Environmental Research Letters

TOPICAL REVIEW

Biological and geophysical feedbacks with fire in the Earth system

OPEN ACCESS

RECEIVED
24 August 2017

REVISED
6 November 2017

ACCEPTED FOR PUBLICATION
1 December 2017

PUBLISHED
6 March 2018

S Archibald[1,2,25], C E R Lehmann[1,3,25], C M Belcher[4], W J Bond[5], R A Bradstock[6], A-L Daniau[7], K G Dexter[3,8], E J Forrestel[9], M Greve[10], T He[11], S I Higgins[12], W A Hoffmann[13], B B Lamont[11], D J McGlinn[14], G R Moncrieff[5], C P Osborne[15], J G Pausas[16], O Price[17], B S Ripley[18], B M Rogers[19], D W Schwilk[20], M F Simon[21], M R Turetsky[22], G R Van der Werf[23] and A E Zanne[24]

1 Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag X3, WITS, Johannesburg, 2050, South Africa
2 Natural Resources and the Environment, CSIR, PO Box 395, Pretoria, 0001, South Africa
3 School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FF, United Kingdom
4 Belcher C.M., wildFIRE Lab, University of Exeter, Exeter, EX4 4PS, United Kingdom
5 South African Environnemental Observation Network, P/Bag X7, Claremont, 7735, South Africa
6 Centre for Environmental Risk Management of Bushfires, Centre for Sustainable Ecosystem Solutions, University of Wollongong, Wollongong NSW 2522, Australia
7 CNRS, UMR 5805–EPOC, Université de Bordeaux, Allée Geoffroy Saint Hilaire, Pessac Cedex, Bordeaux, 33615, France
8 Royal Botanic Garden Edinburgh, Edinburgh EH3 5LR, United Kingdom
9 Department of Viticulture and Enology, University of California, Davis 95616, United States of America
10 Department of Plant and Soil Sciences, University of Pretoria, Pretoria South Africa
11 Department of Environment and Agriculture, Curtin University, Perth, WA 6845, Australia
12 Plant Ecology, University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth, Germany
13 Department of Plant Biology, North Carolina State University, Campus Box 7612, Raleigh, NC, 27695-7612, United States of America
14 Department of Biology, College of Charleston, Charleston, South Carolina, United States of America
15 Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom
16 CIDE-CSIC, Carretera CV-315, Km 10.7, Montcada, Valencia, Spain
17 School of Biological Sciences, University of Wollongong, Wollongong NSW 2522, Australia
18 Department of Botany, Rhodes University, Grahamstown, South Africa
19 Woods Hole Research Center, 149 Woods Hole Road, Falmouth, MA, 02540, United States of America
20 Texas Tech University, Lubbock, Texas, United States of America
21 Embrapa Recursos Genéticos e Biotecnologia, Brasília-DF, 70770-917, Brazil
22 Department of Integrative Biology, University of Guelph, Guelph, Ontario, N1G 2W1, Canada
23 Faculty of Science, Vrije Universiteit Amsterdam, 1081HV, Amsterdam, The Netherlands
24 Department of Biological Sciences, George Washington University, Washington, DC 20052, United States of America
25 Joint first authors to whom any correspondence should be addressed.

E-mail: sally.archibald@wits.ac.za

Keywords: flammability, earth-system feedbacks, niche-construction, evolution, plant traits, vegetation, climate

Supplementary material for this article is available online

Abstract

Roughly 3% of the Earth's land surface burns annually, representing a critical exchange of energy and matter between the land and atmosphere via combustion. Fires range from slow smouldering peat fires, to low-intensity surface fires, to intense crown fires, depending on vegetation structure, fuel moisture, prevailing climate, and weather conditions. While the links between biogeochemistry, climate and fire are widely studied within Earth system science, these relationships are also mediated by fuels—namely plants and their litter—that are the product of evolutionary and ecological processes. Fire is a powerful selective force and, over their evolutionary history, plants have evolved traits that both tolerate and promote fire numerous times and across diverse clades. Here we outline a conceptual framework of how plant traits determine the flammability of ecosystems and interact with climate and weather to influence fire regimes. We explore how these evolutionary and ecological processes scale to impact biogeochemical and Earth system processes. Finally, we outline several research challenges that, when resolved, will improve our understanding of the role of plant evolution in mediating the fire feedbacks driving Earth system processes. Understanding current patterns of fire and vegetation, as well as patterns of fire over geological time, requires research that incorporates evolutionary biology, ecology, biogeography, and the biogeosciences.

Box 1. The fire regime concept at the global scale.

Ecologists use the concept of a fire regime to describe the repeated patterns of fire at a particular location (Bond and Keeley 2005, Gill 1975). A fire regime is characterised by a particular combination of fire characteristics such as frequency, intensity, size, season, spread type, and extent. These characteristics are inter-related (for example systems with intense fires that burn a lot of fuel will burn infrequently) and fire is therefore multi-dimensional (Archibald *et al* 2013). At a global scale broad categories of fire-regime are observed from space. These are termed pyromes because they can be seen as analogous to biomes. Fire regimes therefore represent broad functional categories of the types of fires that occur on Earth—for example crown fire regimes have particular characteristics and ecological impacts that distinguish them from litter fire regimes (Pausas *et al* 2004, Rogers *et al* 2015). Fire regimes respond to changes in climate, vegetation, fauna and human activities (Pausas and Keeley 2014a), and a fully coupled Earth system model would ideally incorporate these underlying mechanisms so that fire regimes are emergent properties of a model rather than imposed (Hantson *et al* 2016, Murphy *et al* 2011). Vegetation properties such as plant growth rates, resprouting, litter quality affecting decomposition rates, plant architecture, branch retention, and tree height all interact with climate and human activities to determine the prevailing fire regime.

Most of the 3099 articles published using the term 'fire regime(s)' between 1945 and 2017 addressed this topic at local or landscape scales (40%, compared with 14% for global and 15% for regional—see SI for methods). Global analyses often do not consider all components of fire regimes but focus only on the 'amount burned'—partly because of lack of data at these scales (for example often paleo analyses have only crude approximations of biomass consumed with which to work). However, advances in remote sensing (Archibald *et al* 2010), and detailed interpretation of paleorecords (Carcaillet *et al* 2001, Duffin *et al* 2008) are making it easier to consider the full complement of fire characteristics, thus shedding light on the evolution of fire in the Earth system.

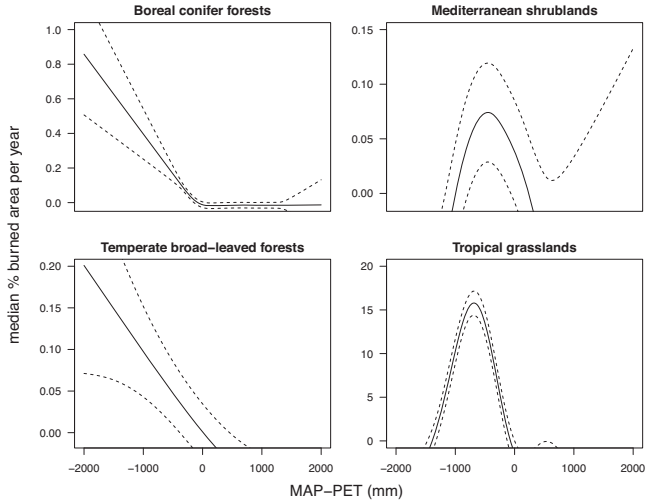

Figure 1. Relationship between the fraction area burned and moisture availability (mean annual precipitation—potential evapotranspiration, MAP–PET), demonstrating that vegetation is an important mediator of climate-fire relationships. The 'intermediate rainfall' hypothesis is apparent in grassy and mediterranean ecosystems, but has less support in broad-leaved and conifer forests where it appears instead that more moisture decreases burned area. Note the different scales of the *y*-axis: global patterns are dominated by the grass signal. Data are the results of a GAM model run on MODIS MCD45 burned area data (Justice *et al* 2011), MAP from CRU (www.cru.uea.ac.uk/), and PET from www.worldclim.org. Vegetation was classified using Olson's ecoregions biome classifications (Olson *et al* 2001).

Introduction

Fires have burned on Earth ever since terrestrial plants evolved and provided a source of fuel and oxygen (Glasspool *et al* 2004, Scott 2000), with subsequent profound impacts on the Earth system. Emissions from fire affect the cycling of carbon, phosphorus, and nitrogen (Crutzen *et al* 1979, van der Werf *et al* 2010, Wittkuhn *et al* 2017), and fires alter surface energy budgets and regional to global climate through emissions of greenhouse gases, aerosols and altering land surface albedo (Kaufman and Fraser 1997, Randerson *et al* 2006, Ward *et al* 2012). Fires also affect Earth system processes through their impacts on vegetation: altering the structure and composition of ecosystems (Pausas and Keeley 2009) and controlling the distribution and diversity of biomes (Bond *et al* 2005, Pausas and Ribeiro 2017).

On the other hand, fire regimes (see Box 1 for a definition) are in turn controlled by atmospheric conditions, climate, and the type of vegetation available as fuel (Krawchuk and Moritz 2011, Pausas *et al* 2004, Swetnam and Betancourt 1990). These two-way interactions (here termed feedbacks) make it difficult to predict how climate interacts with fire and vegetation in a changing world (Archibald *et al* 2013, Bowman *et al* 2009). For example, high temperatures increase the probability of fire occurrence and the intensity of fire for a particular vegetation type (Flannigan *et al* 2009, Westerling *et al* 2006). However, increased temperatures can have negative or positive effects on the productivity of vegetation (Lu *et al* 2013, Pausas and Ribeiro 2013), and can result in shorter fire return periods, which generally result in less fuel and thus less intense fires (Archibald *et al* 2013). The long term

outcome of increased temperatures for fire regimes is a combination of both direct and indirect (via fuels) effects. The same caution should apply when assessing the consequences of human impacts on fire regimes—dense human populations tend to reduce fire due to negative impacts on fuel, despite increased ignition frequency (Andela *et al* 2017, Archibald 2016).

Vegetation is an integral component of the vegetation-fire-climate system, which implies evolutionary and ecological processes need to be adequately represented in any theoretical framework. There are dramatic examples in the paleo-record of changes in global patterns of vegetation and fire linked to the evolution of new leaf properties and plant architecture—e.g. early angiosperms, and subsequently the grass family- Poaceae (Belcher and Hudspith 2017, Bond and Scott 2010, Keeley and Rundel 2005). At shorter time-scales, changes in dominant plant species can also significantly alter fire activity and Earth system feedbacks (D'Antonio and Vitousek 1992, Girardin *et al* 2013). However, these biological processes tend to be overlooked when modelling current fire regimes, predicting changes in fire in the future, or assessing the atmospheric and biogeochemical impacts of fire. New developments in dynamic global vegetation models (DGVMs) are trying to account for these interactions (Scheiter *et al* 2013).

For example, global and regional data analyses have repeatedly indicated that burned area is maximised at intermediate moisture availability (Daniau *et al* 2012, Krawchuk and Moritz 2011, Meyn *et al* 2007)—the explanation being that at low rainfall there is not enough fuel to burn, and at high rainfall the fuel is too moist to burn readily (Bradstock 2010). However, when examined for different vegetation types (figure 1), it becomes clear that this global pattern is largely driven by grass-dominated vegetation (>80% of the area burned currently is grassy (van der Werf *et al* 2006) so it dominates all global analyses when not specifically controlled for). Clearly, explaining global patterns of fire and interactions with climate requires that plant characteristics be explicitly considered (Pausas and Paula 2012).

Collation of the literature indicates that studies on feedbacks between fire and vegetation are less common than ones on feedbacks between climate and vegetation (figure 2). Publications that do consider vegetation are usually local in scope—only 40% of the global papers on fire feedbacks explicitly include vegetation.

Humans have had varied and significant impacts on fire for many millennia. Humans generally increase ignition frequency (Syphard *et al* 2009), reduce area burned (Andela *et al* 2017), extend the length of the fire season, and reduce fire size (Le Page *et al* 2010). Human impacts on global climate, atmospheric properties, and vegetation distributions also feed back to alter fire regimes (Bowman *et al* 2011, Cochrane and Barber 2009). Moreover, because of increasing awareness of feedbacks between fire and Earth system properties, many proposed interventions to mitigate these global changes also involve managing fire and altering its occurrence/type (Moritz *et al* 2014). However, there are several research challenges to successfully assessing the Earth system consequences of our impacts on fire and to identifying opportunities for managing fire for geoengineering purposes. Solving these challenges requires better interactions between plant and Earth system scientists.

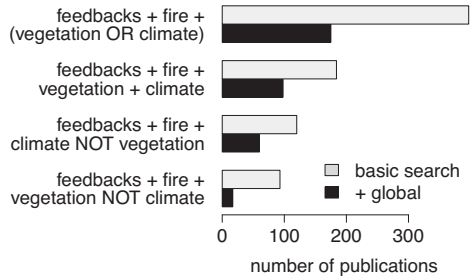

Figure 2. Summary of how fire feedbacks in the Earth system are represented in published literature on Web of Science (see SI for methods available at stacks.iop.org/ERL/13/033003/mmedia). Only about half of the available studies about fire feedbacks consider both vegetation and climate. Global studies on feedbacks with climate are three times more likely than those with feedbacks on vegetation, although vegetation feedbacks appear to be better recognised in local/landscape-level studies.

Here we present a conceptual framework (figure 3) to illustrate how the evolution of key plant traits (see box 2) has driven global scale changes in fire regimes. We start with several modern day examples of 'biogeographic conundrums'—where climate and soils are insufficient for explaining patterns of fire and vegetation. We then outline a conceptual framework of how plant traits influence the flammability of ecosystems, which then feed back to force both the evolution of plant traits and changes in fire characteristics. We explore how these evolutionary and ecological processes scale to impact biogeochemistry and Earth system processes and the potential role of global atmospheric chemistry as a regulatory mechanism influencing changes in fire over geological time. We address this using an approach that includes a collation of published literature.

Biogeographic conundrums

The interdependence of climate, vegetation and fire is illustrated by numerous biogeographic 'conundrums'—examples where abiotic conditions cannot be used without consideration of evolutionary and biogeographic history to predict the distribution of vegetation or fire (figure 4). Biogeographic conundrums are not narrow idiosyncrasies in world vegetation; rather they occur across the majority of the world's biomes and land surface (Moncrieff *et al* 2016). Indeed, these conundrums were recognised by

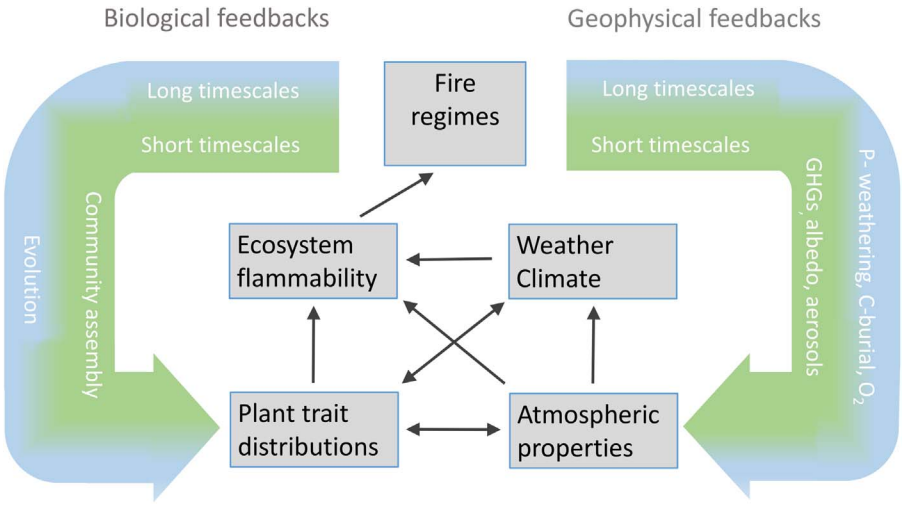

Figure 3. Fire acts through both geophysical processes (exchange of energy and matter between the biosphere and atmosphere) and biological processes (community assembly and evolution). Plant innovations that alter the degree to which vegetation is tolerant of fire and the flammability of the vegetation can alter fire regimes, and potentially impact global biogeochemical processes. With both biological and geophysical feedbacks, the type of processes impacted depend on the time scales involved.

Box 2. Plant functional traits.

Functional traits are defined as morphological, biochemical, physiological, structural, phenological or behavioural characteristics of organisms that influence performance or fitness. They are used to define the ecological roles of species in an environment (Díaz and Cabido 2001).

Traits can be considered in terms of their effect on ecosystem properties and the services that human societies derive from them, or as a response to environmental conditions (Lavorel and Garnier 2002). Thus fire-response traits are associated with fire tolerance and regeneration, and fire-effect traits influence flammability.

There are constraints on the combinations of traits that an individual organism can display, leading to trade-offs among traits. Trait syndromes describe groups of traits that are correlated; i.e. together result in an organism that is able to survive and reproduce in a particular environment, and have been used to define ecological strategies thought to be adaptive in those environments.

Functional traits are at the forefront of efforts to develop a mechanistic understanding of how species diversity influences ecosystem functioning, and are essential for scaling local ecological knowledge to the Earth system. For example, vegetation is represented in Earth system models by characterizing its functional traits such as plant height, maximum photosynthetic rates, and rooting depth, that together determine how plants cycle carbon, water, and energy through the Earth system, and interact with each other. Including fire-related functional traits in these models should likewise enable mechanistic simulations of fire regimes.

many early ecologists (Myers 1936, Whittaker 1975) who noted that the 'climax' vegetation in a region was not always what climate could support, but rather the result of interactions with disturbances such as fire. However, deterministic relationships between climate and vegetation were assumed in the first global vegetation models, which arose in the 1980s (Prentice *et al* 2007, Woodward 1987), and are still employed in species distribution models for a wide variety of purposes (Merow *et al* 2014). It is only in the last decade that the interdependence between climate, vegetation and fire has been quantified at a global scale (Bond *et al* 2005) and recognised as profound.

Biogeographic conundrums arise via two pathways. Divergent fire regimes refer to regions with similar climate but different fire regimes, arising through differences in community assembly (i.e. differences in the types of plants that dominate in two regions). Alternatively, convergent fire regimes refer to regions with different climate that converge on a similar fire regime by having plant traits that render a community similarly flammable. In each case, it is the biological properties of the vegetation that are critical in shaping the fire regime.

One example of divergent fire regimes arises from the difference in plant traits between boreal North America and Eurasia (figure 4). North American fires are largely stand-replacing crown fire events (Fire return interval (FRI) ranging from 80–400 years (Kasischke *et al* 2002)) whereas Eurasian fires are generally surface, litter-fuelled fires (FRI from 15–70 years (Sannikov and Goldammer 1996)). Boreal North American fires emit 53% more carbon (C) per unit area burned but cover one third as much area on an annual basis, emitting half as much C as Eurasia per year. They also have a stronger cooling effect (negative radiative forcing) due to the larger change in surface properties after fire (Rogers *et al* 2015). The climates of these two regions are too similar to explain these differences (Rogers *et al* 2015, de Groot *et al* 2013, figure 4) and there is evidence that plant traits (box 2) of the dominant tree species of each region are

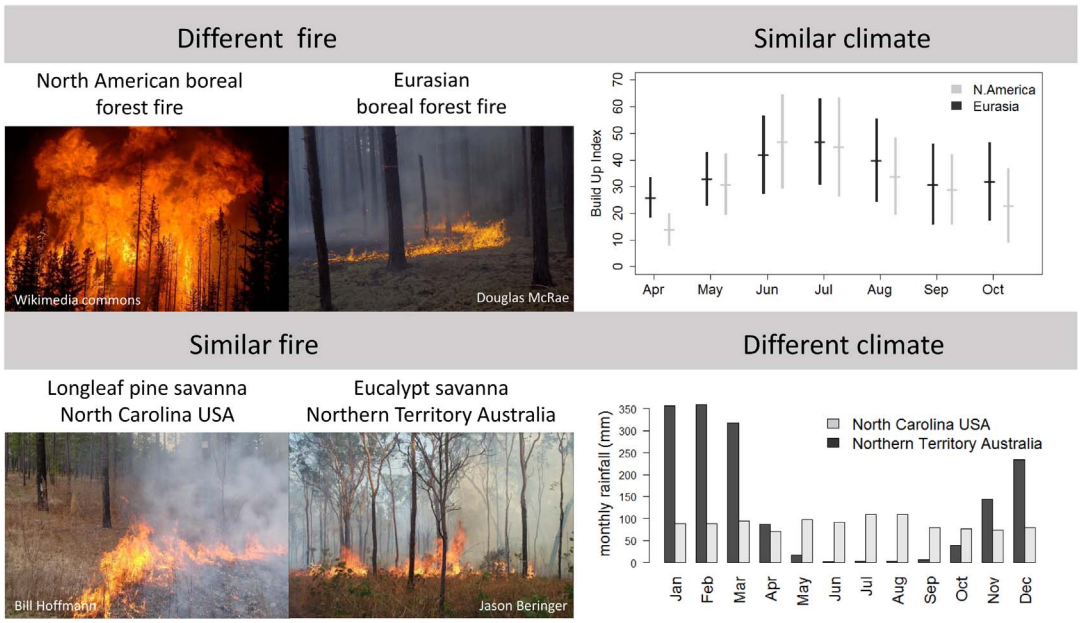

Figure 4. Examples of divergent (top) and convergent (bottom) fire regimes. Boreal North America and Eurasia have different fire regimes (crown fire vs surface fire respectively) but similar climates, and North Carolina, USA and Northern Territory Australia have similar fire regimes but different climates. Rainfall data from CL and WH. Data on build up index (BUI) from de Groot *et al* (2013). The BUI is a measure of the moisture content of the litter fuels (duff) and is a function of temperature and precipitation (Van Wagner and Pickett 1985).

key drivers of the fire dynamics. Fire-embracing black spruce (*Picea mariana*) has highly flammable evergreen needles and retains its dead branches, thereby facilitating crown fire regimes by allowing fires to climb up to the canopy. Spruce (*Picea* spp.) dominate in Alaska and Canada, but comprise only 15% of the tree biomass in Eurasia. By contrast, larch (*Larix* spp.) and pine (*Pinus sylvestris* L.) dominate in Eurasia and tend to resist high-intensity crown fires: larch is deciduous, and the two pine species shed their dead lower branches, so that when fire occurs it usually only spreads in the understory without reaching the canopy. As the same genera are present in both regions, it remains unclear how the differential dominance of particular functional types on each continent has occurred, or how easy it is to shift from one community state to another. It is likely that frequent surface fires in Eurasia kill juvenile *Picea* before they can reproduce (Black and Bliss 1980), and therefore contribute to maintaining the species composition and fire regime of the region. In fact, there are similarities with an even better studied example of divergent fire regimes within a similar climate: alternative stable state dynamics at forest/savanna boundaries (Dantas *et al* 2016, Hennenberg *et al* 2006, Hoffmann *et al* 2012, Staver *et al* 2011), where regions with similar climate either burn frequently (due to a prominent grassy understory in savanna) or hardly ever (due to non-flammable litter and moist microclimate in tropical forests). While mostly studied in the tropics, this process also occurs in temperate ecosystems.

An example of a convergent fire regime, in which regions with very different climates converge on the same fire regime, occurs between pine savannas of the southeastern USA and tropical mesic savannas. These pine savannas are structurally similar to tropical savanna ecosystems, with a continuous grassy understory and an open tree canopy dominated by fire-tolerant longleaf pine (*Pinus palustris*). Like mesic tropical savannas, surface fires occur every ~3 years (range 0.5–12) (Stambaugh *et al* 2011), and without fire they are soon replaced by broad-leaved forest communities that are much less flammable (Kane *et al* 2008). However, rainfall in long-leaf pine savannas is aseasonal (monthly rainfall never <70 mm), in contrast to tropical mesic savannas where seasonal drought is considered a necessary attribute because it both increases the probability of fire and reduces overall tree growth rates (Cole 1960, Lehmann *et al* 2011, Scholes and Walker 1993). How longleaf pine savannas with tropical savanna fire regimes persist in a system without seasonal drought is best explained by the traits of *P. palustris* (Ellair and Platt 2013, Platt *et al* 2016). Their leaves are 20–45 cm in length, more than twice as long as other pine species (Schwilk and Caprio 2011), and, in combination with a tussock-grass understory, they produce an aerated, flammable fuel bed that increases fire temperatures, duration of heating and combustion of fuels (Ellair and Platt 2013), and allows surface fires to burn during most weather conditions (Fill *et al* 2012). Thus, two quite different climate systems have converged to produce similar fire regimes through similarities in fuel structure that arise from biological characteristics of the dominant tree species in the USA.

Finally, the most telling biogeographic conundrum for global modellers are the numerous examples where exotic species (with novel plant traits) have invaded a particular ecosystem and fundamentally altered the fire regime, despite climate/weather conditions remaining unchanged (Brooks *et al* 2004, Pausas and Keeley 2014a). Here plant traits of the invading species are indisputably the factor driving the change in fire regimes (D'Antonio and Vitousek 1992, Fuentes-Ramirez *et al* 2016). These dramatic changes in fire regime are well described in the literature across a range of systems (Brooks *et al* 2004), but the conclusion – that including plant traits is essential for describing fire regimes – has not yet been adequately incorporated into Earth system research.

These biogeographic conundrums provide strong evidence for vegetation as a mediator of fire-climate relationships today. But the types of plants present on Earth have not been static over evolutionary time (Belcher *et al* 2013, Bond and Midgley 2012b), and thus it is necessary to understand both ecological and evolutionary processes when assessing feedbacks between fire and vegetation. Similarly, feedbacks with the Earth system also occur over short (albedo, climate) and longer (nutrient cycling) time scales. With the advent of global meta-databases of plant traits, and global and paleo-ecological datasets on fire, we suggest that it is now possible for evolutionary processes to be incorporated into the study of fire in the Earth system (He and Lamont 2017). Once we understand how plant traits mediate fire regimes and vice versa, we can then incorporate these effects into Earth system models of fire and model their changes through geological time. Below we synthesise current knowledge in this area, describing the pathways by which plant traits both respond to and drive fire regimes.

Ecosystem flammability

Flammability is the propensity of an ecosystem to ignite (given an ignition source) and then propagate a fire. Fire has therefore often been modelled as an infection/percolation process, with flammability being defined as the probability of spread (Cox and Durrett 1988, O'Neill *et al* 1992, Sullivan 2009). The likelihood of an ecosystem burning depends on both abiotic and biotic properties. These properties vary across temporal scales—from millions of years (O_2 concentrations of the atmosphere, evolution of flammable plant traits), to millenia (vegetation distributions, climate), to decades (fuel amount, community assembly), to days and hours (weather conditions and fuel moisture). Consequently, different disciplines emphasise particular aspects of flammability (Whitlock *et al* 2010). For example, paleoecologists focus on fuel type and O_2 levels, Earth system scientists emphasise climate, whereas foresters focus on weather and fuels. Current global predictive models of fire tend towards unidimensional indices of vegetation—e.g. net primary productivity (NPP)—or none at all (Krawchuk *et al* 2009, Moritz *et al* 2012, Spracklen *et al* 2009), although models linked to DGVMs can define fuels more precisely (Page and Morton 2014, Thonicke *et al* 2010). NPP is used as a proxy for of the amount of fuel in a system, but once a certain minimum level of fuel is achieved in a system, how it burns is controlled more by other fuel properties such as arrangement, density, chemical properties, and moisture content (Schwilk 2015, Varner *et al* 2015).

Conceptually, the flammability of a system is controlled by a number of factors: temperature, wind speed, relative humidity, O_2 concentrations, moisture, and the amount and structure of fuels, each of which can compensate or exacerbate others. For example, it is clear from experimental work that non-flammable fuel types become flammable as O_2 concentrations increase (Belcher *et al* 2010b), such that even moist forests would have been easy to ignite in the high O_2 atmospheres of the Carboniferous and Cretaceous periods (Belcher and Hudspith 2017). An example at much shorter timescales is the impact that a sudden rise in relative humidity can have by extinguishing a fire burning through a uniform fuel bed (Cheney *et al* 1993). Moreover, under constant environmental conditions, a change in fuel type can make a non-flammable system flammable (McGranahan *et al* 2012), or transition a surface fire into a crown fire event (Bradstock *et al* 2010). Because fire is a percolation process, it tends to show threshold behaviours (figure 5), implying that small changes in the flammability of the system can have large impacts on the area burned and on other fire characteristics (Archibald *et al* 2012, Cox and Durrett 1988). Thus, changes in plant structure and function that alter vegetation flammability potentially have large impacts on global patterns of fire at time-scales relevant to human management (Pausas and Keeley 2014a) as well as longer timescales (Belcher *et al* 2010a). Below we describe how fuel properties emerge from plant characteristics, and discuss various points of contention relating to the role of evolution in this process.

Plant traits that impact flammability

There is a large and expanding literature that describes how vegetation traits scale to impact fuels, and ultimately fire regimes (Cornwell *et al* 2015, Grootemaat *et al* 2015, Kane *et al* 2008, Schwilk and Caprio 2011). Pausas *et al* (2017) identified three main dimensions of flammability: ignitability, spread rate, and amount of heat released. When scaled up to a whole plant level, these result in three flammability strategies for persisting in fire-prone ecosystems (box 3): *non-flammable* (not easy to ignite), *fast-flammable* (easy to ignite with high spread rates but low heat release), and

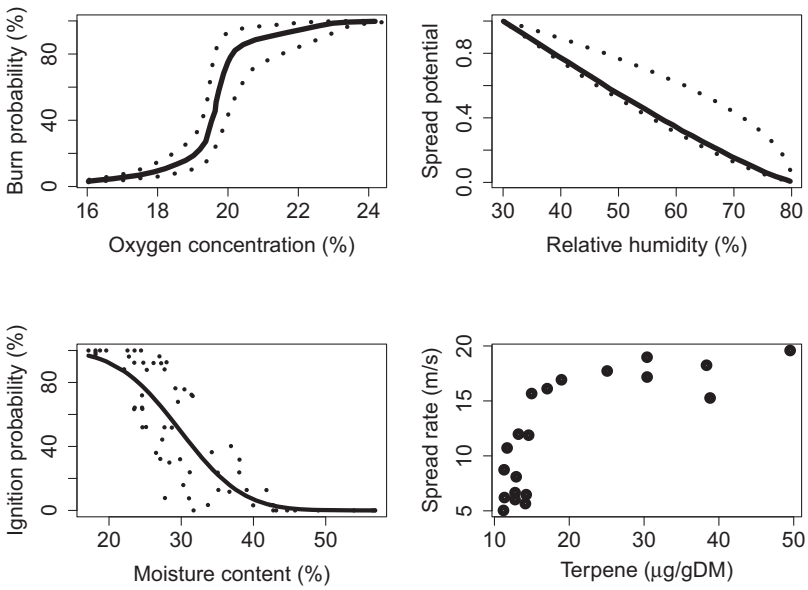

Figure 5. Factors that affect fire spread range from biological to geophysical and vary over spatial and temporal scales. Responses of fire to these drivers are often non-linear, suggesting that small changes can have large effects on fire regimes. Data for O_2 from (Belcher *et al* 2010b), relative humidity (Page and Morton 2014), moisture content (Blackmarr 1972), and leaf terpene concentration (Ormeno *et al* 2009).

hot-flammable (easy to ignite with high heat release). Which of these flammability strategies dominates in an environment will not only affect the environment for other co-occurring species (via niche-construction—e.g. Bowman *et al* 2017), but will also impact nutrient cycling (e.g. N-volatilisation, emission factors), soil properties (water infiltration), and other biogeochemical processes (Wittkuhn *et al* 2017).

Flammability is a property of the intrinsic chemistry and structure of plant parts, how they are arranged on the plant (or in the litter bed), as well as ecophysiological properties such as how quickly they cure, and how quickly they regrow (table 1). At a leaf level, the size and density of the leaf, as well as its nutrient content and presence of volatile oils and resins all affect its tendency to ignite (Cornwell *et al* 2015, Pausas *et al* 2016) (table 1). The arrangement of these leaves on a canopy (plant architecture) can strongly affect flammability: highly branched canopies with high surface area and low bulk density (g cm^{-3}) are better aerated and easier to ignite, although sparse branching may also reduce flammability (Schwilk and Ackerly 2001, Simpson *et al* 2016). Similarly, plants that retain dead leaf material have higher fuel loads and drier canopies and are therefore both more ignitable and have higher heat release (Jaureguiberry *et al* 2011, Schwilk 2003). Correspondingly, litter bed flammability is controlled by the packing ratio: the arrangement of individual leaves based on their morphology (de Magalhaes and Schwilk 2012, Engber and Varner III 2012, Kane *et al* 2008, Scarff and Westoby 2006). The different ways that plant traits alter canopy vs litter fuels (table 1) can reinforce the divergent flammability strategies mentioned above. For example, small leaves increase heat transfer through canopy fuels but pack more closely together as litter, and thus retard surface fire spread (Cornwell *et al* 2015). Traits that make canopy fuels flammable can therefore deter litter fires and vice versa (Pausas *et al* 2017). Moreover, the amount of fuel and its dryness are controlled by plant growth rates, phenology (deciduous vs evergreen) and decomposition rates, that represent the outcome of a range of plant traits and interact with many other aspects of plant ecological strategy (table 1).

Variations in these traits across species can alter ignition probability and fire spread rates by an order of magnitude (Burger and Bond 2015). Many environmental factors interact to select for leaf chemistry, specific leaf area, and plant architecture (Endara and Coley 2011, Wright *et al* 2004). Therefore these traits are not necessarily the product of selection for increased or reduced flammability, although there is a growing body of evidence to suggest that this can sometimes be the case—see box 3. Whatever the evolutionary mechanism by which different flammability strategies emerge and spread in populations, the impact that they can have on fire regimes is substantial (see box 4).

Plant traits that enable fire tolerance

Any organism occurring in an environment that burns needs to have traits that enable survival and/or regeneration after fires. Traits that determine plant performance in post-fire colonisation and regeneration depend on the particular fire regime (Keeley *et al* 2011). For example, serotiny (seed storage and postfire release) is common in ecosystems with stand-replacing canopy fires that have a return interval between maturation age and plant longevity (Lamont *et al* 1991,

Table 1. Plant traits that influence flammability at leaf and whole plant levels, and in terms of life history/physiology. Leaf chemical properties impact heat release rate and propensity of fuel to ignite. Leaf geometry and plant architecture can alter bulk density and moisture content which affect how easily fuel ignites and propagates fire. Moreover, traits such as relative growth rates affect how quickly fuels accumulate after a fire, and can impact fire return times. Decomposition rates are key to defining fuel build up: generally more flammable leaves (higher C:N ratio) have slower decomposition rates, therefore flammability is increased at both the leaf level and through time.

Leaf level (chemistry)	Whole plant level (architecture)	Physiology/phenology
Canopy and surface fuels	**Canopy and surface fuels**	**Canopy and surface fuels**
Leaf carbon:nitrogen ratio	Leaf size (small leaves allow efficient heat transfer)	Curing rates
Resins/volatile oils/waxes	Leaf angle	Decomposition rates
Specific leaf area	Branching patterns	Regrowth rates
Phosphorus concentration	Height to first branching	Deciduousness
Leaf mineral content	Canopy depth	
Leaf moisture content	Retention of dead material	
	Bulk density (packing ratio)	
Litter fuels	**Litter fuels**	**Litter fuels**
Leaf C:N ratio	Leaf size (large leaves increase fuel bed aeration)	Decomposition rate
Resins/volatile oils/waxes	Leaf length	
Specific leaf area	Litter bed density	
P concentration	Fragment sizes in the fuel bed	
	Ratio of leaf to wood	
Moss and peat fuels	**Moss and peat fuels**	**Moss and peat fuels**
Moisture content	Stem density	Decomposition rate
Moisture holding capacity	Bulk density	
Organic matter concentration	Branching architecture	

Pausas and Keeley 2014b): serotinous plants benefit from having all their seeds germinate at a time when resources are abundant (Enright *et al* 1998), but they need time to develop an aerial seedbank between fires and are at risk if fires do not occur before plant death. Serotiny is therefore absent from frequently burned ecosystems like grasslands (Lamont *et al* 2013). In these frequently burned surface fire regimes woody species can persist either via thick bark (Schafer *et al* 2015) and well insulated buds (Charles-Dominique *et al* 2015) or massive underground bud-storing structures—lignotubers, geoxyles and bulbs, (Maurin *et al* 2014)—that allow rapid resprouting. Hence, over time, fire regimes act first as a filter of species traits but also facilitate the development of trait syndromes, where traits such as resprouting and thick bark may be linked as part of an overall plant performance strategy (Lamont *et al* 2013, Simon *et al* 2009).

Such fire-plant interactions have sometimes resulted in convergent evolution: similar sets of traits evolving in different plant lineages exposed to similar fire regimes, so providing compelling evidence that they are adaptations. The mediterranean ecosystems of the world exemplify this. These ecosystems are geographically dispersed and do not share many plant lineages, but fire-related traits (e.g. serotiny, lignotubers, fire-cued flowering and germination) are common across this biome—as are canopy-fuelled fire regimes with moderate (20−80 year) return times (Keeley *et al* 2012). Similarly, fire-adapted woody life forms in tropical savannas that keep most of their biomass below-ground are found in a number of unrelated plant lineages in both African and South American savannas (Maurin *et al* 2014, Simon and Pennington 2012).

Fire regimes are generally determined by the few plant species that dominate a landscape, but co-occurring species—whether flammable or not—need to possess the functional traits that enable resistance to, or tolerance of the fire regime. A classic example is tropical savanna ecosystems where frequent fire is a product of the high annual growth rate of grasses that cure rapidly creating an aerated fuel bed enabling rapid fire spread. Woody species contribute little to the fuel, but all savanna plant species possess traits that confer survival under frequent fire. There is evidence that the most flammable members of a community may have disproportionate effect on the flammability of the ecosystem (Blauw *et al* 2015, de Magalhaes and Schwilk 2012, Van Altena *et al* 2012, Varner *et al* 2017), i.e. yet again, that small changes in the flammability traits of plants can have large ecological, evolutionary, and geophysical impacts.

It has been argued that many of the traits that enable species persistence under various fire regimes could have evolved as responses to other environmental stresses (for example, drought or herbivory) as no traits appear exclusively linked to fire (Axelrod 1980, López-Soria and Castell 1992). However, recent phylogenetic analyses linking the evolution of key fire-tolerant traits (such as bark thickness and serotiny) to changes in fire regimes lend support to the idea that fire has driven the emergence and spread of these plant traits across diverse lineages (Crisp *et al* 2011, He *et al* 2012, 2011, Lamont *et al* 2013). In addition, there is evidence of divergence in fire traits among populations of the same species under different fire regimes (Gómez-González *et al* 2011, Hernández-Serrano *et al* 2013, Pausas *et al* 2012, Vandvik *et al* 2014). Overall, it is now unambiguous that fire has

Box 3. The evolution of flammability.

The idea that flammability (or non-flammability) might be acted on by natural selection has been hotly contested in the literature and there is a suite of theoretical, modeling, and empirical studies exploring this idea. Mutch (1970) originally suggested that species with the capacity to persist after recurrent fires might evolve traits that enhance the flammability of their own community. These arguments suffer from being group-selectionist (Snyder 1984), but can be reformulated within the framework of inclusive fitness theory: flammability-enhancing traits could be favoured in individuals because they increase the mortality of neighbours, and this creates space for the offspring of the flammable individual to recruit ('kill thy neighbour' hypothesis, Bond and Midgley 1995). This hypothesis applies quite narrowly to species for which recruitment is fire-stimulated, with soil or canopy-stored seed banks. Gagnon *et al* (2010) argued that high flammability could also increase individual-level fitness if it resulted in high spread rates: a short residence time would increase survival of below-ground organs and plant propagules. Midgley (2013) criticized these two explanations as being contradictory, but proposed that selection *against* flammability, i.e. selection for non-flammable plant traits, could be both selected for and evolve. Pausas *et al* (2017) integrated all these ideas into a framework that shows that while flammability can be subject to natural selection, the type of selection and resultant plant traits depend on the environment and ecological strategy of the species. They identified three fire strategies 'hot-flammable', 'fast-flammable', and 'non-flammable' that include all examples mentioned above, and presented a framework to predict in which environments these strategies should occur.

There are several studies that demonstrate correlations between serotiny and flammable traits in ecosystems and across phylogenies (Schwilk and Ackerly 2001, He *et al* 2011, Burger and Bond 2015). Moreover, recent experimental evidence supports the idea that different fire regimes can generate within-species variation in flammability (Pausas *et al* 2012), that has a genetic basis (Moreira *et al* 2014). Considering the growing literature showing that plants can have a role in shaping the niches that they occupy (Laland and Sterelny 2006), it seems odd that there is resistance to the idea that plant traits related to flammability or fire suppression can be anything other than an exaptation. An analysis of all papers published in the last 40 years on this topic (see methods in SI) demonstrates that more papers have been published supporting than detracting from the hypothesis, especially those that make conceptual and empirical advances (table B1). Publications in support of selection for flammability traits are growing, and are moving beyond arguments to include modelling and data-driven tests of the theory. However, it is worth noting that most of these tests (77%) consider only serotiny and flammability, not the evolution of flammability more broadly, and that this burgeoning research field is dominated by a few names (65% of the papers are published by four authors).

Table B1. Analysis of publications on the evolution of flammability. Since the idea was mooted in the 1970s more papers have been published supporting the idea than against it and it has more empirical and theoretical support in the literature. See SI for methods.

	Flammability is subject to natural selection	Flammability is NOT subject to natural selection
1970	1	0
1980	0	2
1990	3	0
2000	6	0
2010	17	6
Advancing theory	6	2
Argument	7	4
Data	14	2

had a major role in shaping plant traits in fire-prone environments (He and Lamont 2017).

Given that plant traits influence flammability, and fire regimes affect the traits of plants, we expect to see correlated evolution between traits that enhance flammability and traits that enable fire tolerance and regeneration. In spruce and some pines dead branch retention produces 'ladder fuels' enabling fires that start in the ground layer to reach tree canopies, facilitating stand-replacing crown fire regimes. Branch retention has been demonstrated to have co-evolved with serotiny, which is an effective strategy in crown fire ecosystems (He *et al* 2012, Schwilk and Ackerly 2001). Conversely, branch-shedding to prevent crown fires is also common in pine species, and is associated with thick bark and other fire-resistance traits. In the boreal forest (figure 3) the Eurasian larch species (*Larix sibirica*, *L. gmelinii*), which drop their branches and burn in surface fires, in many cases survive these fire events due to their high bark thickness. Larch also have longer life-spans than the North American spruce and pine species (*Pinus banksiana*, *Picea mariana*) which retain dead branches, are easily killed by fires, and display serotiny (de Groot *et al* 2013, Rogers *et al* 2015).

Geophysical feedbacks: short and long timescales

We have demonstrated above how plant traits and fuel characteristics affect the types of fires that occur globally. Because fire regimes differ in their biogeochemical impacts there are also consequences for the Earth system. Here we discuss some of these consequences and the relevant timescales at which they occur. In the short term the impacts of fire can be summarised into impacts on surface albedo, surface roughness, nutrient cycling, aerosols, greenhouse gas emissions, and the carbon cycle. In the longer term (i.e. millions of years), fire is important in regulating phosphorous weathering, geologic carbon sequestration, and atmospheric oxygen concentrations.

Short-term feedbacks

Annual to decadal scale impacts of fire are emphasised in current research on fire, and are the focus of efforts to manipulate fire to influence the Earth system (Landry and Matthews 2016). In terms of the land surface energy balance, fires initially reduce surface albedo due to the production and deposition of charcoal. However, their overall effect is thought to

Box 4. Evolution of plant-fire feedbacks at geological timescales.

Over short timescales fire can influence community assembly: the types of plants and plant traits that occur in an environment. These, in combination with atmospheric conditions, climate and soils, influence the fire regime, which over longer time scales can result in evolutionary innovations. Therefore, while fire does not evolve itself, it can respond to changes in the composition of its fuel bed that, in turn, are partly a response to the fire regime to which plants are exposed.

The ability to colonise land created fuel where there was previously none and vastly increased productivity and weathering rates on the Earth's surface. By accelerating weathering, early land plants also reduced atmospheric CO_2 to levels that were compatible with the evolution of leaves, leading to a boom in photosynthesis. This high productivity (and associated organic carbon burial) raised atmospheric O_2 to the point where ignition was possible (Belcher *et al* 2010b, Scott 2000), and the first vegetation-fuelled fires occurred. Approximately 300 million years ago plants evolved lignin for structural support (Kenrick and Crane 1997). This new form of organic carbon was difficult to decompose so organic carbon was buried, rather than respired, as evidenced by the huge deposits of coal that formed in the Carboniferous period. This further increased atmospheric O_2 (Lenton 2013). Moreover, these large woody structures increased above-ground fuel, so that with more fuels and higher O_2 concentrations the first forests were associated with a dramatic global rise in fire, and possibly the first 'hot-flammable' (Pausas *et al* 2017) fire regimes.

These fire-prone gymnosperm forests have now been pushed to more extreme climatic regimes on our modern planet. About 135 million years ago (MYA), angiosperm species started to invade the understory of gymnosperm forests. These plants had hydraulic pathways that increased productivity and ultimately led them to dominate most environments on Earth today. The rapid spread of angiosperms from 110-70 MYA is associated with a spike in inertinite levels (fossil charcoal) (figure B1)–i.e. a change in fire regime. Bond and Scott (2010) suggest that the angiosperm leaf traits that increase productivity created new fuels that accumulated very rapidly, and probably resulted in frequent, low-intensity fire regimes ('fast-flammable') that the prevailing gymnosperms were ill-adapted to survive (Bamforth *et al* 2014).

The spread and diversification of angiosperms has led to a range of differing fire regimes. Current forest angiosperms (except eucalypts) tend to have thin, flat leaves with rapid decomposition rates (Cornwell *et al* 2015, Grootemaat *et al* 2015). In contrast, gymnosperm leaves decompose slowly, so while gymnosperm litterbeds can accumulate several meters of fire sustaining 'duff' (non-decomposed plant material), in angiosperm forests there is usually very little litter to burn, even when weather conditions are suitable for fire. Interestingly angiosperms also seem to have evolved a unique relationship with fire, with several of the world's most flammable ecosystems being occupied by pyrophytic angiosperms. These include shrubs that have small but thick volatile-rich leaves that carry intense fires, such as chaparrel communities in California or the Cape Flora of South Africa. These pyrophytic plant communities include plants that have smoke-stimulated flowering or seed germination (Keeley *et al* 2012). Moreover, the expansion of tropical forest in the Palaeogene (Wing *et al* 2009) generated large areas with little fire, creating moist, non-flammable microclimates (Hoffmann *et al* 2011), and reducing rainfall seasonality (Lee *et al* 2012). Amazingly therefore, angiosperms appear to have evolved fire preferences across all fire regimes, from pyrophobic rainforests, to low intensity surface fire regimes in temperate forests, through to some of the most flammable pyrophytic plant communities in the world.

More recently the evolution of grasses (Poaceae) within the angiosperms, and particularly the evolution of open habit tropical savanna C4 grasses, with their fine fuels, low bulk density, rapid regrowth and curing rates have brought frequent and extensive surface fires (Hoetzel *et al* 2013, Keeley and Rundel 2005, Osborne and Beerling 2006) to the planet. While the total biomass burned in these grassy fire regimes is small compared with the conflagrations of the Carboniferious (figure B1), the frequency with which these fires occur has resulted in massive ecological filtering, spreading short-statured grassy ecosystems into vast regions of the world that used to be forest. These fires account for ~70% of annual burned area today, and are largely fuelled by grasses from one clade of Poaceae—the Andropogoneae. The impacts this had on Earth system processes have not yet adequately been addressed, but presumably they altered above-ground biomass stocks and C, N and P cycling rates, with consequent impacts on regional climates (Beerling and Osborne 2006).

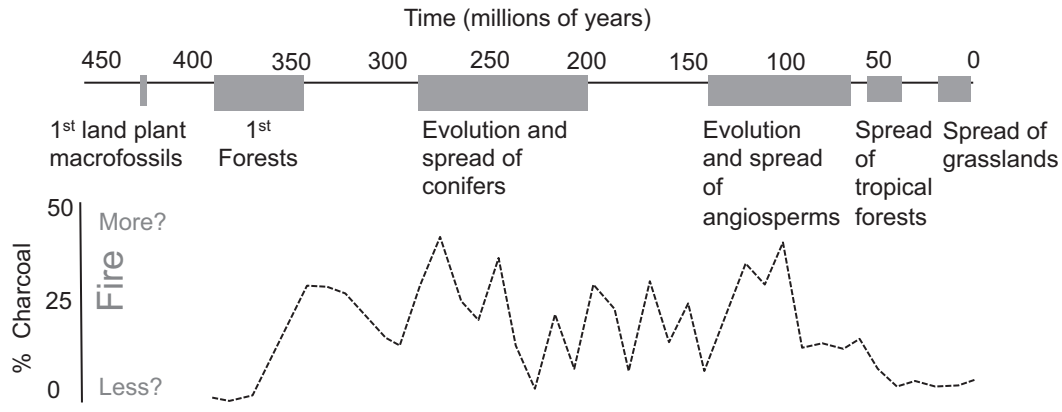

Figure B1. Changes in the abundance of inertinite (fossil charcoal) as preserved in coal deposits tells a robust and long-term story of global trends in fire-activity over the last 400 million years. The first impression is of dramatic changes over time, linked to the evolution of novel plant traits which fundamentally altered the fuel environment, the fire regimes, and the biogeochemistry of the earth. % charcoal taken from Glasspool and Scott (2010), who present the variations in charcoal abundance in a single depositional environment, in different aged rocks, found globally.

be cooling (Landry *et al* 2015, Ward *et al* 2012), as the resulting successional dynamics typically include vegetation types that have higher albedos. This will depend strongly on the albedos of the pre- and post-fire vegetation and land surface, and the rate at which different species recover after a fire (growth rates)—i.e. stronger effects in boreal forest than in grasslands (Kaufman and Fraser 1997, Ward *et al* 2012). Additional short-term land surface impacts result from the reduced surface roughness typical of shorter, more open, vegetation of burned ecosystems. Low surface roughness results in greater wind speeds and warmer surface temperatures (Foley *et al* 2003), which feed back onto greater flammability at local and regional scales (Hoffmann *et al* 2002).

Fires deplete local ecosystems of nitrogen (N) and phosphorus (P) (Pellegrini 2016), but these local losses result in regional and ocean fertilisation (Buendía *et al* 2014, Chen *et al* 2010, Crutzen and Goldammer 1993). The amount of N and P emitted by fires is globally significant (Vitousek *et al* 2013) and depends on the stoichiometry of the fuel: live fuel generally has higher nutrient content than dead fuel (due to translocation of nutrients at senescence), leaves have higher nutrient content than wood, and different plant clades (e.g. angiosperms vs gymnosperms) can differ by orders of magnitude in their nutrient content (Han *et al* 2005). Combustion efficiency (controlled by aeration of fuels and fuel moisture) also affects N loss in fire.

Fire-emitted greenhouse gases such as CH_4, CO and N_2O have a warming effect (Ward *et al* 2012), but fire-emitted aerosols and their precursers scatter (organic carbon) and absorb radiation (black carbon), and the cooling effect is currently thought to predominate (Landry *et al* 2017, Ward *et al* 2012). The aerosols emitted also alter cloud condensation and can affect rainfall patterns regionally (Lohmann and Feichter 2005, Tosca *et al* 2014). Plant traits affect these processes because emission factors (g of particulate matter/chemical compound per kg fuel burned) are strongly influenced by moisture content of the fuel and how aerated it is. Traits such as leaf water content, phenology (deciduous vs evergreen), and architecture will all therefore influence fire emission factors, and consequently, the global energy balance. This is particularly significant in smouldering peat fires because moisture content, bulk density and aeration control the balance of smouldering combustion.

The combustion flux of CO_2 through fire is a major component of the carbon cycle in the short term—contributing to year-to-year variability in carbon storage (van der Werf *et al* 2006). However this carbon is quickly taken up again by regrowing vegetation, so fires will only alter the global carbon cycle if there is a mismatch between rates of burning and regrowth. It has been argued that a focus on fire carbon-fluxes from vegetation to atmosphere is misdirected, and that even at short timescales it is more relevant to consider how fire mediates fluxes from the passive soil carbon pool to the atmosphere (Landry and Matthews 2016). Anthropogenic burning of coal is a key example, but wildfires can affect the soil carbon pool negatively by burning soil carbon and peat (Giglio *et al* 2010, Turetsky *et al* 2011), and positively through char production (passive black carbon (Santín *et al* 2016)). The amount of biomass above-ground, and the amount of peat in the soil, are a function of both vegetation growth rate and decomposition rate (Grootemaat *et al* 2015). Therefore key plant innovations that have resulted in altered fire regimes (see box 4) are often associated with novel photosynthetic pathways/leaf anatomy (Bond and Scott 2010, Bowman *et al* 2009) that will affect both photosynthetic rates and decomposition rates.

It is evident at pluri-millenial and millennial timescales that fire-climate feedbacks are vegetation-dependent. In the extra-tropics biomass burning (figure 6(*c*)) shows the same increasing trend since the last glacial maximum as CO_2 (figure 6(*a*)), CH_4 (figure 6(*b*)) and temperature (figure 6(*f*)) (~20 000 years ago to present) (Carcaillet *et al* 2002, Power *et al* 2008). This is probably due to higher temperatures increasing the opportunities for burning. However, grassy tropical and sub-tropical systems show an opposite trend (figure 6(*d*)) with peaks during periods of low CO_2, CH_4, and temperature—i.e. glacial periods (Daniau *et al* 2013, Haberle and Ledru 2001, Nelson *et al* 2012, van der Kaars *et al* 2000, Wang *et al* 2005). The hydrology (Daniau *et al* 2013) and low CO_2 (Bond and Midgley 2012a) during glacial periods increases grassy fuel loads. Thus, despite low temperatures, tropical biomass burning increases.

Thonicke *et al* (2005) illustrate how a change in the type of fuel can modify fire-Earth system feedbacks. Using a DGVM coupled to a fire model they demonstrate that the expanded grasslands during the last glacial maximum would have increased area burned in the tropics and sub-tropics and reduced it in higher latitudes (corroborating the charcoal data from figure 6). Although total fire emissions were not substantially different from current day, the NO_x emitted in the tropics by grassy fires could have had a significant impact on the oxidative capacity of the atmosphere and might explain why atmospheric CH_4 was so much lower than it is today.

Longer-term feedbacks

Over longer (geological) timescales the fire-feedbacks on radiative forcing and atmospheric CO_2 are dwarfed by feedbacks related to the geochemical cycling of atmospheric O_2 (Mills *et al* 2016). Lenton (2013) suggests that fires are essential for maintaining O_2 within the relatively stable bounds (~16% to ~35%) necessary to sustain life on the planet for 100s of millions of years. When CO_2 is reduced to organic carbon through photosynthesis, O_2 is released. If parts of this reduced organic carbon escape consumption by heterotrophs it is not respired again and when buried in

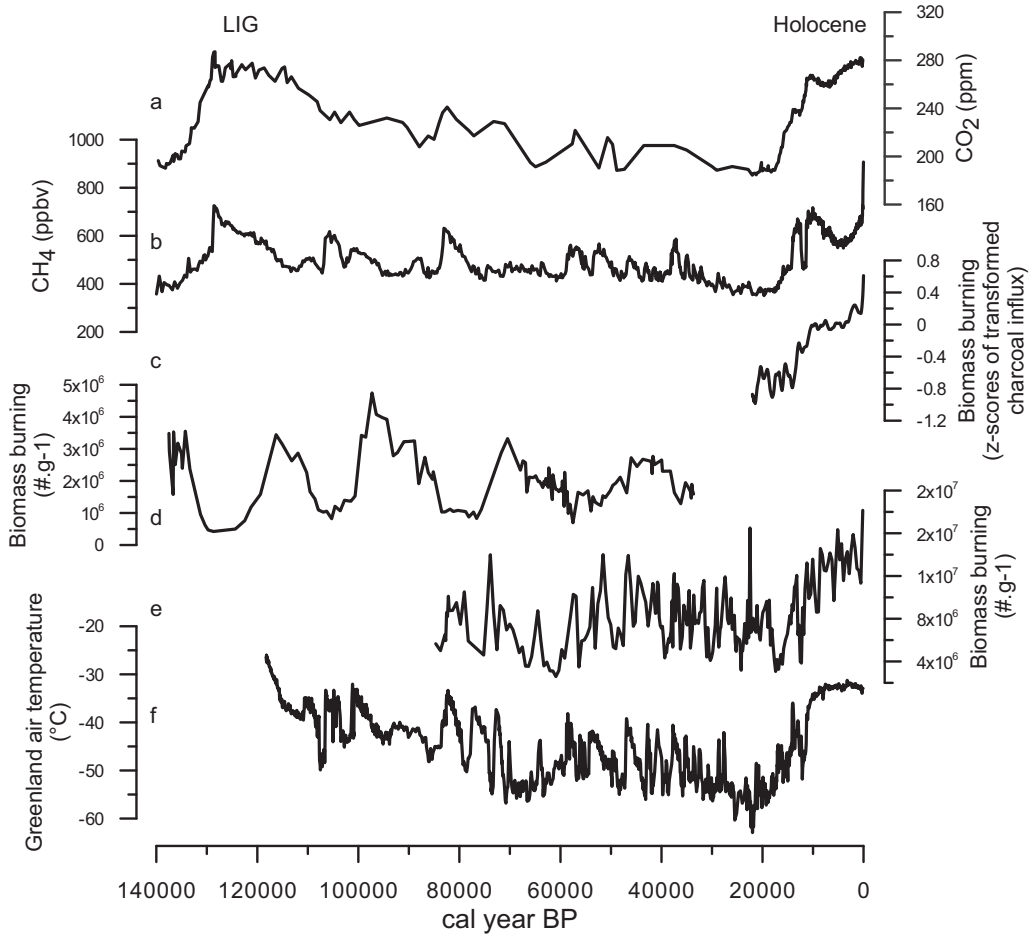

Figure 6. Integrating various paleo-records of charcoal against CO_2 and CH_4 records for the last 140 000 years. Composite records of (*a*) CO_2 and (*b*) CH_4 concentration from Antarctic ice cores (Loulergue *et al* 2008, Lüthi *et al* 2008); (*c*) global biomass burning reconstruction (Daniau *et al* 2012) showing increasing fire when CO_2 and CH_4 increase during our present Holocene interglacial; (*d*) biomass burning reconstruction of southern Africa (Daniau *et al* 2013) (microcharcoal concentration expressed in number of fragments per gram of dried bulk sediment) showing low fire activity during the last warm interglacial (LIG) despite high CO_2 and CH_4 concentrations; (*e*) biomass burning reconstruction of south-western Iberia (Daniau *et al* 2007) showing the rapid response of fire to Dansgaard-Oeschger millenial scale variability recorded in (*f*) Greenland air temperature (data compiled in Sanchez-Goni *et al* 2008).

soils or sediments it represents a net flux of O_2 to the atmosphere. Weathering can draw down this atmospheric O_2, but it goes to completion above ~20% O_2 (present day concentration) meaning there must be some stabilising feedback such that as O_2 concentrations increase, rates of carbon burial decrease. Two main hypotheses have been proposed, both of which involve feedbacks with fire and their redistribution of phosphorus.

Fire is very sensitive to O_2 concentrations (see figure 5(*a*)). At 30% O_2 vegetation as moist as 80% dry weight will ignite (Watson and Lovelock 2013), which implies that even tropical forests could readily carry a fire. Fire exclusion experiments demonstrate that ecosystems which burn often have less above-ground vegetation than climate/soils can support (Bond *et al* 2005)—i.e. increased flammability results in less above-ground biomass. Therefore, under high O_2 we would anticipate more frequent and intense fires (Belcher and Hudspith 2017) that would suppress large land plant biomass, slowing biological weathering rates, and the rate at which key nutrients like phosphorus are released from rocks (Lenton 2001). This is because plant roots actively mine soils for phosphorus, and can increase weathering rates by an order of magnitude (Quirk *et al* 2012). This decline in phosphorus supply from the land to the ocean tends to limit carbon burial over the long-term (Kump 1988, Lenton 2001). Therefore, as O_2 increases fire activity feedbacks kick in causing a decline in terrestrial NPP that ultimately lowers the weathering flux of the nutrient phosphorus, slowing carbon burial, the long-term oxygen source.

Plant traits that would affect this key regulating process include stoichiometry (C:P ratios), root characteristics, and all traits that alter flammability and fire behaviour in ecosystems. Currently fire probably limits forests to approximately half of their potential area (Bond *et al* 2005). We know that higher O_2 concentrations would reduce this further, but the consequences for weathering rates and phosphorus cycling are yet to be quantified. Recent evidence for these proposed mechanisms links major carbon burial

events (known as ocean anoxic events) to increases in atmospheric O_2 and fire (Baker *et al* 2017). As such, fires clearly respond to O_2, and higher resolution studies, combined with models of the final stages of these major disruptions to the carbon cycle, should be capable of exploring the nature of the fire-feedback to rising O_2.

Biological vs geophysical feedbacks and geoengineering

Given that global fire regimes are the outcome of both biological and geophysical processes, understanding the impacts of fire over time requires us to understand these feedbacks and the time scales at which they work. A conceptual framework that summarises these ideas is presented in figure 3:

1. plant traits aggregate to produce fuel properties that drive ecosystem flammability (bulk density, fuel structure, packing ratio, fuel moisture, stoichiometry);
2. ecosystem flammability interacts with climate and weather to affect fire regimes;
3. this is expected to feed back on plant traits in the community both by ecological filtering of species, and through evolution by natural selection (e.g. serotiny and branch retention associated with crown fire regimes);
4. these processes help explain current global patterns of fire, vegetation, and climate (including biogeographic conundrums);
5. the fire regimes that emerge from the climate and vegetation traits present will, over short time scales, impact atmospheric CO_2 levels, surface albedo, and aerosols—which in turn influence atmospheric properties, weather, and plant trait distributions;
6. over longer time scales, carbon burial rates, weathering rates of phosphate-bearing rock, and atmospheric O_2 are all impacted by fire regimes, and this influences the biological and geophysical processes mentioned above.

The relevance of the conceptual model presented here becomes clear as we increasingly consider managing Earth system processes through geoengineering. In the boreal forests, Girardin *et al* (2013) demonstrated that vegetation feedbacks with fire would dampen the impacts of changing climates on the fire regimes if spruce was replaced by deciduous broad-leaved species because it would disrupt the feedbacks between increased temperature and more frequent/intense crown fires. Strategic manipulation of fire through fuels is clearly feasible (Hirsch *et al* 2001, Krawchuk and Cumming 2011, Terrier *et al* 2013), and comprehending the full impacts of these interventions would rely on accurately understanding the feedbacks presented in figure 3.

The potential for mitigating high atmospheric CO_2 levels by manipulating fire regimes is similarly being explored in several other regions (Grace 2011, Russell-Smith *et al* 2013). Information presented here demonstrates how this short-term intervention in the carbon cycle needs to be assessed against alterations of the surface energy balance via albedo and aerosols, as well as considering the inevitable biological feedbacks that will occur.

Research challenges: the role of fire in the Earth system

Research on fire in the Earth system has not yet provided the cross-scale and quantified insights needed to predict future fire regimes when novel ecosystems will undoubtedly emerge, and elucidate the role of fire in shaping the Earth system. We work in a world of unprecedented access to data. The overarching challenge here is to reconcile the scales and types of data to produce useful insights. Our research challenges require interdisciplinary collaboration but also centre on how bringing new data and ideas to a field can replace our understanding of the place of fire in the Earth system.

Research challenge (RC) 1: Linking traits to ecosystems (up-scaling). We need models describing how the fuel properties that define ecosystem flammability emerge from the combination of plant traits. These can be combined with information on species distributions to produce spatially explicit maps of fuel properties.

RC2: Biological vs geophysical drivers. Defining the relative roles of fuel versus weather in a changing climate will be critical to predicting future fire, and to managing unwanted changes in the fire regime. Information on fuel properties (above) will enable modellers to move beyond simple measures of NPP to assess the complex and non-linear responses of fire to changes in climate and species composition associated with global change.

RC3: Evolutionary history. Meta-analyses linking plant phylogenies/chronograms, functional traits and patterns of fire (from remotely sensed imagery or fossil charcoal) can be used to examine the influence of fire on the evolution of plants and to test biogeochemical models of O_2. This requires collaborations across a wide range of research areas.

RC4: Biogeochemical feedbacks. It is becoming clear that geochemical models need to incorporate variations in fuel properties as well as fuel amount and atmospheric properties, as these interact to determine both short and long term C cycling feedbacks. Information from RC3 above can be linked with modelling and fossil based studies to improve our understanding of evolutionary changes in vegetation, climatic drivers and regulation of O_2 through time.

Implications

Human impacts on fire include ignition and suppression, connectivity of landscapes, alteration of geophysical drivers such as temperature, and alteration of biological drivers such as species composition and fuel structure. Often it is the impact on fuels that is most poorly understood and managed. The Anthropocene is a time of unprecedented biotic mixing, where novel plant trait combinations and ecosystems are emerging. Any prediction of future fire regimes that uses climate alone would paint a disturbing picture of wholesale increases in fire across all regions, but we know the reality is more complex than that—largely because the response of plant traits and plant communities to global change can act to both increase and decrease vegetation flammability. Moreover, focus on one or a few time-scales when assessing Earth system feedbacks can mask important processes and result in inappropriate interventions. A longer term view would help to separate transient dynamics from major trends in Earth system drivers. Understanding current patterns of fire and vegetation, as well as patterns of fire over geological time, requires research that integrates evolutionary biology, ecology and the biogeosciences.

Acknowledgments

This work was a result of a National Evolutionary Synthesis Center (NESCENT) catalysis meeting on 'The co-evolution of plants and fire and consequences for the Earth system' November 2013. TH and BL acknowledge the support from the Australian Research Council (DP120103389), and BR acknowledges support from NASA ABoVE (NNX15AU56A). Sally Archibald was funded by the Friedel Sellschop award.

ORCID iDs

S Archibald https://orcid.org/0000-0003-2786-3976
M Greve https://orcid.org/0000-0002-6229-8506
D J McGlinn https://orcid.org/0000-0003-2359-3526
J G Pausas https://orcid.org/0000-0003-3533-5786
M Turetsky https://orcid.org/0000-0003-0155-8666

References

Andela N, Morton D C, Giglio L, Chen Y, van der Werf G R, Kasibhatla P S, DeFries R S, Collatz G J, Hantson S and Kloster S 2017 A human-driven decline in global burned area *Science* **356** 1356–62

Andela N, Van Der Werf G R, Kaiser J W, Leeuwen T T, Van Wooster M J and Lehmann C E R 2016 Biomass burning fuel consumption dynamics in the tropics and subtropics assessed from satellite *Biogeosciences* **13** 3717–34

Archibald S 2016 Managing the human component of fire regimes: lessons from Africa *Phil. Trans. R. Soc. B Biol. Sci.* **371** 20150346

Archibald S, Lehmann C E R, Gómez-Dans J L and Bradstock R A 2013 Defining pyromes and global syndromes of fire regimes *Proc. Natl Acad. Sci. USA* **110** 6442–7

Archibald S, Scholes R J, Roy D, Roberts G and Boschetti L 2010 Southern African fire regimes as revealed by remote sensing *Int. J. Wildl. Fire* **19** 861–78

Archibald S, Staver A C and Levin S A 2012 Evolution of human-driven fire regimes in Africa *Proc. Natl Acad. Sci.* **109** 847–52

Axelrod D I 1980 *History of the Maritime Closed-Cone Pines, Alta and Baja California* (Berkeley, CA: University of California Press)

Baker S J, Hesselbo S P, Lenton T M, Duarte L V and Belcher C M 2017 Charcoal evidence that rising atmospheric oxygen terminated Early Jurassic ocean anoxia *Nat. Commun.* **8** 15018

Bamforth E L, Button C L and Larsson H C E 2014 Paleoclimate estimates and fire ecology immediately prior to the end-cretaceous mass extinction in the Frenchman Formation (66Ma), Saskatchewan, Canada *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **401** 96–110

Beerling D J and Osborne C P 2006 The origin of the savanna biome *Glob. Change Biol.* **12** 2023–31

Belcher C M, Collinson M E and Scott A C 2013 A 450-million-year history of fire *Fire Phenomena and the Earth System: an Interdisciplinary Guide to Fire Science* (Oxford: Wiley) pp 229–49

Belcher C M and Hudspith V A 2017 Changes to cretaceous surface fire behaviour influenced the spread of the early angiosperms *New Phytol.* **213** 1521–32

Belcher C M, Mander L, Rein G, Jervis F X, Haworth M, Hesselbo S P, Glasspool I J and McElwain J C 2010a Increased fire activity at the Triassic/Jurassic boundary in Greenland due to climate-driven floral change *Nat. Geosci.* **3** 426

Belcher C M, Yearsley J M, Hadden R M, McElwain J C and Rein G 2010b Baseline intrinsic flammability of Earth's ecosystems estimated from paleoatmospheric oxygen over the past 350 million years *Proc. Natl Acad. Sci.* **107** 22448–53

Black R A and Bliss L C 1980 Reproductive ecology of Picea mariana (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada *Ecol. Monogr.* **50** 331–54

Blackmarr W H 1972 Moisture content influences ignitability of slash pine litter *Res. Note SE-173. Asheville, NC US Dep. Agric. Forest Serv. Southeast. Forest Exp. Station* **7** 173

Blauw L G, Wensink N, Bakker L, Logtestijn R S P, Aerts R, Soudzilovskaia N A and Cornelissen J H C 2015 Fuel moisture content enhances nonadditive effects of plant mixtures on flammability and fire behavior *Ecol. Evol.* **5** 3830–41

Bond W J and Keeley J E 2005 Fire as a global herbivore: the ecology and evolution of flammable ecosystems *Trends Ecol. Evol.* **20** 387–94

Bond W J and Midgley G F 2012a Carbon dioxide and the uneasy interactions of trees and savannah grasses *Phil. Trans. R. Soc. B Biol. Sci.* **367** 601–12

Bond W J and Midgley J J 1995 Kill thy neighbour: an individualistic argument for the evolution of flammability *OIKOS* **73** 79–85

Bond W J and Midgley J J 2012b Fire and the angiosperm revolutions *Int. J. Plant Sci.* **173** 569–83

Bond W J and Scott A C 2010 Fire and the spread of flowering plants in the Cretaceous *New Phytol.* **188** 1137–50

Bond W J, Woodward F I and Midgley G F 2005 The global distribution of ecosystems in a world without fire *New Phytol.* **165** 525–38

Bowman D M J S *et al* The human dimension of fire regimes on Earth *J. Biogeogr.* **38** 2223–36

Bowman D M J S *et al* 2009 Fire in the Earth system *Science* **324** 481–4

Bowman D M J S, Haverkamp C, Rann K D and Prior L D 2017 Differential demographic filtering by surface fires: how fuel type and fuel load affect sapling mortality of an obligate seeder savanna tree *J. Ecol.* (https://doi.org/10.1111/1365-2745.12819)

Bradstock R A 2010 A biogeographic model of fire regimes in Australia: contemporary and future implications *Glob. Ecol. Biogeogr.* **19** 145–58

Bradstock R A, Hammill K A, Collins L and Price O 2010 Effects of weather, fuel and terrain on fire severity in topographically diverse landscapes of south-eastern Australia *Landsc. Ecol.* **25** 607–19

Brooks M L, D'Antonio C M, Richardson D M, Grace J B, Keeley J E, DiTomaso J M, Hobbs R J, Pellant M and Pyke D 2004 Effects of invasive alien plants on fire regimes *Bioscience* **54** 677

Buendía C, Arens S, Hickler T, Higgins S I, Porada P and Kleidon A 2014 On the potential vegetation feedbacks that enhance phosphorus availability–insights from a process-based model linking geological and ecological timescales *Biogeosciences* **11** 3661–83

Burger N and Bond W J 2015 Flammability traits of cape shrubland species with different post-fire recruitment strategies *South African J. Bot.* **101** 40–8

Carcaillet C, Almquist H, Asnong H, Bradshaw R H W, Carrion J S, Gaillard M-J, Gajewski K, Haas J N, Haberle S G and Hadorn P 2002 Holocene biomass burning and global dynamics of the carbon cycle *Chemosphere* **49** 845–63

Carcaillet C, Bergeron Y, Richard P, Frechette B, Gauthier S and Prairie Y 2001 Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? *J. Ecol.* **89** 930–46

Charles-Dominique T, Beckett H, Midgley G F and Bond W J 2015 Bud protection: a key trait for species sorting in a forest–savanna mosaic *New Phytol.* **207** 1052–60

Chen Y, Randerson J T, van der Werf G R, Morton D C, Mu M and Kasibhatla P S 2010 Nitrogen deposition in tropical forests from savanna and deforestation fires *Glob. Change Biol.* **16** 2024–38

Cheney N P, Gould J S and Catchpole W R 1993 The influence of fuel, weather and fire shape variables on fire-spread in grasslands *Int. J. Wildl. Fire* **3** 31–44

Cochrane M A and Barber C P 2009 Climate change, human land use and future fires in the Amazon *Glob. Change Biol.* **15** 601–12

Cole M M 1960 Cerrado, Caatinga and Pantanal: the distribution and origin of the savanna vegetation of Brazil *Geogr. J.* **126** 168–79

Cornwell W K, Elvira A, Kempen L, Logtestijn R S P, Aptroot A and Cornelissen J H C 2015 Flammability across the gymnosperm phylogeny: the importance of litter particle size *New Phytol.* **206** 672–81

Cox J T and Durrett R 1988 Limit theorems for the spread of epidemics and forest fires *Stoch. Process. Appl.* **30** 171–91

Crisp M D, Burrows G E, Cook L G, Thornhill A H and Bowman D M J S 2011 Flammable biomes dominated by eucalypts originated at the cretaceous-palaeogene boundary *Nat. Commun.* **2** 193

Crutzen P J and Goldammer J G 1993 *Fire in the Environment: the Ecological, Atmospheric and Climatic Importance of Vegetation Fires* (Chichester: Wiley)

Crutzen P J, Heidt L E, Krasnec J P, Pollock W H and Seiler W 1979 Biomass burning as a source of atmospheric gases CO, H_2, N_2O, NO, CH_3Cl and COS *Nature* **282** 253–6

D'Antonio C M and Vitousek P M 1992 Biological invasions by exotic grasses, the grass/fire cycle, and global change *Annu. Rev. Ecol. Syst.* **23** 63–87

Daniau A-L, Goñi M F S, Martinez P, Urrego D H, Bout-Roumazeilles V, Desprat S and Marlon J R 2013 Orbital-scale climate forcing of grassland burning in southern Africa *Proc. Natl Acad. Sci.* **110** 5069–73

Daniau A-L, Sánchez-Goñi M F, Beaufort L, Laggoun-Défarge F, Loutre M-F and Duprat J 2007 Dansgaard–Oeschger climatic variability revealed by fire emissions in southwestern Iberia *Quat. Sci. Rev.* **26** 1369–83

Daniau A *et al* 2012 Predictability of biomass burning in response to climate changes *Glob. Biogeochem. Cycles* **26** GB4007

Dantas V D L, Batalha M A, Pausas J G, Carlos D S, Box P O and Carlos S 2016 Fire drives functional thresholds on the savanna—forest transition *Ecol. Lett.* **94** 2454–63

de Groot W J, Cantin A S, Flannigan M D, Soja A J, Gowman L M and Newbery A 2013 A comparison of Canadian and Russian boreal forest fire regimes *Forest Ecol. Manage.* **294** 23–34

de Magalhaes R M Q and Schwilk D W 2012 Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest *J. Ecol.* **100** 1153–63

Díaz S and Cabido M 2001 Vive la difference: plant functional diversity matters to ecosystem processes *Trends Ecol. Evol.* **16** 646–55

Duffin K I, Gillson L and Willis K J 2008 Testing the sensitivity of charcoal as an indicator of fire events in savanna environments: quantitative predictions of fire proximity, area and intensity *Holocene* **18** 279–91

Ellair D P and Platt W J 2013 Fuel composition influences fire characteristics and understorey hardwoods in pine savanna *J. Ecol.* **101** 192–201

Endara M and Coley P D 2011 The resource availability hypothesis revisited: a meta-analysis *Funct. Ecol.* **25** 389–98

Engber E A and Varner III J M 2012 Patterns of flammability of the California oaks: the role of leaf traits *Can. J. Forest Res.* **42** 1965–75

Enright N J, Marsula R, Lamont B B and Wissel C 1998 The ecological significance of canopy seed storage in fire-prone environments: a model for non-sprouting shrubs *J. Ecol.* **86** 946–59

Fill J M, Welch S M, Waldron J L and Mousseau T A 2012 The reproductive response of an endemic bunchgrass indicates historical timing of a keystone process *Ecosphere* **3** art61

Flannigan M D, Krawchuk M A, de Groot William J and Wotton B M and Gowman Lynn M 2009 Implications of changing climate for global wildland fire *Int. J. Wildl. Fire* **18** 483–507

Foley J A, Costa M H, Delire C, Ramankutty N and Snyder P 2003 Green surprise? How terrestrial ecosystems could affect Earth's climate *Front. Ecol. Environ.* **1** 38

Fuentes-Ramirez A, Veldman J W, Holzapfel C and Moloney K A 2016 Spreaders, igniters, and burning shrubs: plant flammability explains novel fire dynamics in grass-invaded deserts *Ecol. Appl.* **26** 2311–22

Giglio L, Randerson J T, van der Werf G R, Kasibhatla P S, Collatz G J, Morton D C and DeFries R S 2010 Assessing variability and long-term trends in burned area by merging multiple satellite fire products *Biogeosciences* **7** 1171–86

Gill A M 1975 Fire and the Australian flora: a review *Aust. Forest* **38** 4–25

Girardin M P, Ali A A, Carcaillet C, Blarquez O, Hély C, Terrier A, Genries A and Bergeron Y 2013 Vegetation limits the impact of a warm climate on boreal wildfires *New Phytol.* **199** 1001–11

Glasspool I J, Edwards D and Axe L 2004 Charcoal in the Silurian as evidence for the earliest wildfire *Geology* **32** 381–3

Glasspool I J and Scott A C 2010 Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal *Nat. Geosci.* **3** 627

Gómez-González S, Torres-Díaz C, Bustos-Schindler C and Gianoli E 2011 Anthropogenic fire drives the evolution of seed traits *Proc. Natl Acad. Sci.* **108** 18743–7

Grace J 2011 Managing forests to manage the carbon cycle *Carbon Manage.* **2** 499–500

Grootemaat S, Wright I J, Bodegom P M, Cornelissen J H C and Cornwell W K 2015 Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species *Funct. Ecol.* **29** 1486–97

Haberle S G and Ledru M P 2001 Correlations among charcoal records of fires from the past 16 000 years in Indonesia, Papua New Guinea, and Central and South America *Quat. Res.* **55** 97–104

Han W, Fang J, Guo D and Zhang Y 2005 Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China *New Phytol.* **168** 377–85

Hantson S *et al* 2016 The status and challenge of global fire modelling *Biogeosciences* **13** 3359–75

He T and Lamont B B 2017 Baptism by fire: the pivotal role of ancient conflagrations in evolution of the Earth's flora *Natl Sci. Rev.* 0nwx041

He T, Lamont B B and Downes K S 2011 Banksia born to burn *New Phytol.* **191** 184–96
He T, Pausas J G, Belcher C M, Schwilk D W and Lamont B B 2012 Fire-adapted traits of Pinus arose in the fiery Cretaceous *New Phytol.* **194** 751–9
Hennenberg K J, Fischer F, Kouadio K, Goetze D, Orthmann B, Linsenmair K E, Jeltsch F and Porembski S 2006 Phytomass and fire occurrence along forest savanna transects in the Comoe national park, Ivory Coast *J. Trop. Ecol.* **22** 303–11
Hernández-Serrano A, Verdú M, González-Martínez S C and Pausas J G 2013 Fire structures pine serotiny at different scales *Am. J. Bot.* **100** 2349–56
Hirsch K, Kafka V and Todd B 2001 Using forest management techniques to alter forest fuels and reduce wild *Tall Timbers Fire Ecology Conf.* **15** 175
Hoetzel S, Dupont L, Schefuß E, Rommerskirchen F and Wefer G 2013 The role of fire in Miocene to Pliocene C4 grassland and ecosystem evolution *Nat. Geosci.* **6** 1027–30
Hoffmann W A, Jaconis S, Mckinley K L, Geiger E L, Gotsch S G and Franco A C 2012 Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna-forest boundaries *Aust. Ecol.* **37** 634–43
Hoffmann W A, Jaconis S Y, McKinley K L, Geiger E L, Gotsch S G and Franco A C 2011 Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna−forest boundaries *Aust. Ecol.* **37** 634–43
Hoffmann W A, Schroeder W and Jackson R B 2002 Positive feedbacks of fire, climate, and vegetation and the conversion of tropical savanna *Geophys. Res. Lett.* **29** 2052
Jaureguiberry P, Bertone G and Diaz S 2011 Device for the standard measurement of shoot flammability in the field *Aust. Ecol.* **36** 821–9
Justice C O, Giglio L, Roy D, Boschetti L, Csiszar I, Davies D, Korontzi S, Schroeder W, O'Neal K and Morisette J 2010 MODIS-derived global fire products *Land Remote Sensing and Global Environmental Change* (New York: Springer) pp 661–79
Kane J M, Varner J M and Hiers J K 2008 The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeders *Forest Ecol. Manage.* **256** 2039–45
Kasischke E S, Williams D and Barry D 2002 Analysis of the patterns of large fires in the boreal forest region of Alaska *Int. J. Wildl. Fire* **11** 131–44
Kaufman Y J and Fraser R S 1997 The effect of smoke particles on clouds and climate forcing *Science* **277** 1636–9
Keeley J E, Bond W J, Bradstock R A, Pausas J G and Rundel P W 2012 *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management* (Cambridge: Cambridge University Press)
Keeley J E, Pausas J G, Rundel P W, Bond W J and Bradstock R A 2011 Fire as an evolutionary pressure shaping plant traits *Trends Plant Sci.* **16** 406–11
Keeley J E and Rundel P W 2005 Fire and the Miocene expansion of C4 grasslands *Ecol. Lett.* **8** 683–90
Kenrick P and Crane P R 1997 The origin and early evolution of plants on land *Nature* **389** 33–9
Krawchuk M A and Cumming S G 2011 Effects of biotic feedback and harvest management on boreal forest fire activity under climate change *Ecol. Appl.* **21** 122–36
Krawchuk M A and Moritz M A 2011 Constraints on global fire activity vary across a resource gradient *Ecology* **92** 121–32
Krawchuk M A, Moritz M A, Parisien M-A, van Dorn J and Hayhoe K 2009 Global pyrogeography: the current and future distribution of wildfire *PLoS* **4** e5102
Kump L R 1988 Terrestrial feedback in atmospheric oxygen regulation by fire and phosphorus *Nature* **335** 152–54
Laland K N and Sterelny K 2006 Perspective: seven reasons (not) to neglect niche construction *Evolution* **60** 1751–62
Lamont B B, He T and Downes K S 2013 Adaptive responses to directional trait selection in the Miocene enabled Cape proteas to colonize the savanna grasslands *Evol. Ecol.* **27** 1099–115
Lamont B B, Le Maitre D C, Cowling R M and Enright N J 1991 Canopy seed storage in woody plants *Bot. Rev.* **57** 277–317
Landry J-S and Matthews H D 2016 Non-deforestation fire vs. fossil fuel combustion: the source of CO_2 emissions affects the global carbon cycle and climate responses *Biogeosciences* **13** 2137
Landry J-S, Matthews H D and Ramankutty N 2015 A global assessment of the carbon cycle and temperature responses to major changes in future fire regime *Clim. Change* **133** 179–92
Landry J-S, Partanen A-I and Matthews H D 2017 Carbon cycle and climate effects of forcing from fire-emitted aerosols *Environ. Res. Lett.* **12** 25002
Lavorel S and Garnier É 2002 Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail *Funct. Ecol.* **16** 545–56
Le Page Y, Oom D, Silva J, Jönsson P and Pereira J 2010 Seasonality of vegetation fires as modified by human action: observing the deviation from eco-climatic fire regimes *Glob. Ecol. Biogeogr.* **19** 575–88
Lee J, Lintner B R, Neelin J D, Jiang X, Gentine P, Boyce C K, Fisher J B, Perron J T, Kubar T L and Lee J 2012 Reduction of tropical land region precipitation variability via transpiration *Geophys. Res. Lett.* **39** L19704
Lehmann C E R, Archibald S A, Hoffmann W A and Bond W J 2011 Deciphering the distribution of the savanna biome *New Phytol.* **191** 197–209
Lenton T M 2001 The role of land plants, phosphorus weathering and fire in the rise and regulation of atmospheric oxygen *Glob. Change Biol.* **7** 613–29
Lenton T M 2013 Fire feedbacks on atmospheric oxygen *Fire Phenomena and the Earth System: an Interdisciplinary Guide to Fire Science* (Oxford: Wiley) pp 289–308
Lohmann U and Feichter J 2005 Global indirect aerosol effects: a review *Atmos. Chem. Phys.* **5** 715–37
López-Soria L and Castell C 1992 Comparative genet survival after fire in woody Mediterranean species *Oecologia* **91** 493–9
Loulergue L, Schilt A, Spahni R, Masson-Delmotte V, Blunier T, Lemieux B, Barnola J-M, Raynaud D, Stocker T F and Chappellaz J 2008 Orbital and millennial-scale features of atmospheric CH_4 over the past 800 000 years *Nature* **453** 383–6
Lu M, Zhou X, Yang Q, Li H, Luo Y, Fang C, Chen J, Yang X and Li B 2013 Responses of ecosystem carbon cycle to experimental warming: a meta-analysis *Ecology* **94** 726–38
Lüthi D, Le Floch M, Bereiter B, Blunier T, Barnola J-M, Siegenthaler U, Raynaud D, Jouzel J, Fischer H and Kawamura K 2008 High-resolution carbon dioxide concentration record 650 000−800 000 years before present *Nature* **453** 379–82
Maurin O, Davies T J, Burrows J E, Daru B H, Yessoufou K, Muasya A M, van der Bank M and Bond W J 2014 Savanna fire and the origins of the underground forests of Africa *New Phytol.* **204** 201–14
McGranahan D A, Engle D M, Fuhlendorf S D, Miller J R and Debinski D M 2012 An invasive cool-season grass complicates prescribed fire management in a native warm-season grassland *Nat. Areas J.* **32** 208–14
Merow C, Smith M J, Edwards T C, Guisan A, McMahon S M, Normand S, Thuiller W, Wüest R O, Zimmermann N E and Elith J 2014 What do we gain from simplicity versus complexity in species distribution models? *Ecography* **37** 1267–81
Meyn A, White P S, Buhk C and Jentsch A 2007 Environmental drivers of large, infrequent wildfires: the emerging conceptual model *Prog. Phys. Geogr.* **31** 287–312
Midgley J J 2013 Flammability is not selected for, it emerges *Aust. J. Bot.* **61** 102–6
Mills B J W, Belcher C M, Lenton T M and Newton R J 2016 A modeling case for high atmospheric oxygen concentrations during the Mesozoic and Cenozoic *Geology* **44** 1023–6
Moncrieff G R, Bond W J and Higgins S I 2016 Revising the biome concept for understanding and predicting global change impacts *J. Biogeogr.* **43** 863–73

Moreira B, Castellanos M C and Pausas J G 2014 Genetic component of flammability variation in a Mediterranean shrub *Mol. Ecol.* **23** 1213–23
Moritz M A, Batllori E, Bradstock R A, Gill A M, Handmer J, Hessburg P F, Leonard J, McCaffrey S, Odion D C and Schoennagel T 2014 Learning to coexist with wildfire *Nature* **515** 58–66
Moritz M A, Parisien M A, Batllori E, Krawchuk M A, Van Dorn J, Ganz D J and Hayhoe K 2012 Climate change and disruptions to global fire activity *Ecosphere* **3** 1–22
Murphy B P, Williamson G J and Bowman D M J S 2011 Fire regimes: moving from a fuzzy concept to geographic entity *New Phytol.* **192** 316–8
Mutch R W 1970 Wildland fires and ecosystems—a hypothesis *Ecology* **51** 1046–51
Myers J G 1936 Savannah and forest vegetation of the interior Guiana plateau *J. Ecol.* **24** 162–84
Nelson D M, Verschuren D, Urban M A and Hu F S 2012 Long-term variability and rainfall control of savanna fire regimes in equatorial East Africa *Glob. Change Biol.* **18** 3160–70
O'Neill R V, Gardner R H, Turner M G and Romme W H 1992 Epidemiology theory and disturbance spread on landscapes *Landsc. Ecol.* **7** 19–26
Olson D M *et al* 2001 Terrestrial ecoregions of the world: a new map of life on Earth *Bioscience* **51** 933–8
Ormeno E, Cespedes B, Sanchez I A, Velasco-García A, Moreno J M, Fernandez C and Baldy V 2009 The relationship between terpenes and flammability of leaf litter *Forest Ecol. Manage.* **257** 471–82
Osborne C P and Beerling D J 2006 Nature's green revolution: the remarkable evolutionary rise of C4 plants *Phil. Trans. R. Soc. London Ser. B-Biological Sci.* **361** 173–94
Le Page Y and Morton D 2014 HESFIRE: an explicit fire model for projections in the coupled human–earth system *Biogeosciences* **11** 10779–826
Pausas J G, Alessio G A, Moreira B and Corcobado G 2012 Fires enhance flammability in Ulex parviflorus *New Phytol.* **193** 18–23
Pausas J G, Alessio G A, Moreira B and Segarra-Moragues J G 2016 Secondary compounds enhance flammability in a Mediterranean plant *Oecologia* **180** 103–10
Pausas J G, Bradstock R A, Keith D A and Keeley J E 2004 Plant functional traits in relation to fire in crown-fire ecosystems *Ecology* **85** 1085–100
Pausas J G and Keeley J E 2009 A burning story: the role of fire in the history of life *Bioscience* **59** 593–601
Pausas J G and Keeley J E 2014a Abrupt climate-independent fire regime changes *Ecosystems* **17** 1109–20
Pausas J G and Keeley J E 2014b Evolutionary ecology of resprouting and seeding in fire-prone ecosystems *New Phytol.* **204** 55–65
Pausas J G, Keeley J E, Schwilk D W, Naquera C, Ivia K and Ecological W 2017 Flammability as an ecological and evolutionary driver *J. Ecol.* **105** 289–97
Pausas J G and Paula S 2012 Fuel shapes the fire–climate relationship: evidence from Mediterranean ecosystems *Glob. Ecol. Biogeogr.* **21** 1074–82
Pausas J G and Ribeiro E 2013 The global fire–productivity relationship *Glob. Ecol. Biogeogr.* **22** 728–36
Pausas J G and Ribeiro E 2017 Fire and plant diversity at the global scale *Glob. Ecol. Biogeogr.* **26** 889–97
Pausas J G, Keeley J E and Schwilk D W 2017 Flammability as an ecological and evolutionary driver *J. Ecol.* 289–97
Pellegrini A F A 2016 Nutrient limitation in tropical savannas across multiple scales and mechanisms *Ecology* **97** 313–24
Platt W J, Ellair D P, Huffman J M, Potts S E and Beckage B 2016 Pyrogenic fuels produced by savanna trees can engineer humid savannas *Ecol. Monogr.* **86** 352–72
Power M J *et al* 2008 Changes in fire regimes since the last glacial maximum: an assessment based on a global synthesis and analysis of charcoal data *Clim. Dyn.* **31** 887–907
Prentice I C, Bondeau A, Cramer W, Harrison S P, Hickler T, Lucht W, Sitch S, Smith B and Sykes M T 2007 Dynamic global vegetation modelling: quantifying terrestrial ecosystem responses to large-scale environmental change *Terrestrial Ecosystems in a Changing World* ed J G Canadell, D E Pataki and L Pitelka (Berlin: Springer) pp 175–192
Quirk J, Beerling D J, Banwart S A, Kakonyi G, Romero-Gonzalez M E and Leake J R 2012 Evolution of trees and mycorrhizal fungi intensifies silicate mineral weathering *Biol. Lett.* **8** 1006–11
Randerson J T, Liu H, Flanner M G, Chambers S D, Jin Y, Hess P G, Pfister G, Mack M C, Treseder K K and Welp L R 2006 The impact of boreal forest fire on climate warming *Science* **314** 1130–2
Rogers B M, Soja A J, Goulden M L and Randerson J T 2015 Differences in boreal fires and climate feedbacks pp 1–7
Russell-Smith J, Cook G D, Cooke P M, Edwards A C, Lendrum M, Meyer C P and Whitehead P J 2013 Managing fire regimes in north Australian savannas: applying aboriginal approaches to contemporary global problems *Front. Ecol. Environ.* **11** e55–63
Sanchez-Goni M F S, Landais A, Fletcher W J, Naughton F, Desprat S and Duprat J 2008 Contrasting impacts of Dansgaard–oeschger events over a western European latitudinal transect modulated by orbital parameters *Quat. Sci. Rev.* **27** 1136–51
Sannikov S N and Goldammer J G 1996 Fire ecology of pine forests of northern Eurasia *Forest Sci.* **48** 151–67
Santín C, Doerr S H, Kane E S, Masiello C A, Ohlson M, Rosa J M, Preston C M and Dittmar T 2016 Towards a global assessment of pyrogenic carbon from vegetation fires *Glob. Change Biol.* **22** 76–91
Scarff F R and Westoby M 2006 Leaf litter flammability in some semi-arid Australian woodlands *Funct. Ecol.* **20** 745–52
Schafer J L, Breslow B P, Hohmann M G and Hoffmann W A 2015 Relative bark thickness is correlated with tree species distribution along a fire frequency gradient *Fire Ecol.* **11** 74–87
Scheiter S, Langan L and Higgins S I 2013 Next-generation dynamic global vegetation models: learning from community ecology *New Phytol.* **198** 957–69
Scholes R J and Walker B H 1993 *An African Savanna: A Synthesis of the Nylsvlei Study* (Cambridge: Cambridge University Press)
Schwilk D W 2003 Flammability is a niche construction trait: canopy architecture affects fire intensity *Am. Nat.* **162** 725–33
Schwilk D W 2015 Dimensions of plant flammability *New Phytol.* **206** 486–8
Schwilk D W and Ackerly D D 2001 Flammability and serotiny as strategies: correlated evolution in pines *Oikos* **94** 326–36
Schwilk D W and Caprio A C 2011 Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest *J. Ecol.* **99** 970–80
Scott A C 2000 The pre-quaternary history of fire *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **164** 281–329
Simon M F, Grether R, de Queiroz L P, Skema C, Pennington R T and Hughes C E 2009 Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by *in situ* evolution of adaptations to fire *Proc. Natl Acad. Sci.* **106** 20359–64
Simon M F and Pennington T 2012 Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado *Int. J. Plant Sci.* **173** 711–23
Simpson K J, Ripley B S, Christin P, Belcher C M, Lehmann C E R, Thomas G H and Osborne C P 2016 Determinants of flammability in savanna grass species *J. Ecol.* **104** 138–48
Snyder J R 1984 The role of fire: much ado about nothing? *Oikos* **43** 404–5
Spracklen D V, Mickley L J, Logan J A, Hudman R C, Yevich R, Flannigan M D and Westerling A L 2009 Impacts of climate change from 2000 to 2050 on wildfire activity and carbonaceous aerosol concentrations in the western United States *J. Geophys. Res. Atmos.* **114** D20301

Stambaugh M C, Guyette R P and Marschall J M 2011 Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime *J. Veg. Sci.* **22** 1094–104
Staver A C, Archibald S and Levin S 2011 Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states *Ecology* **92** 1063–72
Sullivan A L 2009 Wildland surface fire spread modelling, 1990–2007. 2: Empirical and quasi-empirical models *Int. J. Wildl. Fire* **18** 369–86
Swetnam T W and Betancourt J L 1990 Fire-southern oscillation relations in the south western United States *Science* **249** 1017–20
Syphard A D, Radeloff V C, Hawbaker T J and Steward S I 2009 Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems *Conserv. Biol.* **23** 758–69
Terrier A, Girardin M P, Périé C, Legendre P and Bergeron Y 2013 Potential changes in forest composition could reduce impacts of climate change on boreal wildfires *Ecol. Appl.* **23** 21–35
Thonicke K, Prentice I C and Hewitt C 2005 Modeling glacial-interglacial changes in global fire regimes and trace gas emissions *Glob. Biogeochem. Cycles* **19** GB3008
Thonicke K, Spessa A, Prentice I C, Harrison S P, Dong L and Carmona-Moreno C 2010 The influence of vegetation, fire spread and fire behaviour on biomass burning and trace gas emissions: results from a process-based model *Biogeosciences* **7** 1991–2011
Tosca M G, Diner D J, Garay M J and Kalashnikova O V 2014 Observational evidence of fire-driven reduction of cloud *J. Geophys. Res. Atmos.* **119** 8418–32
Turetsky M R, Kane E S, Harden J W, Ottmar R D, Manies K L, Hoy E and Kasischke E S 2011 Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands *Nat. Geosci.* **4** 27
Van Altena C, van Logtestijn R S P, Cornwell W K and Cornelissen J H C 2012 Species composition and fire: non-additive mixture effects on ground fuel flammability *Front. Plant Sci.* **3** 63
van der Kaars S, Wang X, Kershaw P, Guichard F and Setiabudi D A 2000 A late quaternary palaeoecological record from the Banda Sea, Indonesia: patterns of vegetation, climate and biomass burning in Indonesia and northern Australia *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **155** 135–53
van der Werf G R, Randerson J T, Giglio L, Collatz G J, Kasibhatla P S and Arellano A F Jr 2006 Interannual variability in global biomass burning emissions from 1997 to 2004 *Atmos. Chem. Phys.* **6** 3423–41
van der Werf G R, Randerson J T, Giglio L, Collatz G J, Mu M, Kasibhatla P S, Morton D C, DeFries R S, Jin Y and van Leeuwen T T 2010 Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires 1997–2009 *Atmos. Chem. Phys. Discuss.* **10** 16153–230
Van Wagner C E and Pickett T L 1985 Equations and FORTRAN program for the Canadian forest fire weather index system
Vandvik V, Töpper J P, Cook Z, Daws M I, Heegaard E, Måren I E and Velle L G 2014 Management-driven evolution in a domesticated ecosystem *Biol. Lett.* **10** 20131082
Varner J M, Kane J M, Kreye J K and Engber E 2015 The flammability of forest and woodland litter: a synthesis *Curr. Forest Rep.* **1** 91–9
Varner J M, Kuljian H G and Kreye J K 2017 Fires without tanoak: the effects of a non-native disease on future community flammability *Biol. Invasions* **19** 2307–231
Vitousek P M, Menge D N L, Reed S C and Cleveland C C 2013 Biological nitrogen fixation: rates, patterns and ecological controls in terrestrial ecosystems *Phil. Trans. R. Soc. London B Biol. Sci.* **368** 20130119
Wang X, Peng P A and Ding Z L 2005 Black carbon records in Chinese Loess Plateau over the last two glacial cycles and implications for paleofires *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **223** 9–19
Ward D S, Kloster S, Mahowald N M, Rogers B M, Randerson J T and Hess P G 2012 The changing radiative forcing of fires: global model estimates for past, present and future *Atmos. Chem. Phys.* **12** 10857–86
Watson A J and Lovelock J E 2013 The dependence of flame spread and probability of ignition on atmospheric oxygen *Fire Phenomena and the Earth System: An Interdisciplinary Guide to Fire Science* (Oxford: Wiley) pp 273–87
Westerling A L, Hidalgo H G, Cayan D R and Swetnam T W 2006 Warming and earlier spring increases western US forest wildfire activity *Science* **313** 940–3
Whitlock C, Higuera P E, McWethy D B and Briles C E 2010 Paleoecological perspectives on fire ecology: revisiting the fire-regime concept *Open Ecol. J.* **3** 6–23
Whittaker R H 1975 *Communities and Ecosystems* 2nd edn (New York: MacMillan)
Wing S L, Herrera F, Jaramillo C A, Gómez-Navarro C, Wilf P and Labandeira C C 2009 Late paleocene fossils from the Cerrejón formation, Colombia, are the earliest record of neotropical rainforest *Proc. Natl Acad. Sci.* **106** 18627–32
Wittkuhn R S, Lamont B B and He T 2017 Combustion temperatures and nutrient transfers when grasstrees burn *Forest Ecol. Manage.* **399** 179–87
Woodward F I 1987 *Climate and Plant Distribution* 1st edn (Cambridge: Cambridge University Press)
Wright I J *et al* 2004 The worldwide leaf economics spectrum *Nature* **428** 821–7