberra, ACT, Australia,* [8]*USDA Forest Service Rocky Mountain Research Station, Fire Modeling Institute, Missoula, MT, USA,* [9]*Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT, USA,* [10]*Department of Biodiversity and Conservation, Landcare Research, Lincoln 7640, New Zealand,* [11]*School of Environment, University of Auckland, Private Bag 92019, Auckland, New Zealand,* [12]*School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand,* [13]*Landcare Research, Lincoln 7640, New Zealand*

*Correspondence: Dave McWethy, Department of Earth Sciences, Montana State University, Bozeman, MT 59717, USA.
E-mail: dmcwethy@montana.edu

ABSTRACT

Aim The increased incidence of large fires around much of the world in recent decades raises questions about human and non-human drivers of fire and the likelihood of increased fire activity in the future. The purpose of this paper is to outline a conceptual framework for examining where human-set fires and feedbacks are likely to be most pronounced in temperate forests world-wide and to establish and test a methodology for evaluating this framework using palaeoecological records.

Location Tasmania, north-western USA, southern South America and New Zealand.

Methods We outline a conceptual framework for predicting the sensitivity of ecosystems to human impacts on fire regimes and then use a circum-Pacific comparison of existing historical reconstructions of fire, climate, human settlement and vegetation to evaluate this approach.

Results Previous research investigating important controls on fire activity shows that the sensitivity of temperate ecosystems to human-set fires is modulated by the frequency of natural fire occurrence, fuel moisture and fuel type and availability. Palaeoecological data from four temperate regions suggest that the effects of anthropogenic burning are greatest where fire is naturally rare, vegetation is poorly adapted to fire and fuel biomass is abundant and contiguous. Alternatively, where fire activity is naturally high and vegetation is well adapted to fire, evidence of human influence on fire and vegetation is less obvious.

Main conclusions Palaeofire records suggest that the most dynamic and persistent ecosystem transitions occur where human activities increase landscape flammability through fire–vegetation feedbacks. Rapid forest transitions in biomass-rich ecosystems such as New Zealand and areas of Tasmania and southern South America illustrate how landscapes experiencing few fires can shift past tipping points to become fire-prone landscapes with new alternative stable state communities. Comparisons of palaeoecological data from different regions with similar biophysical gradients but different human settlement histories can provide new opportunities for understanding ecosystem vulnerability to fire–climate–human interactions.

Keywords
Biome sensitivity, climate, fire regimes, global change, human impacts, tipping points.

DOI: 10.1111/geb.12038

INTRODUCTION

Fire influences nearly all biomes of the world and plays a critical role in transferring carbon from the terrestrial biosphere to the atmosphere. Despite its importance, the drivers of fire and its ecosystem consequences over a range of temporal and spatial scales remain poorly understood. In recent decades, fire activity has increased in many temperate forests world-wide, even in ecosystems where natural ignitions are scarce, and this increase begs questions of whether climate change, human ignitions, land-use change and/or altered vegetation are responsible. Some of the largest fires occur in forests that are highly vulnerable to climate change, have little natural resilience to fire and are undergoing rapid land-use change (Meyn *et al*., 2007). The increased frequency of large fires has been attributed to drier than average summers and longer fire seasons (e.g. Westerling *et al*., 2006), and recent severe drought and increased plant mortality have exacerbated fire hazard, raising concerns about the trajectory of post-fire vegetation dynamics and future fire regimes (van Mantgem *et al*., 2009). Compounding the climatic drivers of fire are forest clearance, fire suppression and related fuel changes, invasion by exotic fire-prone plants and livestock grazing.

A number of recent studies have revisited alternative stable state theory to explain dynamic shifts in the distribution of forest and non-forest systems, many suggesting that abrupt changes in fire frequency often result in rapid transitions between seemingly stable vegetation states (Staver *et al*., 2011; Kitzberger *et al*., 2012). These studies illustrate the role of fire in maintaining multiple vegetation states through promoting and reducing landscape flammability depending on the starting point (Fig. 1). Palaeoecological studies from lake-sediment, tree-ring and anthropological records have revealed critical linkages among fire, vegetation, human activities and climate that cannot be inferred from modern observations alone. This research offers unique opportunities to consider climate–fuel–ignition feedbacks under different states of climate, vegetation and human influences across multiple temporal and spatial scales, and, coupled with conceptual models, it provides critical context for understanding dynamic vegetation transitions and vulnerabilities to future change.

A suite of biophysical conditions is required for fire to ignite and spread, and the significant driving variables change with spatial and temporal scale (Whitlock *et al*., 2010). At fine scales, fire requires a heat source, oxygen and fuel. At the scale of an individual fire event, weather, fuels and topography influence the rate of fire spread and intensity (Rothermel, 1972; Sullivan *et al*., 2012). A fire regime comprises the pattern of fire activity (e.g. fire frequency, intensity, seasonality and type) at landscape to regional spatial scales and decadal to centennial temporal scales (Gill, 1975); and more broadly, fire's role in an ecosystem (Krebs *et al*., 2010). At broader scales is the concept of a metafire regime, defined as the ensemble of fire regimes that characterize a biome during the duration of its existence (Whitlock *et al*., 2010).

Fires are frequent where flammable fuels are abundant, ignitions are frequent and weather conditions are conducive to fire spread (Krawchuk *et al*., 2009). Climate affects fuel characteristics (vegetation type, fuel moisture, continuity and abundance), rates of natural ignitions and fire weather (precipitation, humid-

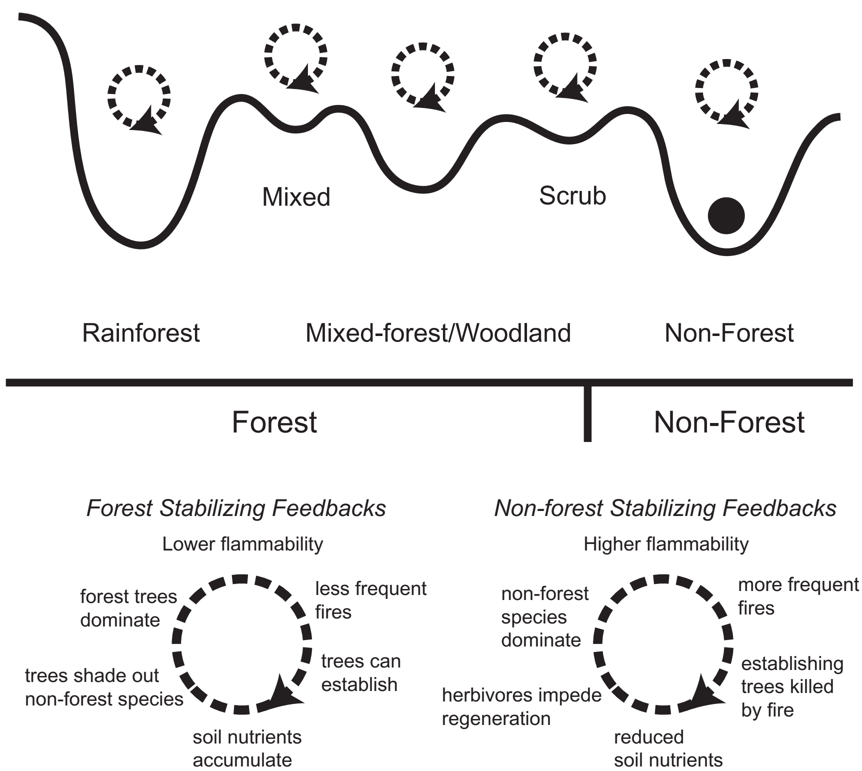

Figure 1 Conceptual model of vegetation dynamics (originally developed for south-west Tasmania) illustrated with the 'ball and cup' (or 'stability landscapes') commonly used to describe alternative stable states (ISLSCP2; Olson *et al*., 2001). In Jackson's 'alternative stable states' model, each vegetation community can occupy any possible underlying environmental setting. Each vegetation state is represented as resilient 'basins of attraction' that are modified by the effects of fire–vegetation–soil feedbacks. The community is initially resilient to disturbance by fire and will return to the original state, but if pushed beyond the threshold by repeated stand-replacing fires (or lack thereof), positive feedbacks from the alternative stable state will take over and the system will undergo transition to another stable state (Warman & Moles, 2009). Figure adapted from Wood & Bowman (2012).

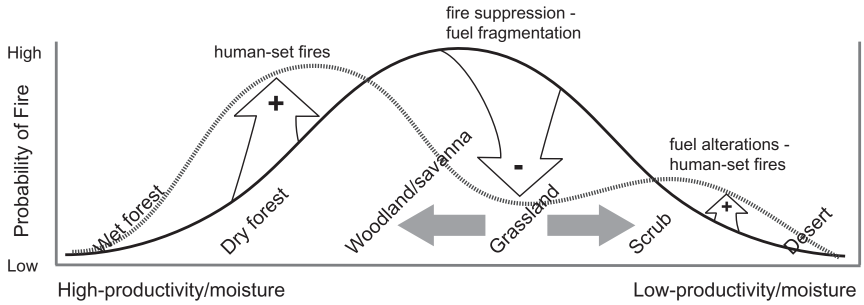

Figure 2 Human influence on fire activity along a productivity/moisture gradient. The natural or background distribution of fire activity (i.e. frequency and area burned; solid black curve) can be altered by human impacts via increasing ignitions, actively suppressing fires, and altering vegetation by introducing new plants and land-use activities (e.g. promoting grazing, clearing forests) (modified from Whitlock *et al*., 2010; Krawchuk & Moritz, 2011). The dashed line indicates how human impacts can alter the natural distribution of fire activity, in some cases resulting in a persistent shift in biome type. For example, active suppression of fires in grassland biomes can result in a shift to woodland/savanna or scrub biomes depending on how this activity interacts with climatic controls and land use impacts on vegetation structure and composition.

ity, air temperature and wind conditions). High-productivity/high-moisture (e.g. net primary productivity) fire regimes are supported by abundant, connected fuels, but fuel moisture is generally too high to allow for fire spread (Bradstock, 2010). In these systems, large fires occur during unusually dry years, when low fuel moisture and fire weather promote rapid fire spread (e.g. Bessie & Johnson, 1995). In less productive, drier, fuel-limited ecosystems, sparse or discontinuous fuels impede fire spread, even where low fuel moisture and weather conditions are suitable for burning. Hence, at extremes of productivity and environmental moisture gradients, fires are limited either by sparse, discontinuous plant cover (e.g. deserts) or by high fuel moisture (e.g. rain forests) (Krawchuk & Moritz, 2011).

Humans have altered fire regimes for millennia, although their ultimate impact relative to climate alone is still contested (Bowman *et al*., 2011). Human actions include igniting fires when and where they were naturally rare, modifying fuel composition and structure, synchronizing ignitions to match times of low fuel moisture and suppressing or eliminating fires (Fig. 2; Whitlock *et al*., 2010). Although it is widely known that dense, agricultural-based populations significantly altered past fire regimes and vegetation, evidence suggests that strong deviations from natural fire activity are also related to cultural practices and land-use histories linked to small, nomadic populations (e.g. Bush & Silman, 2007). Pre-European deforestation of island environments demonstrates that even small, mobile populations were able to transform large landscapes through the use of fire (e.g. McWethy *et al*., 2010). The role of humans in altering past and present fire regimes centres on three questions: (1) Which settings are most vulnerable to shifts in fire regimes resulting from human activities? (2) Where have humans promoted fire where it would not otherwise occur? (3) At what scales are human influences most relevant?

Anthropogenic alteration of natural fire regimes has been greatest in high-productivity/moisture environments where fuels are abundant and natural ignitions are infrequent or asynchronous with times of low fuel moisture, and in low-productivity/moisture environments, where fuels are limiting (Fig. 3; Bowman *et al*., 2011). In high-productivity/moisture environments, spatial targeting of ignitions in more flammable, early-seral vegetation can initiate feedbacks that increase the amount of flammable vegetation and fire activity across the landscape promoting irreversible change in the vegetation (Kitzberger *et al*., 2012; Perry *et al*., 2012b). Ignitions deliberately timed to coincide with weather conducive to fire spread have amplified and extended the duration and intensity of the natural fire season (Holz & Veblen, 2011). In ecosystems where fire is fuel limited, introduced non-native species have increased fuel continuity and fire spread (Miller *et al*., 2010). In many intermediate-productivity grassland/savannas, anthropogenic ignitions have shifted the spatial distribution and timing of fires to reduce fire risk (i.e. spread), but deliberate burning has generally not altered natural fire frequency or area burned (van Wilgen *et al*., 2004). Human activities at the tails of the productivity/moisture gradient result in strong positive feedbacks that alter fuel conditions and landscape flammability. Our objective here is to outline a conceptual framework for understanding ecosystem sensitivity to human influence on fire regimes with particular attention to feedbacks driving widespread forest transitions in more productive forest ecosystems. To evaluate this framework we draw upon examples from four temperate forest regions in a circum-Pacific region: the northwestern United States, southern South America, Tasmania and New Zealand.

HYPOTHESES

We propose that efforts to disentangle human versus climate drivers of past fire regimes can advance by examining the effects of climate and humans across a productivity/moisture gradient:

Drivers of fire activity

H1a: At millennial to centennial scales, fire activity is governed by both long-term variations in climate and decadal- to

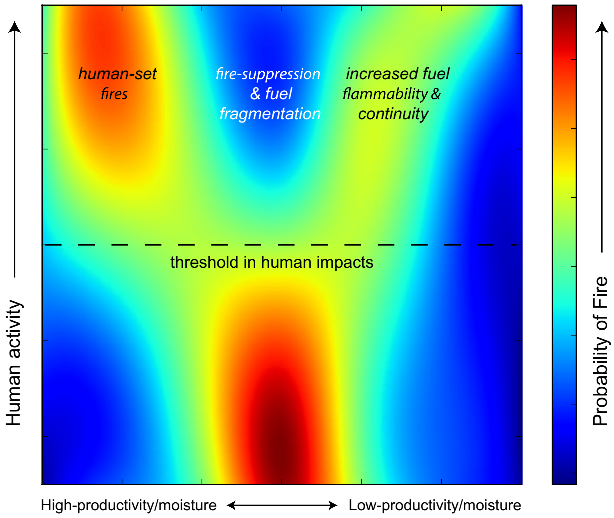

Figure 3 Hypothesized distribution of fire activity in relation to a productivity/moisture gradient (*x*-axis) and increased human activity (left *y*-axis). Probability of fire (right *y*-axis) is defined as the likelihood of ignition and fire spread. In the absence of human activity (y = 0), background fire activity is greatest (red = high fire activity, blue = low fire activity) where fuel is abundant and continuous and variation in climate provides seasonally dry fuels (centre of *x*-axis, e.g. grassland/savannas). Fire activity is low where fuel moisture is consistently high and/or ignitions are infrequent or asynchronous with conditions conducive to fire spread and where fuels are sparse or discontinuous (far left and right lower quadrants). Human activity has the greatest potential to increase fire activity in settings where fuels are abundant and fire activity is naturally low (upper left quadrant); here, targeted ignitions in time and space can initiate feedbacks that promote the development of fire-prone landscapes.

interannual-scale climate variability, which directly affect fire-conducive climate and weather, and indirectly shape fuel composition and structure.

H1b: Departures from the expectations imposed by climate can be ascribed to non-climatic variables, such as land-cover change, human-set ignitions, edaphic controls and interactions among these variables (Fig. 4).

Sensitivity of vegetation to anthropogenic alteration of fire regimes

H2: The importance of non-climatic controls on fire regimes varies across gradients of productivity (e.g. net primary productivity) and moisture (Fig. 4; Bowman *et al.*, 2011).

H2a: Fire regimes in high-productivity/moisture systems are most sensitive to human influences because human activities can create conditions that overcome or reinforce natural limits on fire. Deliberate fires in these settings may initiate positive feedbacks that maintain highly flammable, early-seral vegetation and prevent development of less flammable, late-seral vegetation (Kitzberger *et al.*, 2012). In these settings, humans may also target ignitions to coincide with times that abundant, but normally wet biomass, is available for burning [e.g. periods of drought related to interannual variations in climate such as El Niño–Southern Oscillation (ENSO)]. Alternatively, human activity can limit fires in these settings through fire suppression and landscape fragmentation.

H2b: Fuel-limited systems are most sensitive to the introduction of non-native plants that increase fuel continuity and/or flammability, and to interannual variations in climate that can increase fuels in one year, and then promote fire through fuel-drying in the following year (e.g. ENSO). Human-set fires that are synchronous with periods of abundant flammable fuels can have dramatic impacts on fire activity (Bradstock, 2010).

H2c: Abundant and continuous fine fuels promote high fire activity in intermediate-productivity/moisture settings, such as in woodland or forest–steppe ecotones. Human-set fires alter the timing of fires but do little to increase fire frequency in these fire-prone settings. Fire suppression and landscape fragmentation may decrease fire activity.

CIRCUM-PACIFIC COMPARISON

Changes in fire regimes following pre-European human and European arrival in temperate high-productivity regions (Fig. 4, Table 1) illustrate how our conceptual framework and hypotheses can be evaluated. The approach builds on and complements palaeofire reconstructions within particular regions and those under way at a continental and global scale (e.g. Marlon *et al.*, 2009). We seek to identify where background fire activity deviates from a system driven by climate alone (H1a) by comparing biophysical gradients, flammability traits of native vegetation and records of past fire, vegetation and climate, and examine where humans have had the greatest influence in shaping past fire regimes (H1b). While palaeofire records themselves cannot identify the causal mechanisms of past fire activity, comparing fire–climate–human relationships across four temperate forest regions helps evaluate alternative hypotheses about the sensitivity of fire regimes to human activity. Ultimately, landscape-scale fire and ecosystem modelling, which can isolate and test alternative mechanisms linking climate, vegetation, humans and fire, are necessary to help infer potential mechanisms causing past changes.

The mid-latitude forests of Tasmania, North and South America and New Zealand lend themselves well to such a comparison because they feature: (1) similar gradients in key fire controls such as productivity and climate; (2) different durations and intensities of human use; and (3) contrasting flammability traits in the native vegetation that shape the natural fire regime (Fig. 5, Table 1). In general, each region supports a west-to-east moisture gradient with wet forests experiencing low ignition frequencies and resource-focused pockets of human settlement in the west, and non-forest grassland/scrubland ecosystems with high natural ignition frequencies and more intense land use in the east.

The regions have different histories of human arrival, occupation and prehistoric land use, with people present first in

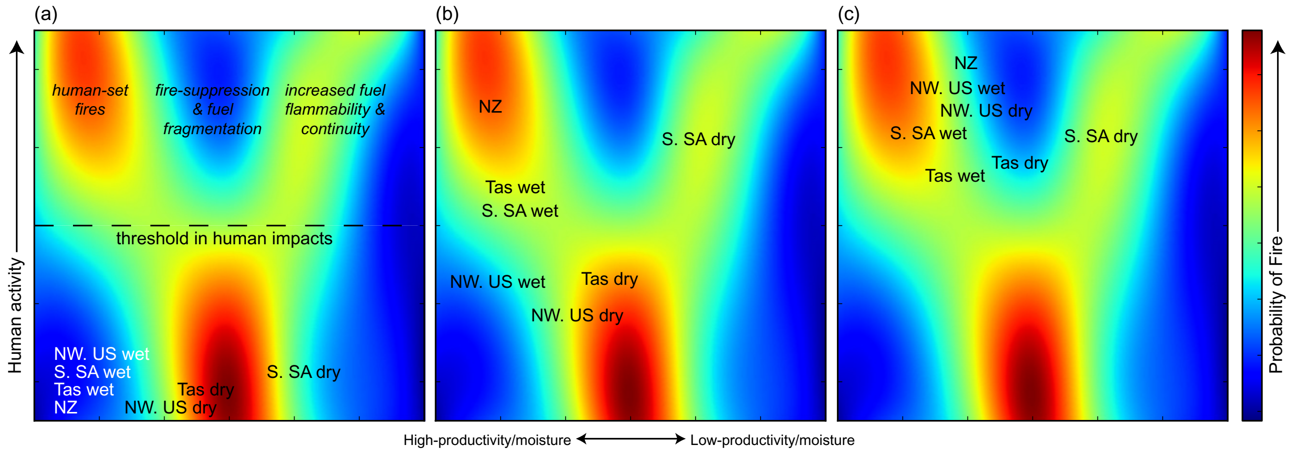

Figure 4 Hypothesized fire activity (probability of fire ignition and spread, right *y*-axis) at sites in New Zealand (NZ), Tasmania (Tas), north-western United States (NW. US) and southern South America (S. SA) along gradients in productivity/moisture (*x*-axis) and human presence (left *y*-axis) for pre-human (a), early-human (b) and European era (c) fire regimes. We identify a threshold at which human activity strongly alters natural fire regimes, whether through increased ignitions, fire suppression or shifts in fuel type, abundance and availability.

Tasmania *c.* 35,000 cal. yr BP (Cosgrove, 1999), in the Americas and Patagonia by 12,000 cal. yr BP (Borrero, 1999; Meltzer, 2009) and in New Zealand only in the last 700–800 years (Wilmshurst *et al.*, 2008). In all regions, the influence of Europeans on fire regimes was most profound in the 19th and 20th centuries.

Tasmania

Tasmania, to the south of mainland Australia, receives high annual rainfall on its west coast, has a somewhat drier climate in the interior lowlands due to a rain shadow effect and experiences a more seasonal and drier climate on its east coast. The geology of the island results in infertile soils (quartz-rich bedrock) on the rugged west coast to more fertile soils (e.g. dolerite bedrock) on the central and eastern half of the island. Both climate and edaphic controls create a vegetation mosaic of buttongrass moorland (sedge- and low-shrub-dominated vegetation of poorly drained sites), *Nothofagus* (southern beech) temperate rain forest and tall eucalypt forests in the west. The midlands and east coast support dry eucalypt forests, heathlands and fire-sensitive *Callitris* forests. Charcoal and pollen records suggest that fires were infrequent in west coast rain forests prior to human arrival, but midland and east coast forests experienced more frequent, low-severity fires (Fig. 4a; Fletcher & Thomas, 2010).

Pre- and early human fire regime

Along the west coast, the mosaic of tall forest to moorland vegetation has been ascribed to fire–vegetation–soil interactions and a long history of Aboriginal occupancy (> 30,000 years, Cosgrove, 1999). Jackson (1968) and later Bowman (1986) and Fletcher & Thomas (2010) proposed that the co-occurrence of forest and treeless vegetation in western Tasmania arose from interactions among fire-resistant and fire-prone vegetation related to anthropogenic burning. However, current assessments suggest that millennia without fire are required for buttongrass moorland to convert to forest (Wood & Bowman, 2012). It remains unclear if aboriginal burning created the current vegetation patterns in western Tasmania, or if aboriginal-set fires simply maintained vegetation patterns resulting from late Pleistocene and Holocene climatic changes (Wood & Bowman, 2012). Likewise, anomalous grasslands on fertile substrates may be the legacy of sustained aboriginal fire use, possibly maintaining Pleistocene plant communities (Gammage, 2008; Bowman *et al.*, 2012).

European fire regime

European colonization of Tasmania and subsequent land clearance and settlement resulted in an initial increase in fire activity, potentially amplifying the influence of drought linked to inter-annual ENSO variability (Nichols & Lucas, 2007). Even with more intensive land use, Tasmania's wet forests experienced infrequent fires because of strong climatic controls on fire spread (H1a; Fig. 4c) but were more vulnerable to human-set fires than the fuel-limited regions of eastern Tasmania where fire closely tracks ENSO variability (H2b,c; Fig. 4c).

In western Tasmania, the prevalence of sharp boundaries between fire-prone moorlands and fire-sensitive forests suggest that early human activities may have played a large role in altering fire regimes and vegetation (H2a; Fig. 4b). Alternatively, in open grassland/savannas and drier eucalypt forests found in Tasmania's midlands and east coast, early human-set fires, while potentially frequent, appear less ecologically significant (H2b,c; Fig. 4b). With a long history of human presence, the challenge remains to clarify the scale at which human activities altered fire and vegetation from conditions governed by climate alone.

Table 1 Human-settlement and biophysical gradients represented by palaeodata used in this study. Monthly temperature and precipitation data are from the Climate Research Unit (New *et al.*, 1999), and net primary productivity (NPP) data are from the International Satellite Land-Surface Climatology Project II (ISLSCP2; Olson *et al.*, 2001).

Gradient/parameter	Tasmania	North-western United States	Southern South America	New Zealand
Early human occupation (years)	> 30,000	> 12,000	12,000	800
European occupation (years)	200	200	500	200
Predominant early human economy	Hunter-gatherer	Hunter-gatherer/localized intensive cultivation	Hunter-gatherer/localized intensive agriculture	Localized intensive cultivation (the North Island), hunter-gather (the South Island)
Total annual precip. (mm) min.-max.	744–2226	373–2974	250–2508	643–4076
Mean temp. of the warmest month (°C) min.-max.	18–22	17–31	12–27	18–25
NPP (gC m^{-2} $year^{-1}$) min.-max.	661–911	177–857	190–962	356–1039
Historical fire regimes				
Pre-human	Infrequent, small, and mostly ecologically insignificant fire activity in west and more frequent fires in mixed forests and non-forest in east	Infrequent, stand-replacing fires in subalpine and mixed conifer forests; frequent low-intensity surface fires in drier environments	Infrequent, small and mostly ecologically insignificant fire activity in the west and more frequent fires in mixed forests and non-forest in the east	Infrequent, small, and mostly ecologically insignificant fire activity with slightly more frequent fires in the east
Early human	Frequent, deliberate targeting of fires increased distribution of buttongrass moorlands in the west, forest/non-forest mosaic elsewhere	Localized burning targeting expansion of valley grasslands and forest margins – larger impact debated	Frequent but localized targeting of fires in wet forests increasing distribution of non-forested environments, scale of transitions still unclear	Dramatic increase in fire activity resulting in conversion of forest to non-forest
European settlement	Expansion of early-human deforestation followed by recent fire suppression	Large and severe fires follow timber harvests *c.* early 1900s followed by recent fire suppression	Expansion of deforestation to increase pasture followed by recent fire suppression	Expansion of early-human deforestation followed by recent fire suppression *c.* 1970s

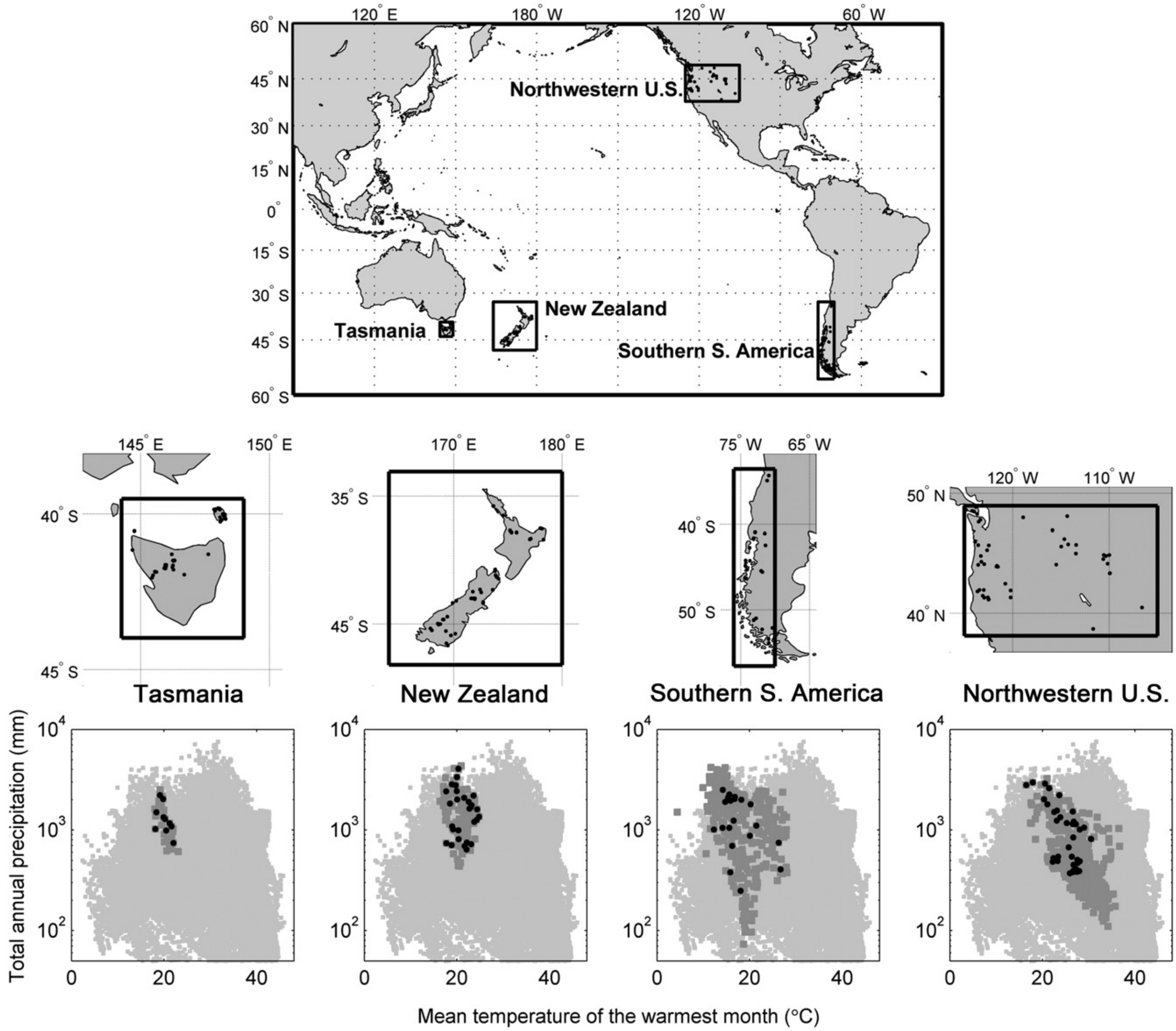

Figure 5 Location of paleofire records from four regions (black dots) in geographic space (top and middle rows) and climate space. Rectangles within maps identify each study region, and black dots indicate sediment charcoal records included in Version 2 of the Global Charcoal Database and additional sites targeted for future sampling. Climate space plots (Daniau *et al.*, 2012) include each site (black dots), all land within each study region (dark grey squares) and all land across the globe (small, light grey squares), plotted using the biophysical variables most important for global fire activity. Monthly temperature and precipitation data are from the Climate Research Unit (bottom row; similar to Marlon *et al.*, 2008) and have a spatial resolution of 0.5°.

North-western United States

The north-western United States is a large, diverse region hosting multiple mountain systems. In general, climate varies widely from the Pacific slope, where mesic forests of *Pseudotsuga, Tsuga*, *Picea* and *Thuja* dominate, to the interior northern Rocky Mountains, where strong elevational gradients support wet-to-dry coniferous forests dominated by *Pinus*, *Picea*, *Abies* and *Pseudotsuga*. Prior to the arrival of humans (>12,000 yr BP), fire return intervals on the order of centuries, and large infrequent stand-replacing fires characterized subalpine forests, and frequent, low-severity surface fires shaped the driest low-elevation forests of ponderosa pine (*Pinus ponderosa*). In middle-elevation mixed-coniferous forests of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*) and western larch (*Larix occidentalis*), the pre-European fire regime was characterized by a mixture of surface and stand-replacing fires occurring at intervals from decades to centuries (Baker, 2009).

Pre- and early human fire regime

Palaeoecological records from wet forests of the west-side Cascades of Oregon and Washington suggest that late Holocene fire regimes have maintained much of the 'old-growth' forest in an intermediate successional state dominated by *Pseudotsuga* (Hemstrom & Franklin, 1982). Pre-European fire return intervals varied spatially along a climatic gradient with long fire intervals (i.e. several centuries) in wetter forests and shorter intervals (i.e. decades) in drier forests, and it is difficult to disentangle the relative influence of humans and climate, except to note that past fire activity has closely tracked changes in climate, suggesting a minor role for anthropogenic fires (Fig. 4b; Whitlock & Knox, 2002).

In the Rocky Mountains, hunter-gatherers were present for at least 12,000 years (Meltzer, 2009) but the extent and impacts of deliberate burning seem to have been spatially variable. High-elevation mesic conifer forests in Yellowstone, for example, where humans probably had minimal year-round presence, show variations in fire frequency that are consistent with climate change. Fires in these forests were more frequent during the early Holocene insolation maximum, when much of the region experienced warm and dry summer conditions (Millspaugh *et al*., 2000), and decreased in the last 7000 years as summers became cooler and wetter. There is little evidence that this climate-limited system was modified by human activities, except perhaps locally (Fig. 4b).

European fire regime

In general, across the north-western United States, EuroAmerican settlement resulted in increased fire activity in the late 19th century and early 20th century, followed by widespread suppression of fires and interruption of fuels by grazing through the mid 20th century, and then increased fire risk in recent decades, particularly in dry forests (Fig. 4c). Invasive grasses, forbs and shrubs have aggressively colonized recently burned forests at all elevations, and their life history (e.g. *Bromus tectorum*) has increased fire frequency in some locations. Logging and other land-cover changes, however, have fragmented the most flammable vegetation types and limited large fires to unusually dry years. Thus, the alteration of fuels and fire season with EuroAmerican land use has created feedbacks that perpetuate the presence of annual invasive plants.

Palaeoecological records from wet forests in the north-western United States indicate few natural fires in the last several millennia as a result of cooler wetter conditions in the late Holocene (Fig. 4a; Long *et al*., 2007). Prehistoric use of fire by hunter-gatherers may have been important in oak-dominated regions, but even there, their impact on the vegetation was local in scale (Walsh *et al*., 2010). Indigenous burning practices may have been more significant in shaping the fire regimes of mixed-conifer forests in the Rocky Mountains, but again examples point to local use of fire, not broad-scale burning. This localized use of fire by indigenous people stands in contrast to the large areas burned by EuroAmerican settlers (Fig. 4c).

Southern South America

Pre-human fire regime

In southern South America, westerly circulation and the Andes result in a steep rainfall gradient that supports wet forests and moorlands in the west and extensive grassland steppe ecosystems towards the east. Empirical research has documented that tall, closed *Nothofagus* forests inhibit fire spread, whereas post-fire successional communities dominated by resprouting shrubs (e.g. *Nothofagus antarctica*, *Schinus* spp.) are highly flammable (Mermoz *et al*., 2005; Veblen *et al*., 2011). Initial burning of tall *Nothofagus* forests that are dominated by obligate seeders is dependent on extreme drought, whereas tall shrublands are highly flammable under less severe drought. As in the north-western United States, palaeoecological data suggest shifts from fuel-limited fire regimes in the early Holocene to climate-limited fire regimes in the late Holocene, as a result of climate-driven vegetation changes (Fig. 4a; Whitlock *et al*., 2007). In the early Holocene (c. 12,000 cal. yr BP) nearly all sites south of latitude 40° S on both sides of the Andes experienced higher fire activity than today, and this period of regional burning has been attributed to a weakening and southward shift of the westerlies in response to the annual insolation maximum (Huber *et al*., 2004; Whitlock *et al*., 2007).

Early-human fire regime

Humans have been present in the region for > 12,000 years (Borrero, 1999). Heusser (1990) claims a broad impact of human-set fires on the landscape; however, Huber *et al*. (2004) argue that the human impact was probably local. It is difficult to imagine widespread fires in Tierra del Fuego where natural ignitions are rare today, and humans may have been the critical source of ignitions in the early Holocene (H2a; Fig. 4b); alternatively, climate conditions then may have included more convectional storms than today. In most regions, fire activity declined with the expansion of closed *Nothofagus* forest in the late Holocene; however, the pattern of fire occurrence has been spatially heterogeneous in the last few millennia, which may relate to the local use of fire as opposed to broad-scale burning. For most of southern South America few records show clear evidence of human influence on patterns of pre-European anthropogenic fire.

European era fire regime

Europeans arrived in southern South America about 500 years ago, and were accompanied by increased fires as well as the introduction of non-native plant species (Huber & Markgraf, 2003). European settlement in the late 19th to mid-20th centuries greatly increased fire activity (Veblen *et al*., 1999; Holz & Veblen, 2011), and replacement of burned *Nothofagus* forests by resprouting shrubs has been further exacerbated by introduced herbivores (livestock, exotic deer and European hares) which impede the regeneration of the obligate seeding tree species (Raffaele *et al*., 2011). As in other regions, xeric woodlands on the east side of the Andes have experienced increased fuel accumulation as a result of land-use practices and fire suppression (Veblen *et al*., 1999).

Palaeoecological reconstructions of fire activity over the past several centuries show the importance of interannual to interdecadal climate variability related to ENSO and the Southern

Annual Mode (SAM) on both sides of the Andes (Kitzberger *et al.*, 1997; Veblen *et al.*, 1999; Holz & Veblen, 2012). European conversion of wet forests to shrublands, grazing and the spread of non-native plant species have increased landscape flammability, maintaining more fire-prone landscapes. In dry shrub ecosystems, the most evident human impact has been a reduction of fires due to pre-European depopulation and fire suppression (H2b; Fig. 4b & c). In recent decades, climate appears to be driving changes in fire activity as synchronous widespread fire activity is strongly linked to the intensification of interannual climate variability and associated drought conditions (Holz & Veblen, 2011). In addition, planting of introduced pines as well as invasion of the native vegetation by escaped pines is creating large areas of more homogeneous and highly flammable woody fuels over extensive areas of former steppe.

Examples from more productive and wet settings, such as Tierra del Fuego and western Patagonia, suggest that early human and European activities had a larger role in altering fire regimes and vegetation through increased fire activity than elsewhere in southern South America, where climate acted as the primary driver of changes in fire activity (H2a; Figure 4b). Land-use activities following European arrival have interacted with climate variability to alter landscape flammability, both promoting and inhibiting fire activity through fire suppression, grazing and the introduction of non-native plant species (Fig. 4c).

New Zealand

Pre-human fire regime

New Zealand has a maritime climate, with strong north–south temperature and east–west rainfall gradients as the primary broad-scale climatic controls on vegetation. Before initial human settlement in the 13th century AD (Wilmshurst *et al.*, 2008), forest covered 85–90% of the New Zealand landscape (McGlone & Wilmshurst, 1999). The palaeoecological record suggests that while fires occurred in New Zealand prior to Māori settlement they were too infrequent to have had a widespread ecological effect (Ogden *et al.*, 1998). With a few notable exceptions [e.g. *Leptopsermum scoparium* (mānuka) and *Kunzea ericoides* (kānuka)] New Zealand's plant species are poorly adapted to fire, with fire-stimulated resprouting, epicormic budding or germination being rare (Ogden *et al.*, 1998). New Zealand's woody ecosystems were, however, highly susceptible to fire and were probably ignition-limited rather than inherently non-flammable (McGlone, 2001; Perry *et al.*, 2012a). The rarity of pre-human fire in New Zealand was the consequence of the low rate of lightning and its association with high-rainfall frontal activity not conducive to ignition. Prior to human arrival, New Zealand's fire regimes were limited by infrequent ignitions that rarely occurred when and where fuels were sufficiently dry to facilitate fire spread (H1a; Fig. 4a).

Early-human fire regime

The arrival of humans dramatically altered New Zealand's forest landscapes, primarily via the introduction of fire. McWethy *et al.* (2009, 2010) describe an 'initial burning period' (IBP) which occurred asynchronously across the South Island between 700 and 500 years ago, depending on location. In regions that prehistorically supported forest, the IBP was characterized by a short period of intense fire and loss of forest. Pollen and charcoal records from the North Island tell a similar story (Wilmshurst *et al.*, 1997). The addition of fire to New Zealand's landscapes led to a dramatic transformation in vegetation, slope stability and limnology. In a period of 200 years or less 40–50% of New Zealand's forest cover was lost and converted to open shrubland and fernland, which in some regions has persisted until the present-day.

European fire regime

European settlement of New Zealand in the 19th century AD was accompanied by a second period of burning such that forest cover is now around 20% and rare in the lowland eastern areas. European fires and land use further expanded forest conversion to more flammable vegetation, although this trend was halted by active fire suppression in recent decades, with an average of < 6000 ha burned per year since 1991 (Anderson *et al.*, 2008) (Fig. 4c). In the last century, invasive pyrophytic non-native plant species, such as gorse (*Ulex europaeus*) and *Pinus* spp., have altered landscape flammability setting the stage for increased fire activity. Feedbacks between land use, non-native species and fire regimes in recent times are thought to be critical for explaining the persistence of fire-prone landscapes in New Zealand (Perry *et al.*, 2010) and fire risk is predicted to increase under future climate conditions (Pearce *et al.*, 2005).

The abrupt and widespread increase in fire activity following Polynesian arrival indicates a dramatic deviation from a strongly climate- and ignition-limited fire regime (H1b) and suggests that New Zealand's native, fuel-rich forests, were highly sensitive to landscape flammability feedbacks responsible for the forest transitions that persist today (H2a; Fig. 4b). European fires and land use further expanded forest conversion to more flammable vegetation, even though recent fire suppression limits the extent of fire spread (Fig. 4c).

DISCUSSION

In circum-Pacific temperate forests, the greatest human impacts, both prehistoric and European, occur where human activities initiate self-reinforcing feedbacks that alter landscape flammability and underlie alternative stable state theory as described in seminal studies by Sauer (1944), Jackson (1968), Jones (1969), McGlone (1983), Denevan (1992) and Bowman & Prior (2004). Sauer (1944) proposed that the presence of grassland and savanna systems in climates that could support forests was largely a consequence of human-set fires in North America. In Australia, humans ('fire-stick farmers') are considered as the primary agents of fire that shape the distribution and structure of vegetation, especially where human activities and travel are pronounced (Jones, 1969; Bowman & Prior, 2004; Bird *et al.*, 2008). Similarly, Jackson (1968) proposed that temperate rainforest would dominate most of western Tasmania were it not for human-set fires that promote flammable sclerophyll and buttongrass moorland vegetation. Jackson's model highlights how anthropogenic ignitions in areas with limited natural ignitions can lead to new stable states through altered landscape flammability. The ecological significance of human-set fires varies across biophysical gradients that shape fire regimes, and some of the most striking examples of human influence come from settings where human activities increase ignitions when and where they are naturally rare or alter fuel conditions in ways that overcome strong natural limits on fire.

Fuel-rich wet forests in New Zealand rarely experienced fires prior to human settlement, largely because few ignitions occurred when fuels were sufficiently dry to carry fire. The rapid anthropogenic transformation of the fire regime and extensive loss of forest when people arrived was a consequence of forests that were sensitive to fire but not inherently unburnable. The New Zealand story illustrates the vulnerability of fuel-rich ecosystems to fire–vegetation feedbacks and the fact that human ignitions can have dramatic impacts in settings where natural ignitions are rare. The loss of *Nothofagus–Podocarpus* forest represents an extreme case of vegetation modification by anthropogenic fire and one of the best examples where the influence of humans on fire risk and fire hazard can be isolated from those of climate change. Widespread forest transitions in New Zealand also show how ignition-limited ecosystems can be pushed past fire regime tipping points, shifting landscapes that rarely experience fire to fire-prone systems.

In contrast to New Zealand, where human-set fires initiated feedbacks that altered landscape flammability (Perry *et al.*, 2012b), human impacts on past fire activity and vegetation in the north-western United States, southern South America and Tasmania, appear to have been limited in geographic extent and impact. Palaeofire records from wet forests of Tierra del Fuego and western Tasmania suggest that human-set fires may have been partially responsible for the creation of landscape mosaics of forest/non-forest vegetation with sharp boundaries between fire-prone and relatively fire-proof vegetation. Why much larger populations in the north-western United States had little impact on fire and vegetation remains unresolved. Wet forests here would have been vulnerable to early human-set fires but historical shifts in fire regimes closely track past climate variation. The lack of a strong human signal may be a consequence of different resource utilization strategies, the degree to which Douglas-fir forests are fire resistant, the frequency of natural spring–summer ignitions, the low flammability of early and middle-successional Douglas-fir forests or some combination of these factors. For example, the ecological impact of deliberate fires in the north-western United States may have been limited by a short period (years) of post-fire landscape flammability such that human-set fires resulted in little fire spread and, unlike New Zealand beech forests, mature Douglas-fir forests are resistant to widespread fire-caused mortality and are able to quickly recolonize extensive burned areas (Larson & Franklin, 2005). Thus, anthropogenic burning in the north-western United States appears to have had minimal ecological effect in widespread Douglas-fir forests, although early fire–human–climate interactions are still poorly resolved.

During the European era, all four regions experienced a similar sequence of conversion of native grasslands and adjacent forest margins to pasture, followed by grazing and forest fragmentation, and all show an expansion of forest cover in the 20th century as a result of fire suppression and elimination, although rates of expansion vary greatly (e.g. slow in button-grass moorlands of Tasmania). In recent decades, examination of changes in fire activity across regions suggests that even recent fire activity is strongly linked to interannual climate variability and its effects on fuel type and abundance, drought and fire-weather.

CONCLUSIONS

Our understanding of fire as a process in the Earth system has increased as a result of analyses of global fire-related datasets (e.g. the International Multiproxy Paleofire Database) yet our knowledge of how fire–climate–human interactions are contributing to persistent biome transitions is still limited (Bowman *et al.*, 2011). Under future climate scenarios (without human influence), fire activity is predicted to increase in temperate forests and decrease in tropical broadleaf forests and savannas (Moritz *et al.*, 2012), yet human activities may interact with climate in ways that reverse or amplify these projections. Hence, it is increasingly important to identify environmental settings that may be most vulnerable to these climate–fire–human interactions.

To address these key topics, fire scientists are calling for multiproxy approaches across wide biophysical gradients, yet studies of this nature are rare, probably because they require an intensive sampling effort and replication, and collaboration across disciplines. Utilizing a comparison of palaeoenvironmental and climatological data across four temperate regions is an example of an approach that can provide new insights into the role of anthropogenic burning, climate change and their impacts on global distributions of forest and non-forest biomes. Integrating these palaeofire records into multiscale mechanistic models for scenario testing is a logical next step in further evaluating ecosystem vulnerabilities to fire–human–climate feedbacks and anticipating where these feedbacks are likely to be most pronounced.

ACKNOWLEDGEMENTS

This research was supported in part by National Science Foundation Grants OISE-0966472 (D.M., P.H., C.W., T.V., B.M.), BCS-1024413 and BCS-0956552 (D.M., C.W.), Australian Research Council grant DP110101950 (D.B., T.V., C.W.), New Zealand Foundation for Research Science and Technology funding (J.W., M.M.) and Royal Society of New Zealand Marsden funding (M.M., J.W., C.W.). We thank Patrick Bartlein for the suggestion of plotting sites in climate space and helping access the NPP dataset, and Mitch Power for providing access to Version 2 of the Global Charcoal Database. We also appreciate comments from Jed Kaplan and two anonymous referees.

REFERENCES

Anderson, S.A.J., Doherty, J.J. & Pearce, H.G. (2008) Wildfires in New Zealand from 1991 to 2007. *New Zealand Journal of Forestry*, **53**, 19–22.

Baker, W. (2009) *Fire ecology in Rocky Mountain landscapes*. Island Press, Washington, DC.

Bessie, W.C. & Johnson, E.A. (1995) The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology*, **76**, 747–762.

Bird, B.R., Bird, D.W., Codding, B.F., Parker, C.H. & Jones, J.H. (2008) The 'fire stick farming' hypothesis: Australian aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *Proceedings of the National Academy of Sciences USA*, **105**, 14796–14801.

Borrero, L.A. (1999) The prehistoric exploration and colonization of Fuego-Patagonia. *Journal of World Prehistory*, **13**, 321–355.

Bowman, D.M.J. (1986) Stand characteristics, understorey associates and environmental correlates of *Eucalyptus tetrodonta* F. Muell. forests on Gunn Point, northern Australia. *Vegetatio*, **65**, 105–113.

Bowman, D.M.J. & Prior, L.D. (2004) Impact of aboriginal landscape burning on woody vegetation in *Eucalyptus tetrodonta* savanna in Arnhem Land, northern Australia. *Journal of Biogeography*, **31**, 807–817.

Bowman, D.M.J., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'Antonio, C.M., DeFries, R., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Mack, M., Moritz, M.A., Pyne, S., Roos, C.I., Scott, A.C., Sodhi, N.S. & Swetnam, T.W. (2011) The human dimension of fire regimes on earth. *Journal of Biogeography*, **38**, 2223–2236.

Bowman, D.J.M.S., Wood, S.W., Neyland, D., Sanders, G.J. & Prior, L.D. (2012) Contracting Tasmanian montane grasslands within a forest matrix is consistent with cessation of Aboriginal fire management. *Austral Ecology*, doi:10.1111/aec.12008.

Bradstock, R.A. (2010) A biogeographic model of fire regimes in Australia: current and future implications. *Global Ecology and Biogeography*, **19**, 145–158.

Bush, M.B. & Silman, M.R. (2007) Amazonian exploitation revisited: ecological asymmetry and the policy pendulum. *Frontiers in Ecology and the Environment*, **5**, 457–465.

Cosgrove, R. (1999) Forty-two degrees south: the archaeology of Late Pleistocene Tasmania. *Journal of World Prehistory*, **13**, 357–402.

Daniau, A.L., Bartlein, P.J., Harrison, S.P. *et al.* (2012) Predictability of biomass burning in response to climate changes. *Global Biogeochemical Cycles*, **26**, doi:10.1029/2011GB004249.

Denevan, W. (1992) The pristine myth: the landscape of the Americas in 1492. *Annals of the Association of American Geographers*, **83**, 369–385.

Fletcher, M.-S. & Thomas, I. (2010) The origin and temporal development of an ancient cultural landscape. *Journal of Biogeography*, **37**, 2183–2196.

Gammage, B. (2008) Plain facts: Tasmania under aboriginal management. *Landscape Research*, **33**, 241–254.

Gill, A.M. (1975) Fire and the Australian flora: a review. *Australian Forestry*, **38**, 4–25.

Hemstrom, M.A. & Franklin, J.F. (1982) Fire and other disturbances of the forests in Mount Rainier National Park. *Quaternary Research*, **18**, 32–51.

Heusser, C.J. (1990) Late-glacial and Holocene vegetation and climate of subantarctic South America. *Review of Palaeobotany and Palynology*, **65**, 9–15.

Holz, A. & Veblen, T.T. (2011) The amplifying effects of humans on fire regimes in temperate rainforests in western Patagonia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **311**, 82–92.

Holz, A. & Veblen, T.T. (2012) Wildfire activity in rainforests in western Patagonia linked to the Southern Annular Mode. *International Journal of Wildland Fire*, **21**, 114–126.

Huber, U.M. & Markgraf, V. (2003) European impact on fire regimes and vegetation dynamics at the steppe–forest ecotone of southern Patagonia. *Holocene*, **13**, 567–579.

Huber, U.M., Markgraf, V. & Schabitz, F. (2004) Geographical and temporal trends in Late Quaternary fire histories of Fuego-Patagonia, South America. *Quaternary Science Reviews*, **23**, 1079–1097.

Jackson, W.D. (1968) Fire, air, water and earth – an elemental ecology of Tasmania. *Proceedings of the Ecological Society of Australia*, **3**, 9–16.

Jones, R. (1969) Fire-stick farming. *Australian Natural History*, **16**, 224–228.

Kitzberger, T., Veblen, T.T. & Villalba, R. (1997) Climatic influences on fire regimes along a rain forest to xeric woodland gradient in northern Patagonia, Argentina. *Journal of Biogeography*, **24**, 35–47.

Kitzberger, T., Aráoz, E., Gowda, J., Mermoz, M. & Morales, J. (2012) Decreases in fire spread probability with forest age promotes alternative community states, reduced resilience to climate variability and large fire regime shifts. *Ecosystems*, **15**, 97–112.

Krawchuk, M., Moritz, M., Parisien, M.-A., Van Dorn, J. & Hayhoe, K. (2009) Global pyrogeography: the current and future distribution of wildfire. *PLoS ONE*, **4**, e5102.

Krawchuk, M.A. & Moritz, M.A. (2011) Constraints on global fire activity vary across a resource gradient. *Ecology*, **92**, 121–132.

Krebs, P., Pezzatti, G., Mazzoleni, S., Talbot, L. & Conedera, M. (2010) Fire regime: history and definition of a key concept in disturbance ecology. *Theory in Biosciences*, **129**, 53–69.

Larson, A.J. & Franklin, J.F. (2005) Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. *Forest Ecology and Management*, **218**, 25–36.

Long, C.J., Whitlock, C. & Bartlein, P.J. (2007) Holocene vegetation and fire history of the Coast Range, western Oregon, USA. *The Holocene*, **17**, 917–926.

McGlone, M.S. (1983) Polynesian deforestation of New Zealand: a preliminary synthesis. *Archaeology in Oceania*, **18**, 11–25.

McGlone, M.S. (2001) The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. *New Zealand Journal of Ecology*, **25**, 1–15.

McGlone, M.S. & Wilmshurst, J.M. (1999) Dating initial Maori environmental impact in New Zealand. *Quaternary International*, **59**, 5–16.

McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S. & Li, X. (2009) Rapid deforestation of South Island, New Zealand by early Polynesian fires. *The Holocene*, **19**, 883–897.

McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S., Fromont, M., Li, X., Dieffenbacher-Krall, A., Hobbs, W.O., Fritz, S.C. & Cook, E.R. (2010) Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proceedings of the National Academy of Sciences USA*, **107**, 21343–21348.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. (2009) Widespread increase of tree mortality rates in the western United States. *Science*, **323**, 521–524.

Marlon, J., Bartlein, P., Carcaillet, C., Gavin, D.G., Harrison, S.P., Higuera, P.E., Joos, F., Power, M.J. & Prentice, C.I. (2008) Climate and human influences on global biomass burning over the past two millennia. *Nature Geoscience*, **1**, 697–702.

Marlon, J.R., Bartlein, P.J., Walsh, M.K. *et al.* (2009) Wildfire responses to abrupt climate change in North America. *Proceedings of the National Academy of Sciences USA*, **106**, 2519–2524. doi: 10.1073/pnas.0808212106.

Meltzer, D.J. (2009) *First peoples in a new world: colonizing Ice Age America*. University of California Press, Berkeley.

Mermoz, M., Kitzberger, T. & Veblen, T. (2005) Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. *Ecology*, **86**, 2705–2715.

Meyn, A., White, P.S., Buhk, C. & Jentsch, A. (2007) Environmental drivers of large, infrequent wildfires: the emerging conceptual model. *Progress in Physical Geography*, **31**, 287–312.

Miller, G., Friedel, M., Adam, P. & Chewings, V. (2010) Ecological impacts of buffel grass (*Cenchrus ciliaris* L.) invasion in central Australia – does field evidence support a fire-invasion feedback? *The Rangeland Journal*, **32**, 353–365.

Millspaugh, S.H., Whitlock, C. & Bartlein, P.J. (2000) Variations in fire frequency and climate over the past 17 000 yr in central Yellowstone national park. *Geology*, **28**, 211–214.

Moritz, M.A., Parisien, M.-A., Batllori, E., Krawchuk, M.A., Van Dorn, J., Ganz, D.J. & Hayhoe, K. (2012) Climate change and disruptions to global fire activity. *Ecosphere*, **3**, art49.

New, M., Hulme, M. & Jones, P. (1999) Representing twentieth-century space–time climate variability. Part I: development of a 1961–90 mean monthly terrestrial climatology. *Journal of Climate*, **12**, 829–856.

Nichols, N. & Lucas, C. (2007) Interannual variations of area burnt in Tasmanian bushfires: relationships with climate and predictability. *International Journal of Wildland Fire*, **16**, 540–546.

Ogden, J., Basher, L. & McGlone, M. (1998) Fire, forest regeneration and links with early human habitation: evidence from New Zealand. *Annals of Botany*, **81**, 687–696.

Olson, R.J., Scurlock, J.M.O., Prince, S.D., Zheng, D.L. & Johnson, K.R. (2001) *NPP multi-biome: global primary production data initiative products*. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN.

Pearce, H.G., Mullan, A.B., Salinger, M.J., Opperman, T.W., Woods, D. & Moore, J.R. (2005) *Impact of climate change on long-term fire danger*. New Zealand Fire Service Commission Research Report, Number 50. New Zealand Fire Service Commission, Wellington, New Zealand.

Perry, G.L.W., Ogden, J., Enright, N.J. & Davy, L.V. (2010) Vegetation patterns and trajectories in disturbed landscapes, Great Barrier Island, northern New Zealand. *New Zealand Journal of Ecology*, **34**, 311–323.

Perry, G.L.W., Wilmshurst, J.M., McGlone, M.S. & Napier, A. (2012a) Reconstructing spatial vulnerability to forest loss by fire in pre-historic New Zealand. *Global Ecology and Biogeography*, **21**, 1029–1041.

Perry, G.L.W., Wilmshurst, J.M., McGlone, M.S., McWethy, D.B. & Whitlock, C. (2012b) Explaining fire-driven landscape transformation during the initial burning period of New Zealand's prehistory. *Global Change Biology*, **18**, 1609–1621.

Raffaele, E., Veblen, T.T., Blackhall, M. & Tercero-Bucardo, N. (2011) Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia, Argentina. *Journal of Vegetation Science*, **22**, 59–71.

Rothermel, R.C. (1972) *A mathematical model for predicting fire spread in wildland fuels*. Research Paper INT-115. USDA Forest Service, Intermountain Forest and Range Research Station, Ogden, UT.

Sauer, C.O. (1944) A geographic sketch of early man in America. *Geographical Review*, **34**, 529–573.

Staver, A.C., Archibald, S. & Levin, S.A. (2011) The global extent and determinants of savanna and forest as alternative biome states. *Science*, **334**, 230–232.

Sullivan, A.L., McCaw, W.L., Cruz, M.G., Matthews, W. & Ellis, P.F. (2012) Fuel, fire weather and fire behaviour in Australian ecosystems. *Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world* (ed. by R. Bradstock, A. Gill and R. Williams), pp. 51–79. CSIRO Publishers, Melbourne.

Veblen, T.T., Kitzberger, T., Villalba, R. & Donnegan, J. (1999) Fire history in northern Patagonia: the roles of humans and climatic variation. *Ecological Monographs*, **69**, 46–67.

Veblen, T.T., Holz, A., Paritsis, J., Raffaele, E., Kitzberger, T. & Blackhall, M. (2011) Adapting to global environmental change in Patagonia: what role for disturbance ecology? *Austral Ecology*, **36**, 891–903.

Walsh, M.K., Pearl, C.A., Whitlock, C., Bartlein, P.J. & Worona, M.A. (2010) An 11,000-year-long record of fire and vegetation history at Beaver Lake, Oregon, central Willamette Valley. *Quaternary Science Reviews*, **29**, 1093–1106.

Warman, L. & Moles, A.T. (2009) Alternative stable states in Australia's wet tropics: a theoretical framework for the field data and a field-case for the theory. *Landscape Ecology*, **24**, 1–13.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. (2006) Warming and earlier spring increase western US forest wildfire activity. *Science*, **313**, 940–943.

Whitlock, C. & Knox, M.A. (2002) Prehistoric burning in the Pacific Northwest. *Fire, native peoples and the natural landscape* (ed. by T.R. Vale), pp. 195–231. Island Press, Washington, DC.

Whitlock, C., Moreno, P.I. & Bartlein, P. (2007) Climatic controls of Holocene fire patterns in southern South America. *Quaternary Research*, **68**, 28–36.

Whitlock, C., Higuera, P.E., McWethy, D.B. & Briles, C.E. (2010) Paleoecological perspective on fire ecology: revisiting the fire regime concept. *The Open Ecology Journal*, **3**, 6–23.

van Wilgen, B.W., Govender, N., Biggs, H.C., Ntsala, D. & Funda, X.N. (2004) Response of savanna fire regimes to changing fire-management policies in a large African national park. *Conservation Biology*, **18**, 1533–1540.

Wilmshurst, J.M., McGlone, M.S. & Partridge, T.R. (1997) A late Holocene history of natural disturbance in lowland podocarp/hardwood forest, Hawke's Bay, New Zealand. *New Zealand Journal of Botany*, **35**, 79–96.

Wilmshurst, J.M., Anderson, A.J., Higham, T.F.G. & Worthy, T.H. (2008) Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. *Proceedings of the National Academy of Sciences USA*, **105**, 7676–7680.

Wood, S. & Bowman, D. (2012) Alternative stable states and the role of fire–vegetation–soil feedbacks in the temperate wilderness of southwest Tasmania. *Landscape Ecology*, **27**, 13–28.

BIOSKETCH

David McWethy is currently an assistant research professor at Montana State University, Bozeman, USA. His research focuses on how past and present human and natural disturbances shape vegetation and influence the structure and function of ecosystems. McWethy and contributing authors are currently collaborating on research efforts aimed at better understanding the causes and consequences of fire in the past, present and future (http://www.wildfirepire.org/).

Editor: Greg Jordan