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To cite this article before publication: Sally Archibald *et al* 2017 *Environ. Res. Lett.* in press <https://doi.org/10.1088/1748-9326/aa9ead>

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# Biological and geophysical feedbacks with fire in the Earth system

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## Keywords:

Evolution, flammability, Earth-system feedbacks, niche-construction, vegetation, climate, plant traits

## 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 – which are the product of evolutionary and ecological processes. Fire is a powerful selective force and, over their evolutionary history, plants across diverse clades have evolved numerous traits that either tolerate or promote fire. 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 biogeochemistry 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.

## Tweetable abstract:

Plant ecology and evolution mediate fire feedbacks in the Earth system

## 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 by changing 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; Pausas and Ribeiro, 2013). For example, increased temperatures raise 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).

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, 2014), 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 (Andela et al., 2016; 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.

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 later, 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 are trying to account for these interactions (Scheiter et al., 2013).

For example, global and regional data analyses have repeatedly suggested that burned area is maximised at intermediate moisture availability (Daniau et al., 2012; Krawchuk and Moritz, 2011; Meyn et al., 2007). The explanation is that at low rainfall there is not enough fuel to burn, whereas 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).

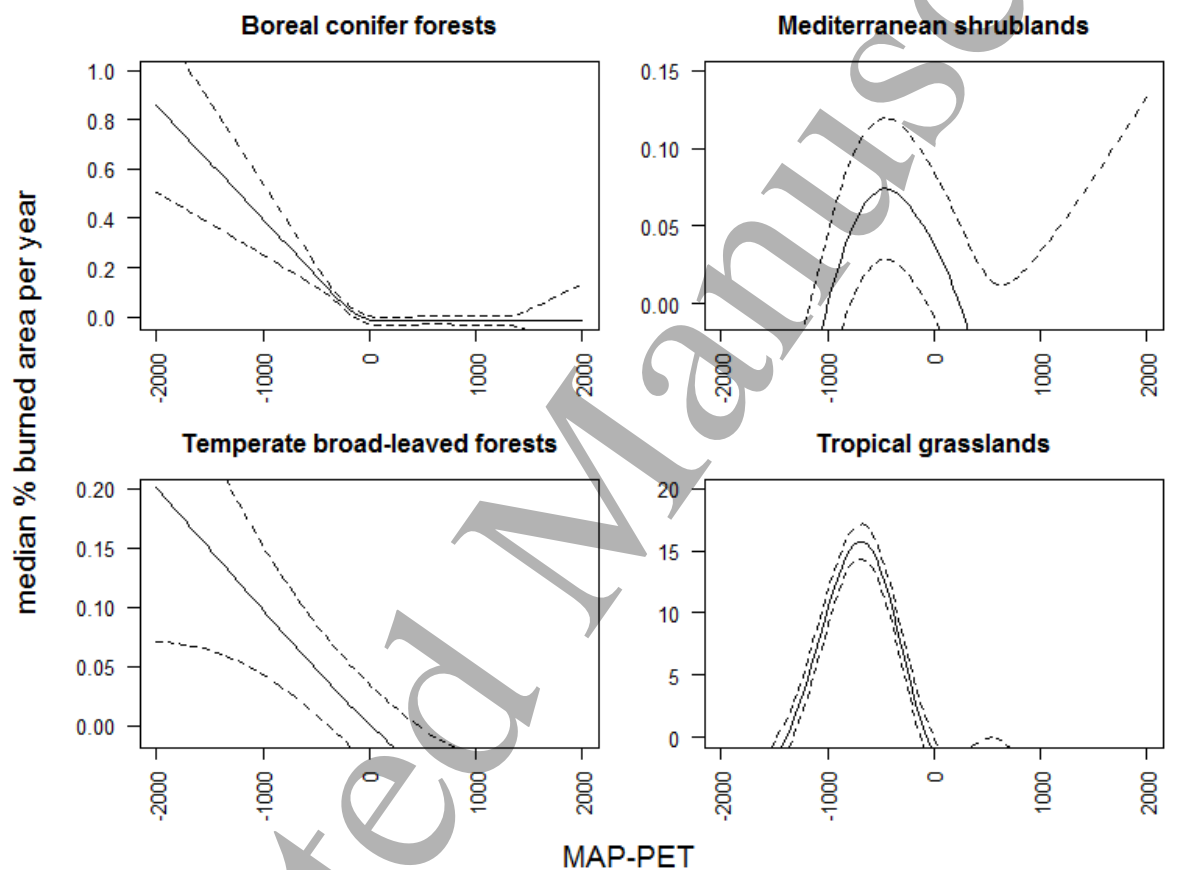


Figure 1: Relationship between the fraction of total area burned and moisture availability (mean annual precipitation – potential evapotranspiration, MAP –PET), demonstrating that vegetation is an important mediator of climate-fire relationships. The “intermediate rainfall” hypothesis is apparent in 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/](http://www.cru.uea.ac.uk/)), and PET from [www.worldclim.org](http://www.worldclim.org). Vegetation was classified using Olson’s ecoregions biome classifications (Olson et al., 2001).

Collation of the literature indicates that studies on feedbacks between fire and vegetation are less common than those 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.

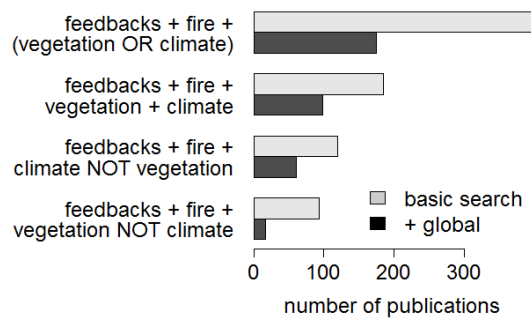


Figure 2: Summary of how fire feedbacks in the Earth system are represented in published literature on the Web of Science (see SI for methods). Only half of the available studies about fire feedbacks consider both vegetation and climate. Global studies on feedbacks with climate are three times more likely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

Humans have had varied and significant impacts on fire for 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 wider consequences of our impacts on fire and to identifying opportunities in managing fire for geoengineering purposes. Solving these challenges requires better interactions between plant and Earth system scientists.

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 collation of relevant 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 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 1980’s (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.

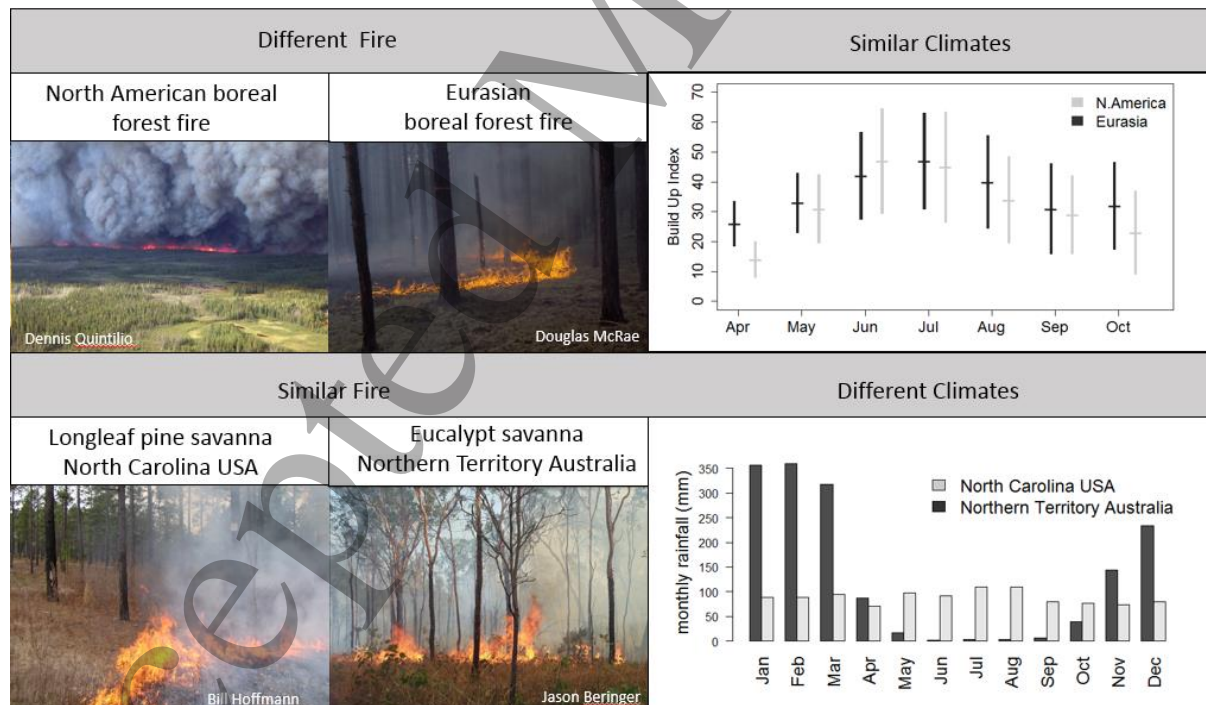


Figure 4: Examples of divergent (top) and convergent (bottom) fire regimes. Boreal North America and Eurasia have different fire regimes (crown fire vs surface fire respectively) but similar climates, and North Carolina, USA and Northern Territory Australia have similar fire regimes but different climates. 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 1985).



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3 One example of divergent fire regimes arises from the difference in plant traits between boreal North  
4 America and Eurasia (Figure 4). North American fires are largely stand-replacing crown fire events (Fire  
5 return interval (FRI) ranging from 80-400 years (Kasischke et al., 2002)) whereas Eurasian fires are  
6 generally surface, litter-fuelled fires (FRI from 15-70 years (Sannikov and Goldammer, 1996)). Boreal  
7 North American fires emit 53% more Carbon (C) per unit area burned but burn one third as much area  
8 on an annual basis, emitting half as much C as Eurasia per year in total. They also have a stronger  
9 cooling effect (radiative negative forcing) due to the larger change in surface properties after fire  
10 (Rogers et al., 2015). The climates in these two regions are too similar to explain these differences  
11 (Rogers et al. 2015; de Groot et al. 2013, Figure 4) and there is evidence that plant traits (Box 2) of the  
12 dominant tree species of each region are key drivers of the fire dynamics (Rogers et al., 2015). Fire-  
13 embracing black spruce (*Picea mariana*) has highly flammable evergreen needles and retains dead  
14 branches, thereby facilitating crown fire regimes by allowing fires to climb up to the canopy. Spruce  
15 (*Picea* spp.) dominate in Alaska and Canada, but comprise only 15% of the tree biomass in Eurasia. By  
16 contrast, larch (*Larix* spp.) and pine (*Pinus sylvestris* L.) dominate in Eurasia and tend to resist high-  
17 intensity crown fires: larch is deciduous, and the two pine species shed their dead lower branches, so  
18 that when fire occurs it usually only spreads in the understory without reaching the canopy. As the  
19 same genera are present in both regions, it remains unclear how the differential dominance of  
20 particular functional types on each continent has occurred, or how easy it is to shift from one  
21 community state to another. It is likely that frequent surface fires in Eurasia kill juvenile *Picea* before  
22 they can reproduce (Black and Bliss, 1980), and therefore contribute to maintaining the species  
23 composition and fire regime of the region. In fact, there are similarities with an even better studied  
24 example of divergent fire regimes within a similar climate: alternative stable state dynamics at  
25 forest/savanna boundaries (Dantas et al., 2016; Hennenberg et al., 2006; Hoffmann et al., 2012; Staver  
26 et al., 2011), where regions with similar climate either burn frequently (due to a prominent grassy  
27 understory in savanna) or hardly ever (due to non-flammable litter and microclimate in tropical  
28 forests). While mostly studied in the tropics, this process also occurs in temperate ecosystems

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38 An example of a convergent fire regime, in which regions with very different climates converge on the  
39 same fire regime, occurs between pine savannas of the southeastern USA and tropical mesic savannas.  
40 These pine savannas are structurally similar to tropical savanna ecosystems, with a continuous grassy  
41 understory and an open tree canopy dominated by fire-tolerant longleaf pine (*Pinus palustris*). Like  
42 mesic tropical savannas, surface fires occur every ~3 years (range 0.5-12) (Stambaugh et al., 2011),  
43 and without fire they are soon replaced by broad-leaved forest communities that are much less  
44 flammable (Kane et al., 2008). However, rainfall in long-leaf pine savannas is aseasonal (monthly  
45 rainfall never less than 70mm), in contrast to tropical mesic savannas where seasonal drought is  
46 considered a necessary attribute because it both increases the probability of fire and reduces overall  
47 tree growth rates (Cole, 1960; Lehmann et al., 2011; Scholes and Walker, 1993). How longleaf pine  
48 savannas and tropical savanna fire regimes persist in a system without seasonal drought is best  
49 explained by the traits of *P. palustris* (Ellair and Platt, 2013; Platt et al., 2016). Their leaves are 20-45  
50 cm in length, more than twice as long as other pine species (Schwilk and Caprio, 2011), and, in  
51 combination with a tussock-grass understory, they produce an aerated, flammable fuel bed that  
52 increases fire temperatures, duration of heating and combustion of fuels (Ellair and Platt 2013), and  
53 allows surface fires to burn during most weather conditions (Fill et al., 2012). Thus, two very different  
54 climate systems have converged to produce similar fire regimes through similarities in fuel structure  
55 that arise from biological characteristics of the dominant tree species in the USA.  
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3 Finally, the most telling biogeographic conundrum for global modellers are the numerous examples  
4 where exotic species (with novel plant traits) have invaded a particular ecosystem and fundamentally  
5 altered the fire regime, despite climate/weather conditions remaining unchanged (Brooks et al., 2004;  
6 Pausas & Keeley, 2014). Here plant traits of the invading vegetation are indisputably the factor driving  
7 the change in fire regimes (D'Antonio and Vitousek, 1992; Fuentes-Ramirez et al., 2016). These  
8 dramatic changes in fire regime are well described in the literature across a range of systems (Brooks  
9 et al., 2004), but the conclusion – that including plant traits is essential for describing fire regimes –  
10 has not been adequately incorporated into Earth system research.  
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14 These biogeographic conundrums provide strong evidence for vegetation as a mediator in fire-climate  
15 relationships today. But the types of plants present on Earth have not been static over evolutionary  
16 time (Belcher et al., 2013; Bond and Midgley, 2012b), and thus it is necessary to understand both  
17 ecological and evolutionary processes when assessing feedbacks between fire and vegetation.  
18 Similarly, feedbacks with the Earth system also occur over short (albedo, climate) and longer (nutrient  
19 cycling) time scales. With the advent of global meta-databases of plant traits, and global and paleo-  
20 ecological datasets on fire, we suggest that it is now possible for evolutionary processes to be  
21 incorporated into the study of fire in the Earth system (He and Lamont, 2017). Once we understand  
22 how plant traits mediate fire regimes and *vice versa*, we can then incorporate these effects into Earth  
23 system models of fire and model their changes through geological time. Below we synthesise current  
24 knowledge in this area, describing the pathways by which plant traits both respond to and drive fire  
25 regimes.  
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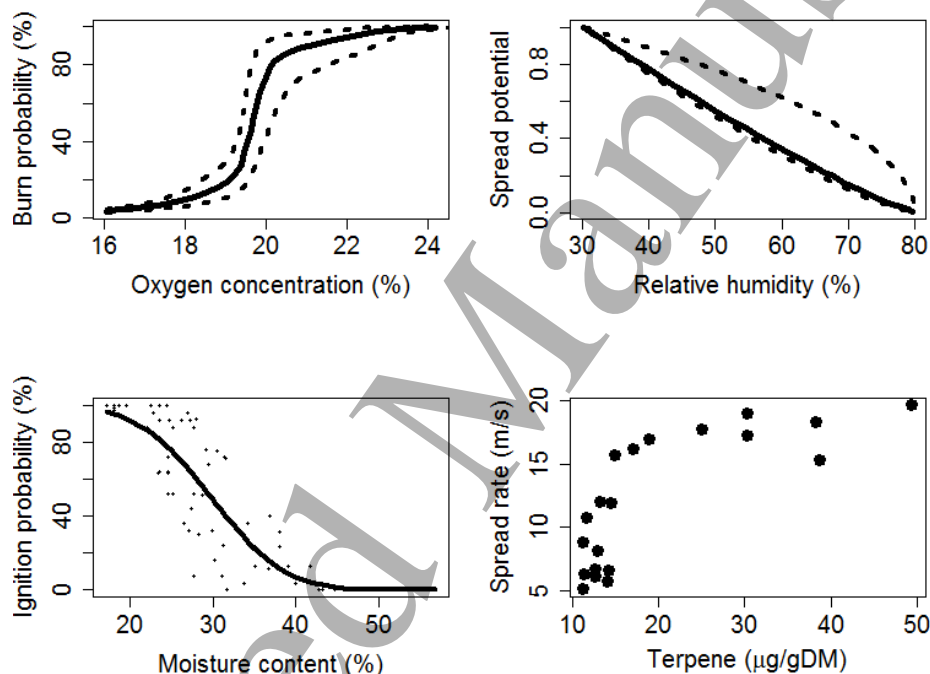
### 31 Ecosystem Flammability

32 Flammability is the propensity of an ecosystem to ignite (given an ignition source) and then propagate  
33 a fire. Fire has therefore often been modelled as an infection/percolation process, with flammability  
34 being defined as the probability of spread (Cox and Durrett, 1988; O'Neill et al., 1992; Sullivan, 2009).  
35 The likelihood of an ecosystem burning depends on both abiotic and biotic properties. These  
36 properties vary across temporal scales – from millions of years ( $O_2$  concentrations of the atmosphere,  
37 evolution of flammable plant traits), to millenia (vegetation distributions, climate), to decades (fuel  
38 amount, community assembly), to days and hours (weather conditions and fuel moisture).  
39 Consequently, different disciplines emphasise particular aspects of flammability (Whitlock 2010). For  
40 example, paleoecologists focus on fuel type and  $O_2$ , Earth system scientists emphasise climate, while  
41 foresters focus on weather and fuels. Current global predictive models of fire tend towards  
42 unidimensional indices of vegetation - e.g. net primary productivity (NPP) - or none at all (Krawchuk  
43 et al., 2009; Moritz et al., 2012; Spracklen et al., 2009), although models linked to DGVMs can define  
44 fuels more precisely (Page and Morton, 2014; Thonicke et al., 2010). NPP is used as a proxy for of the  
45 amount of fuel in a system, but once a certain minimum level of fuel is achieved in a system, how it  
46 burns is controlled more by other fuel properties such as arrangement, density, chemical properties,  
47 and moisture content (Pausas et al., 2017; Schwilk, 2015; Varner et al., 2015).  
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54 Conceptually, the flammability of a system is controlled by a number of factors: temperature, wind  
55 speed, relative humidity,  $O_2$  concentrations, moisture, and the amount and structure of fuels, each of  
56 which can compensate or exacerbate others. For example, it is clear from experimental work that non-  
57 flammable fuel types become flammable as  $O_2$  concentrations increase (Belcher et al., 2010b), such  
58 that even moist forests may have been easy to ignite in the high  $O_2$  atmospheres of the Carboniferous  
59 and Cretaceous periods (Belcher and Hudspeth, 2017). An example at much shorter timescales is the  
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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 of 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 very small changes in the flammability of the system can have large impacts on the area burned and 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 (Juli G. Pausas and Keeley, 2014) 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.



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*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<sub>2</sub> from (Belcher et al., 2010b), relative humidity (Page and Morton, 2014), moisture content (Blackmarr, 1972), and leaf terpene concentration (Ormeno et al., 2009).*

### 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 (2017) identifies 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

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3 flammability strategies for persisting in fire-prone ecosystems (Box 3): *non-flammable* (not easy to  
4 ignite), *fast-flammable* (easy to ignite with high spread rates but low heat release), and *hot-flammable*  
5 (easy to ignite with high heat release). Which of these flammability strategies dominates in an  
6 environment will not only affect the environment for other co-occurring species (via niche-  
7 construction – e.g. Bowman et al., 2017), but will also impact nutrient cycling (eg N-volatilisation,  
8 emission factors), soil properties (water infiltration), and other biogeochemical processes (Wittkuhn  
9 et al., 2017).  
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13 Flammability is a property of the intrinsic chemistry and structure of plant parts, how they are  
14 arranged on the plant (or in the litter bed), as well as ecophysiological properties such as how quickly  
15 they cure, and how quickly they regrow (Table 1). At a leaf level, the size and density of the leaf, as  
16 well as its nutrient content and presence of volatile oils and resins all affect its tendency to ignite  
17 (Cornwell et al., 2015; Pausas et al., 2016) (Table 1). The arrangement of these leaves on a canopy  
18 (plant architecture) can strongly affect flammability: highly branched canopies with high surface area  
19 and low bulk density ( $\text{g cm}^{-3}$ ) are better aerated and easier to ignite, although very sparse branching  
20 can also reduce flammability (Schwilk and Ackerly, 2001; Simpson et al., 2016). Similarly, plants which  
21 retain dead leaf material have higher fuel loads and drier canopies and are therefore both more  
22 ignitable and have higher heat release (Jaureguiberry et al., 2011; Schwilk, 2003). Correspondingly, in  
23 the litter bed flammability is controlled by the packing ratio: the arrangement of individual leaves  
24 based on their morphology (de Magalhaes and Schwilk, 2012; Engber and Varner III, 2012; Kane et al.,  
25 2008; Scarff and Westoby, 2006). The different ways that plant traits alter canopy vs litter fuels (Table  
26 1) can reinforce the divergent flammability strategies mentioned above. For example small leaves  
27 increase heat transfer through canopy fuels but pack more closely together as litter, and thus retard  
28 surface fire spread (Cornwell et al., 2015). Traits that make canopy fuels flammable can therefore  
29 deter litter fires and vice versa (Pausas et al., 2017). Moreover, the amount of fuel and its dryness are  
30 controlled by growth rates, phenology (deciduous vs evergreen trees) and decomposition rates, which  
31 represent the outcome of a range of plant traits and interact with many other aspects of plant  
32 ecological strategy (Table 1).  
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40 *Table 1: Plant traits that influence flammability at leaf and whole plant level, and in terms of life*  
41 *history/physiology. Leaf chemical properties impact heat release rate and propensity of fuel to ignite. Leaf*  
42 *geometry and plant architecture can alter bulk density and moisture content which affect how easily fuel ignites*  
43 *and propagates fire. Moreover, traits such as relative growth rates affect how quickly fuels re-grow after a fire,*  
44 *and can impact fire return times. Decomposition rates are key to defining fuel build up. Generally more*  
45 *flammable leaves (higher C:N ratio) also have slower decomposition rates, therefore flammability is increased at*  
46 *both the leaf level and through time.*  
47

| Leaf level (chemistry)   | Whole plant level (geometry)  | Physiology/phenology  |
|--|---|---|
| <b>Canopy and surface fuels</b><br>Leaf carbon:nitrogen ratio<br>Resins/volatile oils/waxes<br>Specific leaf area<br>Phosphorus concentration<br>Leaf mineral content<br>Leaf moisture content | <b>Canopy and surface fuels</b><br>Leaf size (small leaves allow<br>efficient heat transfer)<br>Leaf angle<br>Branching patterns<br>Height to first branching<br>Canopy depth<br>Retention of dead material<br>Bulk density (packing ratio) | <b>Canopy and surface fuels</b><br>Curing rates<br>Decomposition rates<br>Regrowth rates<br>Deciduousness |

|  |  |  |
|--|--|--|
| <b>Litter fuels</b><br>Leaf C:N ratio<br>Resins/volatile oils/waxes<br>Specific leaf area<br>P concentration | <b>Litter fuels</b><br>Leaf size (large leaves increase fuel bed aeration)<br>Leaf length<br>Litter bed density<br>Fragment sizes in the fuel bed<br>Ratio of leaf to wood | <b>Litter fuels</b><br>Decomposition rate        |
| <b>Moss and peat fuels</b><br>Moisture content<br>Moisture holding capacity<br>Organic matter concentration  | <b>Moss and peat fuels</b><br>Stem density<br>Bulk density<br>Branching architecture   | <b>Moss and peat fuels</b><br>Decomposition rate |

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 plant traits are not necessarily the product of selection for increased or reduced flammability, although there is 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).

**Box 3: The evolution of flammability:**

The idea that flammability (or lack of flammability) might be acted on by natural selection has been hotly contested in the literature and there are 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 the 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 in which recruitment is fire-stimulated, with dormant soil seed banks or serotiny. Gagnon et al (2010) argued that flammability could also increase individual-level fitness if it results 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 of these ideas into a framework which 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 organism. He identified three fire strategies “hot-flammable”, “fast-flammable”, and “non-flammable” which include all examples mentioned above, and presented a framework to predict which environments these strategies should be found.

There are numerous studies demonstrating correlations between serotiny and flammable traits in ecosystems and across phylogenies (Schwilk 2001, Ne’eman 2012, He, 2011, Burger 2015). Moreover,

recent experimental evidence supports the idea that different fire regimes can generate within-species variation in flammability (Pausas et al., 2012), which 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 so much 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 theory, especially those that make conceptual and empirical advances (Figure B1). The 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).

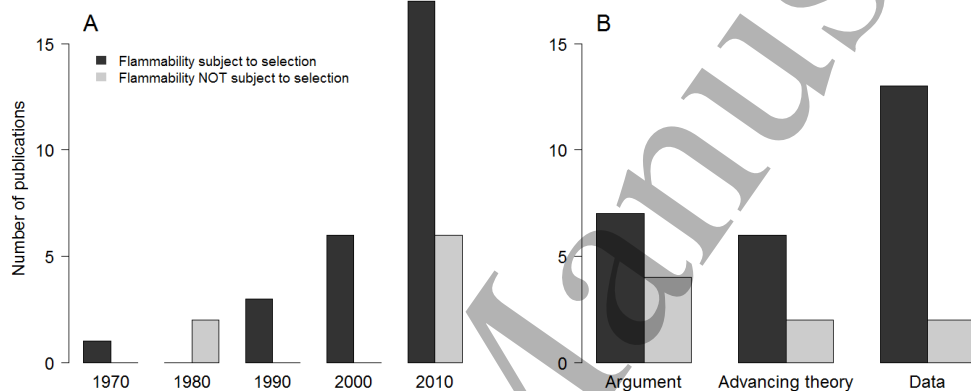


Figure B1: Analysis of publications on the evolution of flammability. More papers have been published supporting the idea than against it (a) and it has more empirical and theoretical support in the literature (b) See SI for methods.

### 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. Plant traits that determine plant performance in post-fire colonisation and regeneration depend on the particular fire regime (Keeley et al., 2011b). 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; Pausas and Keeley, 2014): 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) - which 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

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3 resprouting and thick bark may be linked as part of an overall plant performance strategy (Lamont et  
4 al., 2013; Simon et al., 2009).  
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7 Such fire-plant interactions have sometimes resulted in convergent evolution: similar sets of traits  
8 evolving in different plant lineages exposed to similar fire regimes, which provides compelling  
9 evidence that they are adaptations. The mediterranean ecosystems of the world exemplify this. These  
10 ecosystems are geographically dispersed and do not share many plant lineages, but fire-related traits  
11 (e.g., serotiny, lignotubers, fire-cued flowering and germination) are common across this biome – as  
12 are canopy-fuelled fire regimes with moderate (20–80 year) return times (Keeley et al. 2011, Rundel  
13 et al. 2016). Similarly, in tropical savannas fire-adapted woody life forms which keep most of their  
14 biomass below-ground are found in a number of unrelated plant lineages in both African and South  
15 American savannas (Maurin et al., 2014; Simon and Pennington, 2012).  
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19 Fire regimes are generally determined by the few plant species dominating a landscape, but co-  
20 occurring species - whether flammable or not - need to possess the functional traits that enable  
21 resistance or tolerance of the fire regime. A classic example is tropical savanna ecosystems where  
22 frequent fire is a product of the high annual growth rate of grasses that cure rapidly creating an  
23 aerated fuel bed enabling rapid fire spread. Woody species contribute fairly little to the fuel, but all  
24 savanna plant species possess traits that confer survival under frequent fire. There is evidence that  
25 the most flammable members of a community may have disproportionate effect on the flammability  
26 of the ecosystem (Blauw et al., 2015; de Magalhaes and Schwilk, 2012; Van Altena et al., 2012; Varner  
27 et al., 2017), i.e. yet again, that small changes in the flammability traits of plants can have large  
28 ecological, evolutionary, and geophysical impacts.  
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33 It has been argued that many of the traits that enable species persistence under varied fire regimes  
34 could have evolved as responses to other environmental stresses (for example, drought or herbivory)  
35 as no traits appear exclusively linked to flammability (Axelrod, 1980; López-Soria and Castell, 1992).  
36 However, recent phylogenetic analyses linking the evolution of key fire-tolerant traits (such as bark  
37 thickness and serotiny) to changes in fire regimes lend support to the idea that fire has driven the  
38 emergence and spread of these plant traits across diverse lineages (Crisp et al., 2011; He et al., 2012,  
39 2011; Lamont et al., 2013). In addition, there is evidence of divergence in fire traits among populations  
40 of the same species under different fire regimes (Gómez-González et al., 2011; Hernández-Serrano et  
41 al., 2013; Pausas et al., 2012; Vandvik et al., 2014). Overall, it is now unambiguous that fire has had a  
42 major role in shaping plant traits in fire-prone environments (He and Lamont, 2017).  
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46 Given that plant traits influence flammability, and fire regimes affect the traits of plants, we expect to  
47 see correlated evolution between traits that enhance flammability and traits that enable fire tolerance  
48 and regeneration. In spruce and some pines dead branch retention produces 'ladder fuels' enabling  
49 fires that start in the ground layer to reach tree canopies, facilitating stand-replacing crown fire  
50 regimes. Branch retention has been demonstrated to have co-evolved with serotiny – which, as  
51 discussed above, is an effective strategy in crown fire ecosystems (He et al., 2012; Schwilk and Ackerly,  
52 2001). Conversely, branch-shedding to prevent crown fires is also common in pine species, and is  
53 associated with thick bark and other fire-resistance traits. In the boreal forest, (Figure 4) the Eurasian  
54 larch species (*Larix sibirica*, *Larix gmelinii*), which drop their branches and burn in surface fires in many  
55 cases survive these fire events due to high bark thickness. Larch also have longer life-spans than the  
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3 North American spruce and pine species (*Pinus banksiana*, *Picea mariana*) which retain dead branches,  
4 are easily killed by fires, and display serotiny (de Groot et al., 2013; Rogers et al., 2015).  
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## 9 Geophysical feedbacks: short and long timescales

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

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25 Annual to decadal scale impacts of fire are emphasised in current research on fire, and are the focus  
26 of efforts to manipulate fire to influence the Earth system (Landry and Matthews, 2016). In terms of  
27 the land surface energy balance, fires initially reduce surface albedo due to the production and  
28 deposition of charcoal. However, their overall effect is thought to be cooling (Landry et al., 2015; Ward  
29 et al., 2012), as the resulting successional dynamics typically include vegetation types that have higher  
30 albedos. This will depend strongly on the albedos of the pre- and post-fire vegetation and land surface,  
31 and the rate at which different species recover after a fire (growth rates) - i.e. stronger effects in boreal  
32 forest than in grasslands (Kaufman and Fraser, 1997; Ward et al., 2012). Additional short-term land  
33 surface impacts result from the reduced surface roughness typical of shorter, more open, vegetation  
34 of burned ecosystems. Low surface roughness results in greater wind speeds and warmer surface  
35 temperatures (Foley et al., 2003), which feed back onto greater flammability at local and regional  
36 scales (Hoffmann et al., 2002).  
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42 Fires deplete local ecosystems of nitrogen (N) and phosphorus (P) (Pellegrini, 2016), but these local  
43 losses result in regional and ocean fertilisation (Buendía et al., 2014; Chen et al., 2010; Crutzen and  
44 Goldammer, 1993). The amount of N and P emitted by fires is globally significant (Vitousek et al., 2013)  
45 and depends on the stoichiometry of the fuel: live fuel generally has higher nutrient content than dead  
46 fuel (due to translocation of nutrients at senescence), leaves have higher nutrient content than wood,  
47 and different plant clades (eg angiosperms vs gymnosperms) can differ by orders of magnitude in their  
48 nutrient content (Han et al., 2005). Combustion efficiency (controlled by aeration of fuels and fuel  
49 moisture) also affects N loss in fire.  
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53 Fire-emitted greenhouse gases such as CH<sub>4</sub>, CO and N<sub>2</sub>O have a warming effect (Ward et al., 2012),  
54 but fire-emitted aerosol precursors and aerosols scatter (organic carbon) and absorb radiation (black  
55 carbon), and the cooling effect is currently thought to predominate (Landry et al., 2017; Ward et al.,  
56 2012). However, the aerosols emitted also alter cloud condensation and can affect rainfall patterns  
57 regionally (Lohmann and Feichter, 2005; Tosca et al., 2014). Plant traits affect these processes because  
58 emission factors (g of particulate matter/chemical compound per kg fuel burned) are strongly  
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3 influenced by moisture content of the fuel and how aerated it is. Traits such as leaf water content,  
4 phenology (deciduous vs evergreen), and architecture will all therefore influence fire emission factors,  
5 and consequently, the global energy balance. This is particularly significant in smouldering peat fires  
6 because moisture content, bulk density and aeration control the balance of smouldering combustion.  
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9 The combustion flux of CO<sub>2</sub> through fire is a major component of the carbon cycle in the short term –  
10 contributing to year-to-year variability in carbon storage (van der Werf et al., 2006). However this  
11 carbon is quickly taken up again by regrowing vegetation, so fires will only alter the global carbon cycle  
12 if there is a mismatch between rates of burning and regrowth. It has been argued that a focus on fire  
13 carbon-fluxes from vegetation to atmosphere is misdirected, and that even at short timescales it is  
14 more relevant to consider how fire mediates fluxes from the passive soil carbon pool to the  
15 atmosphere (Landry and Matthews, 2016). Anthropogenic burning of coal is a key example, but  
16 wildfires can affect the soil carbon pool negatively by burning soil carbon and peat (Giglio et al., 2010;  
17 Turetsky et al., 2011), and positively through char production (passive black carbon (Santín et al.,  
18 2016)). The amount of biomass above-ground, and the amount of peat in the soil, are a function of  
19 both vegetation growth rate and decomposition rate (Grootemaat et al., 2015). Therefore key plant  
20 innovations which have resulted in altered fire regimes (see Box 4) are often associated with novel  
21 photosynthetic pathways/leaf/ anatomy (Bond and Scott, 2010; Bowman et al., 2009) which will affect  
22 both photosynthetic rates and decomposition rates.  
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28 It is evident at pluri-millennial and millennial timescales that fire-climate feedbacks are vegetation-  
29 dependent. In the extra-tropics biomass burning (Figure 6c) shows the same increasing trend since  
30 the last glacial maximum as CO<sub>2</sub> (Figure 6a), CH<sub>4</sub> (Figure 6b) and temperature (Figure 6f) (~ 20 000  
31 years ago to present) (Carcaillet et al., 2002; Power et al., 2008). This is probably due to higher  
32 temperatures increasing the opportunities for burning. However, grassy tropical and sub-tropical  
33 systems show an opposite trend (Figure 6d) with peaks during periods of low CO<sub>2</sub>, CH<sub>4</sub>, and  
34 temperature – i.e. glacial periods (Daniau et al., 2013; Haberle and Ledru, 2001; Nelson et al., 2012;  
35 van der Kaars et al., 2000; Wang et al., 2005). The hydrology (Daniau et al 2013) and low CO<sub>2</sub> (Bond  
36 and Midgley, 2012a) during glacial periods increases flammable grass fuel at the expense of trees.  
37 Thus, despite low temperatures, tropical biomass burning increases.  
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41 Thonicke et al. (Thonicke et al., 2005) illustrate how a change in the type of fuel can modify fire-Earth  
42 system feedbacks. Using a DGVM coupled to a fire model they demonstrate that the expanded  
43 grasslands during the last glacial maximum would have increased area burned in the tropics and sub-  
44 tropics and reduced it in higher latitudes (corroborating the charcoal data from Figure 6). Although  
45 total fire emissions were not substantially different from current day, the NO<sub>x</sub> emitted in the tropics  
46 by grassy fires could have had a significant impact on the oxidative capacity of the atmosphere and  
47 might explain why atmospheric CH<sub>4</sub> was so much lower than it is today.  
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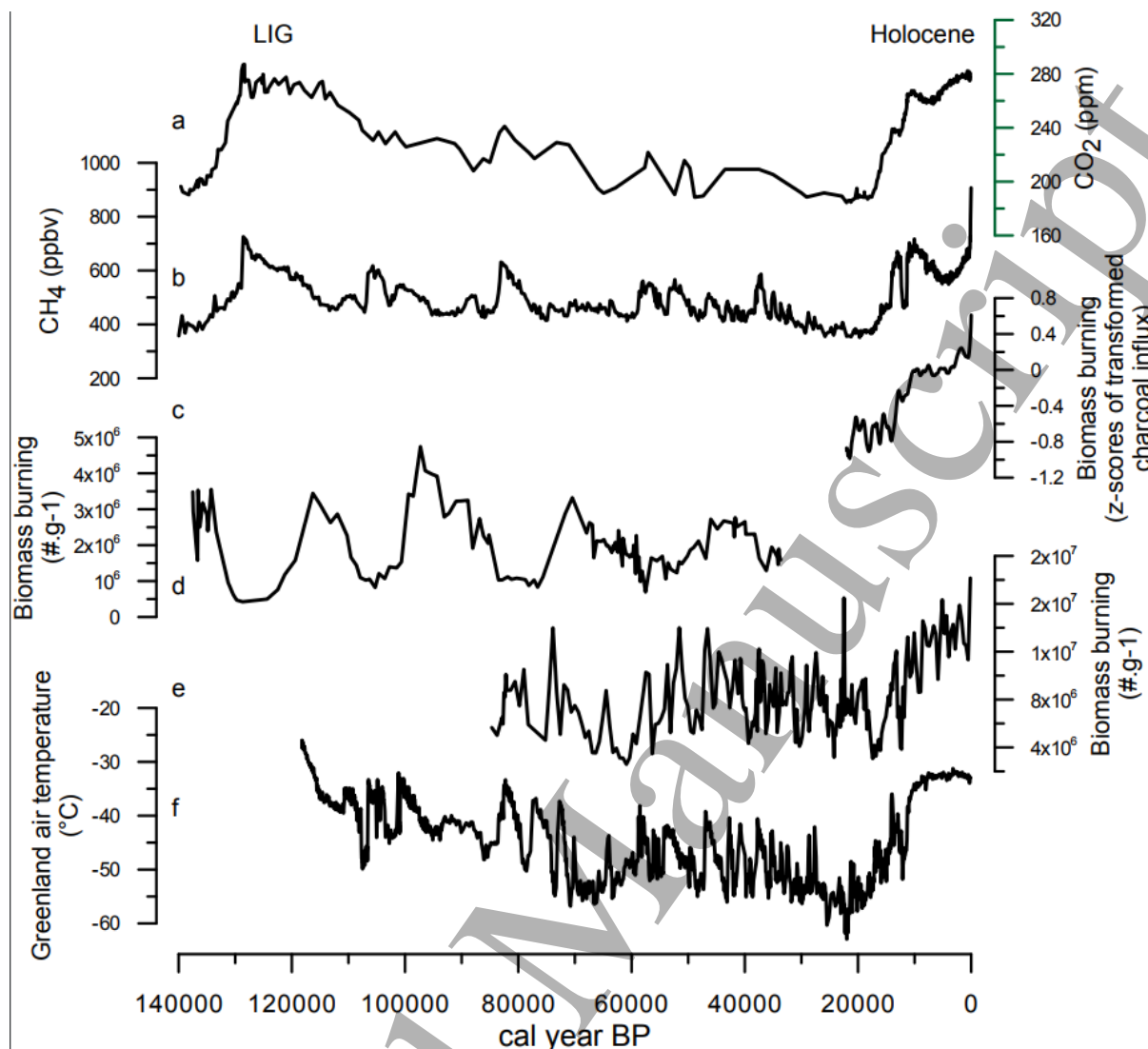


Figure 6: Integrating several different paleo-records of charcoal against CO<sub>2</sub> and CH<sub>4</sub> records for the last 140 000 years. Composite records of a) CO<sub>2</sub> and b) of CH<sub>4</sub> concentration from antarctic ice cores (Loulergue et al., 2008; Lüthi et al., 2008); c) global biomass burning reconstruction (Danialou et al., 2012) showing increasing fire when CO<sub>2</sub> and CH<sub>4</sub> increase during our present Holocene interglacial; d) biomass burning reconstruction of southern Africa (Danialou 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<sub>2</sub> and CH<sub>4</sub> concentrations; e) biomass burning reconstruction of south-western Iberia (Danialou et al., 2007) showing the rapid response of fire to Dansgaard-Oeschger millennial scale variability recorded in f) Greenland air temperature (data compiled in (Goni et al., 2008)).

### Longer-term feedbacks

Over longer (geological) timescales the fire-feedbacks on radiative forcing and atmospheric CO<sub>2</sub> are dwarfed by feedbacks related to the geochemical cycling of oxygen (Mills et al., 2016). These might be key to maintaining atmospheric O<sub>2</sub> within the relatively stable bounds (~16% and ~35%) necessary to sustain life on the planet for 100s of millions of years (Lenton, 2013). When photosynthesis occurs CO<sub>2</sub>

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3 is reduced to organic carbon and  $O_2$  is released. Some of this reduced organic carbon escapes  
4 consumption by heterotrophs and is not respired again: when buried in soils or sediments it represents  
5 a net flux of  $O_2$  to the atmosphere. Weathering can draw down this atmospheric  $O_2$ , but it goes to  
6 completion above  $\sim 20\%$   $O_2$  (present day concentration) meaning there must be some stabilising  
7 feedback such that as  $O_2$  concentrations increase, rates of carbon burial decrease. Two main  
8 hypotheses have been mooted, both of which involve feedbacks with fire and their redistribution of  
9 phosphorus.  
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13 Fire is very sensitive to  $O_2$  concentrations (see Figure 5a). At 30%  $O_2$  vegetation as moist as 80% dry  
14 weight will ignite easily (Watson and Lovelock, 2013), which implies that even tropical forests could  
15 readily carry a fire. Fire exclusion experiments demonstrate that ecosystems that burn often have less  
16 above-ground vegetation than climate/soils can support (Bond et al., 2005); i.e., increased  
17 flammability results in less above-ground biomass. Therefore under high  $O_2$  we would anticipate more  
18 frequent and more intense fires (Belcher and Hudspeth, 2017) that would suppress large land plant  
19 biomass, slowing biological weathering rates, and the rate at which key nutrients like phosphorus are  
20 released from rocks (Lenton, 2001). This is because plant roots actively mine soils for phosphorus, and  
21 can increase weathering rates by an order of magnitude (Quirk et al., 2012). This decline in phosphorus  
22 supply from the land to the ocean tends to limit carbon burial over the long-term (Kump, 1988; Lenton,  
23 2001). Therefore when  $O_2$  increases fire stabilising feedbacks kick in causing a decline in terrestrial  
24 NPP, that ultimately lowers the weathering flux of the nutrient phosphorus, slowing carbon burial, the  
25 long-term oxygen source.  
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31 Plant traits that would affect this key regulating process include stoichiometry (C:P ratios), root  
32 characteristics, and all traits that alter flammability and fire behaviour in ecosystems. Currently fire  
33 probably limits forests to approximately half of their potential area (Bond et al., 2005). We know that  
34 higher  $O_2$  concentrations would reduce this further, but the consequences for weathering rates and  
35 phosphorus cycling are yet to be quantified. Recent evidence for these proposed mechanisms links  
36 major carbon burial events (known as Ocean Anoxic Events) to increases in atmospheric  $O_2$  and fire  
37 (Baker et al., 2017). Fires clearly respond to  $O_2$ , and higher resolution studies, combined with models  
38 of the final stages of these major disruptions to the carbon cycle, might be capable of exploring the  
39 nature of the fire-feedback to rising  $O_2$ .  
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#### Box 4: Evolution of plant-fire feedbacks on geological timescales

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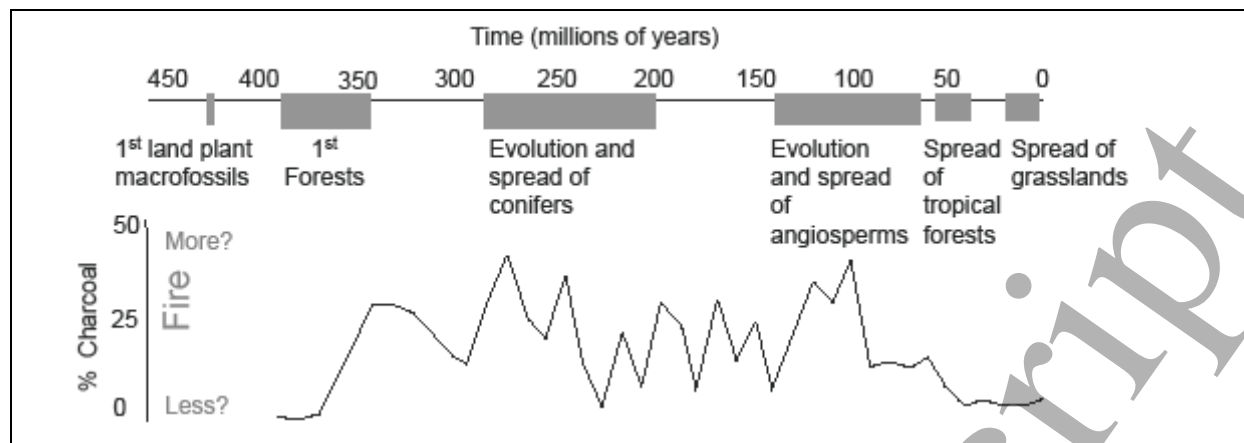


Figure B2: Changes in the abundance of inertinite (charcoal) as preserved in coal deposits tells a robust and long-term story of global trends in fire-activity over the last 400 million years. The first impression is of dramatic changes over time, linked to the evolution of novel plant traits, which fundamentally altered the fuel environment, the fire regimes, and the biogeochemistry of the earth. Charcoal curve modified from Glasspool and Scott (2010), who present the variations in charcoal abundance in a single depositional environment, in different aged rocks, found globally.

The ability to grow on land created fuel where there was previously none and increased productivity and weathering rates on the Earth's surface. By accelerating weathering, early land plants also reduced atmospheric CO<sub>2</sub> 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<sub>2</sub> to the point where ignition was possible (Belcher et al., 2010b; Scott, 2000), and the first vegetation-fueled 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<sub>2</sub> (Lenton, 2013). Moreover, these large woody structures increased above-ground fuel, so with more fuels and higher O<sub>2</sub> concentrations the first forests are 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 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 B2) – i.e. a change in fire regime. Bond and Scott (2010) suggest that the angiosperm leaf traits that increase productivity created new fuels, which 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 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

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3 suitable for fire. Interestingly angiosperms also seem to have evolved a unique relationship with fire,  
4 with several of the world's most flammable ecosystems being occupied by pyrophytic angiosperms.  
5 These include shrubs that have small but thick volatile-rich leaves that carry intense fires, such as  
6 chaparral communities in California or the Cape Flora of South Africa. Both these pyrophytic plant  
7 communities include plants that have smoke-stimulated flowering or seed germination (Keeley et al.,  
8 2011a). Moreover, the expansion of tropical forest in the Palaeogene (Wing et al., 2009) generated  
9 large areas with little fire, creating moist, non-flammable microclimates (Hoffmann et al., 2011), and  
10 reducing rainfall seasonality (Lee et al., 2012). Amazingly therefore, angiosperms appear to have  
11 evolved fire preferences across all fire regimes, from pyrophobic rainforests, to low intensity surface  
12 fire regimes in temperate forests, through to some of the most flammable pyrophytic plant  
13 communities in the world. No other plant group has such a varied relationship with fire and so  
14 significantly influences it. This diversity of relationships with fire over this plant group's 135 million  
15 year history has been set against an overall decline in atmospheric O<sub>2</sub>; perhaps due to this new varied  
16 nature of fire regimes.

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22 More recently the evolution of grasses (Poaceae) within the angiosperms, and particularly the  
23 evolution of open habit tropical savanna C4 grasses, with their fine fuels, low bulk density, rapid  
24 regrowth rates, and rapid curing rates have brought frequent and extensive surface fires (Hoetzel et  
25 al., 2013; Keeley and Rundel, 2005; Osborne and Beerling, 2006) to the planet. While the total biomass  
26 burned in these grassy fire regimes is small compared with the conflagrations of the Carboniferous  
27 (Figure B2), the frequency with which these fires occur has resulted in massive ecological filtering,  
28 spreading short-statured grassy ecosystems into vast regions of the world that used to be forest. These  
29 fires account for ~70% of annual burned area today, and are largely fuelled by grasses from one clade  
30 of Poaceae – the Andropogoneae (Lehmann in prep). The impacts this had on Earth system processes  
31 have not yet adequately been addressed, but presumably they altered above-ground biomass stocks  
32 and C,N and P cycling rates, with consequent impacts on regional climates (Beerling and Osborne,  
33 2006).  
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### 38 39 40 Biological vs geophysical feedbacks and geoengineering

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42 Given that global fire regimes are the outcome of both biological and geophysical processes,  
43 understanding the impacts of fire over time requires us to understand these feedbacks and the time  
44 scales at which they work. A conceptual framework that summarises these ideas is presented in Figure  
45 3:  
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- 47 a) Plant traits aggregate to produce fuel properties which drive ecosystem flammability (bulk  
48 density, fuel structure, packing ratio, fuel moisture, stoichiometry);
- 49 b) Ecosystem flammability interacts with climate and weather to affect fire regimes;
- 50 c) This is expected to feed back on plant traits in the community both by ecological filtering of  
51 species, and through evolution by natural selection (e.g., serotiny and branch retention  
52 associated with crown fire regimes);
- 53 d) These processes help explain current global patterns of fire, vegetation, and climate (including  
54 biogeographic conundrums);  
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3 e) The fire regimes that emerge from the climate and vegetation traits present will, over short  
4 time scales, impact atmospheric CO<sub>2</sub> levels, surface albedo, and aerosols – which in turn  
5 influence atmospheric properties, weather, and plant trait distributions;  
6  
7 f) Over longer time scales, carbon burial rates, weathering rates of phosphate-bearing rock, and  
8 atmospheric O<sub>2</sub> are all impacted by fire regimes, and this influences the biological and  
9 geophysical processes mentioned above.  
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13 The relevance of the conceptual model presented here becomes clear as we increasingly consider  
14 managing Earth system processes through geoengineering. In the boreal forests, (Girardin et al., 2013)  
15 demonstrate that vegetation feedbacks on fire would dampen the impacts of changing climates on  
16 the fire regimes if spruce was replaced by deciduous broad-leaved species because it would disrupt  
17 the feedbacks between increased temperature and more frequent/intense crown fires. Strategic  
18 manipulation of fire through fuels is clearly feasible (Hirsch et al., 2001; Krawchuk and Cumming, 2011;  
19 Terrier et al., 2013), and comprehending the full impacts of these interventions would rely on  
20 accurately understanding the feedbacks presented in Figure 3.  
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24 The potential for mitigating high atmospheric CO<sub>2</sub> levels by manipulating fire regimes is similarly being  
25 explored in several other regions (Grace, 2011; Russell-Smith et al., 2013). Information presented here  
26 demonstrates how this short-term intervention in the carbon cycle needs to be assessed against  
27 alterations of the surface energy balance via albedo and aerosols, as well as considering the inevitable  
28 biological feedbacks that will occur.  
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### 34 Research Challenges: The role of fire in the Earth system

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36 Research on fire in the Earth system has not yet provided the cross-scale and quantified insights  
37 needed to predict future fire regimes when novel ecosystems will undoubtedly emerge, and elucidate  
38 the role of fire in shaping the Earth system. We work in a world of unprecedented access to data. The  
39 overarching challenge here is to reconcile the scales and types of data to produce useful insights. Our  
40 research challenges require interdisciplinary collaboration but also centre on how bringing new data  
41 and ideas to a field can drive forward our understanding of the place of fire in the Earth system.  
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45 **RC1: Linking traits to ecosystems (up-scaling)** We need models describing how the fuel properties  
46 that define ecosystem flammability emerge from the combination of plant traits. These can be  
47 combined with information on species distributions to produce spatially explicit maps of fuel  
48 properties.  
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50 **RC2: Biological vs geophysical drivers.** Defining the relative roles of fuel versus weather in a changing  
51 climate will be critical to predicting future fire, and to managing unwanted changes in the fire regime.  
52 Information on fuel properties (above) will enable modellers to move beyond simple measures of NPP  
53 to assess the complex and non-linear responses of fire to changes in climate and species composition  
54 associated with global change.  
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58 **RC3: Evolutionary history:** Meta-analyses linking plant phylogenies, functional traits and patterns of  
59 fire (from remotely sensed imagery or fossil charcoal) can be used to examine the influence of fire on  
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3 the evolution of plants and to test biogeochemical models of O<sub>2</sub>. This requires collaborations across a  
4 wide range of research areas.  
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6 **RC4: Biogeochemical feedbacks:** It is becoming clear that geochemical models need to incorporate  
7 variations in fuel properties as well as fuel amount and atmospheric properties, as these interact to  
8 determine both short and long term C cycling feedbacks. Information from RC3 above can be linked  
9 with modelling and fossil based studies to improve our understanding of evolutionary changes in  
10 vegetation, climatic drivers and regulation of O<sub>2</sub> through time.  
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## 14 15 Implications

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

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