



Climate–vegetation–fire interactions and feedbacks: trivial detail or major barrier to projecting the future of the Earth system?

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Edited by Josef Settele, Domain Editor, and Mike Hulme, Editor-in-Chief

Fire is a complex process involving interactions and feedbacks between biological, socioeconomic, and physical drivers across multiple spatial and temporal scales. This complexity limits our ability to incorporate fire into Earth system models and project future fire activity under climate change. Conceptual, empirical, and process models have identified the mechanisms and processes driving fire regimes, and provide a useful basis to consider future fire activity. However, these models generally deal with only one component of fire regimes, fire frequency, and do not incorporate feedbacks between fire, vegetation, and climate. They are thus unable to predict the location, severity or timing of fires, the socioecological impacts of fire regime change, or potential non-linear responses such as biome shifts into alternative stable states. Dynamic modeling experiments may facilitate more thorough investigations of fire–vegetation–climate feedbacks and interactions, but their success will depend on the development of dynamic global vegetation models (DGVMs) that more accurately represent biological drivers. This requires improvements in the representation of current vegetation, plant responses to fire, ecological dynamics, and land management to capture the mechanisms behind fire frequency, intensity, and timing. DGVMs with fire modules are promising tools to develop a globally consistent analysis of fire activity, but projecting future fire activity will ultimately require a trans-disciplinary synthesis of the biological, atmospheric, and socioeconomic drivers of fire. This is an important goal because fire causes substantial economic disruption and contributes to future climate change through its influence on albedo and the capacity of the biosphere to store carbon. © 2016 Wiley Periodicals, Inc.

How to cite this article:

WIREs Clim Change 2016, 7:910–931. doi: 10.1002/wcc.428

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Conflict of interest: The authors have declared no conflicts of interest for this article.

Additional Supporting Information may be found in the online version of this article.

INTRODUCTION

The temporal and spatial patterns and ecological effects of fire in a region (the fire regime) are determined by interactions between the biosphere and atmosphere. The atmospheric drivers of fire, at both macro and microclimate scales, are relatively well known, with precipitation, temperature, wind and lightning playing important roles in fuel drying, ignition, spread and extinction of fires (reviewed by Ref 1–3). However, quantifying the biological and socioeconomic drivers of fire remains a major challenge, even under current climate conditions, because of the interactions and feedbacks between fire, vegetation, human intervention, and climate. Consequently, projecting changes in vegetation growth and fuel dynamics under future climatic conditions, necessary to predict future fire activity, is an even more challenging problem.^{4,5}

This challenge is important, firstly because the ability to predict future fire activity could greatly reduce the impacts of fire on human and natural systems. But future fire activity also has the potential to drive climate change by impacting vegetation, the surface radiative balance, terrestrial water cycle, and cloud distributions. If such effects occur at the continental scale, they could result in planetary wide change, including a significant change in the capacity of the biosphere to store carbon. If this is the case, fire has the potential to reframe our understandings of the global carbon cycle, and needs to be better represented in climate models.

Fire activity is inextricably linked to the fire regime. The fire regime can be described simply in terms of the intensity, frequency, seasonality, and type of fire at a site,⁶ but it also encompasses a range of time periods and scales (past, present, or future; a single fire or many fires over years, decades or centuries); different spatial scales affected (e.g. a single ecosystem or vegetation type, a particular geographical area); and whether a fire is of natural or anthropogenic origin. Additionally, the fire regime incorporates the variability of fire intensity, frequency, and seasonality across space and time, the conditions that affect fire occurrence (e.g. fuel type, fire weather), and the ecological impact of the fire.⁷ Attempts have been made to develop a global assessment of fire regimes, but a wide variation in the state of knowledge about the drivers of fire regimes in different geographic regions remains. Generalizations are difficult, because the density, duration, and variability of fire activity within global groupings of fire regimes, or pyromes, do not directly relate to different global vegetation units (biomes).^{8,9} Since a single biome can

contain several different fire regimes, and, alternatively, very different biomes can belong to the same pyrome, the development of future fire regimes in response to changes in climate and human activity is likely to be difficult to predict.⁹

This review aims to identify those aspects of fire activity that can be understood or modeled in the context of climate change, and those which represent unpredictable responses and feedbacks. In order to achieve this, we firstly outline the challenges that exist in projecting fuel loads under future climatic conditions. We do not consider one particular time frame or scenario of future emissions, because the challenges exist regardless of the extent of change. These include the uncertainties inherent in predicting biological responses to future change, uncertainties in the many biological, socioeconomic, and physical drivers, and difficulties in measuring, let alone predicting, the multiscale interactions and feedbacks that exist amongst all drivers. We then assess the contributions that conceptual, empirical, and process models of fire have made towards our understanding of the evolving nature of fire activity in a warming world. And finally, we conclude with recommendations on how progress could be made and future research directions.

CHALLENGES IN PROJECTING FUEL LOADS UNDER FUTURE CLIMATE CONDITIONS

It has been claimed that predictions of ‘the outcomes of climate interactions with future fire regime(s) are almost pure conjecture’ (Ref 10, p. 254). While this claim was made in relation to one forest type in Australia, it is likely to be just as applicable to other biomes around the world. Moving beyond conjecture requires an appreciation of what elements can be projected into the future, which elements cannot, and which could be better understood with more research. Identifying those aspects able to be controlled or modified by humans and those that cannot is also important.

Biological Drivers

Biological responses to increased temperature, carbon dioxide (CO₂), extreme events, and changes to rainfall patterns, as well as shifts in species distributions and interactions, represent one of the greatest challenges to predicting future fire regimes. However, some generalizations are possible. Increased tree mortality is expected in response to drought, increased temperatures and interactions with other

climate-mediated processes such as insect outbreaks.^{11,12} Large trees in particular exhibit reduced growth and biomass production at high temperatures.^{13,14} Fuel loads may increase in the short term as a result of drought responses such as leaf and bark shedding, or, alternatively, compensatory responses such as decreased productivity with decreased rainfall could lead to reduced fuel loads. Increased leaf longevity in response to elevated CO₂¹⁵ may also have consequences for fuel accumulation. Changes in ecosystem processes such as water use, photosynthesis, growth and regeneration, mortality, and litter decomposition are likely to occur in response to changing temperature and precipitation.¹⁶ Increased temperature and CO₂ are expected to increase plant growth through the 'fertilization' effect^{17,18} in ecosystems where rainfall and temperature are not limiting.^{19,20} Alternatively, reduced rainfall may have the opposite effect, although improved water use efficiency with elevated CO₂ could counteract to some extent the reduction in water availability, by reducing water demand and soil drying due to reductions in total transpiration.^{17,21,22} This compensatory effect may be particularly important in water limited systems.²³ These changes have the potential to affect the flammability of forests and fuel loads by changing vegetation structure, species abundance, and species attributes such as wood density or leaf nutrient status, in turn affecting herbivory and decomposition.

Many generalizations, however, have been found to be overly simplistic when scrutinized closely within different ecosystems (e.g. Ref 16,24). Plant growth and regeneration following fire can be affected by disturbance regime,²⁵ competition,^{26,27} or nutrient and water availability. The fertilization effect under elevated CO₂ may not apply in nutrient limited ecosystems, because plants are unable to match the increased carbon with equivalent concentrations of nitrogen. This causes a decline in C:N ratio and a subsequently greater reduction in photosynthesis when nutrient availability is low.^{17,28} Changes to the C:N content of leaves may alter rates of decomposition^{29–32} and palatability to herbivores,^{33–35} with consequent effects on fuel accumulation. Free air enrichment experiments (FACE) have made strong contributions to understanding the range of whole plant responses to atmospheric CO₂ enrichment across diverse ecosystems around the world.^{21,36} Contrasting responses and mechanisms have been demonstrated in different forest types and regions.²¹ Extensive comparative research is therefore still required to develop general models of plant physiological responses and how they influence ecosystems processes and fire activity amongst global vegetation types.

Changes to the extent and species composition of vegetation types are likely to occur³⁷ as species' distributions shift in response to changing climate conditions^{38–40} and human assisted migration or accidental introductions.^{41,42} Changes to vegetation structure may lead to microclimatic changes that can substantially affect fire behavior and severity. Novel ecosystems may emerge, with previously unseen species assemblages and interactions, and new responses to fire. For instance, the spread of invasive species is expected to increase in the future, as the productivity of native species declines,⁴³ and the invasive potential of species changes.^{44–47} Such changes have the potential to alter fuel continuity and flammability across the landscape.^{48–50}

Extensive debate has focused on the competitive interactions between C4 grasses and C3 woody plants under climate change, because invasive C4 species such as Gamba Grass (*Andropogon gayanus*) now drive grass fire cycles in many woody ecosystems around the world.⁵¹ In general, it is expected that climate change will increase the dominance of C4 grasses, because they have higher water use efficiency, greater drought tolerance, and greater persistence in warmer climates compared to C3 species.^{52,53} However, the combined effect of elevated CO₂ and competitive interactions between C4 and C3 plants under different nutrient conditions and seasonality is not well understood, and can lead to idiosyncratic responses.^{52,54} C3 trees, for example, may come to dominate in savannahs under the combination of increasingly frequent fires and elevated CO₂, because they are able to store more non-structural carbohydrate in underground storage organs than grasses, and recover to fire-resistant sizes faster under high CO₂ conditions.²⁵

Positive feedbacks can in some cases cause ecosystem-level transformations, with shifts in fire regime into alternative stable states. One mechanism by which this can occur is if the spread of an invasive species increases flammability and fire spread, excluding fire sensitive native species, and promoting further increases in fire frequency and intensity.⁴⁸ For example, Gamba Grass (*A. gayanus*) and Buffel Grass (*Cenchrus ciliaris*) are very successful invaders in semiarid and savannah ecosystems in Australia, Mexico, Hawaii and the western United States,⁵⁵ forming dense monocultures that exclude native species, causing huge increases in fuel loads and altering the fire regime and functioning of the system.^{56–59} Alternatively, fire may be suppressed when invasive species out-compete dense understory species with lower fuel moisture.⁴⁸ Frequent fire in tropical forests, interacting with climate, resources and species

traits, can cause a shift towards savannah, radically changing fire regimes.^{60,61} This represents a dramatic transformational change, from the most carbon dense and least flammable of all biomes, to the most frequently burnt biome with substantially lower carbon storage capacity. However, biome switching is not always a gradual process. In forests dominated by obligate seeders adapted to fire regimes with relatively long fire return intervals and low intensity fires, for example, increased frequency of severe fire can cause a change in vegetation state following population collapse.^{62,63}

All of these biological responses have the potential to cause a change in the fire regime in different regions. Changes to the fire regime not only affect fuel accumulation, but can have long-term effects on the vegetation structure, composition, and flammability. In combination with demographic changes such as reduced seed production under warmer and drier conditions, more frequent fire may result in ‘interval squeeze,’ leading to greater extinction risk for woody plants, and changed ecosystem structure, composition, and carbon storage.⁶⁴ These unpredictable responses and interactions limit our ability to predict whether fuel loads will increase or decrease at a particular point, let alone predict how fire regimes and fuel loads may change across the landscape or in different ecosystems or regions of the world.

Socioeconomic Drivers

Fire management by humans is a major driver of global fire regimes,^{65–67} and the extent and impact of the sociopolitical drivers of fire is increasing.⁶⁸ Land use change is a key driver of changes to fire activity.⁶⁹ Anthropogenic changes to the frequency, intensity, and timing of fire may lead to shifts in vegetation structure, composition, and flammability. Increased fire frequency is associated with agriculture, afforestation as well as deforestation, arson and prescribed burning to protect biodiversity, infrastructure and population centers.^{70–72} The relationship between humans and fire activity is non-linear, with the highest frequency of fire and largest area burned occurring at intermediate levels of population density and urbanization, declining beyond certain thresholds of ignition rates.⁷³ The impacts of anthropogenic burning are likely to be greatest in systems where fire is naturally rare, fuel load is high, and vegetation is poorly adapted to fire.⁷⁴ Fire suppression to protect assets or resulting from land use change, habitat fragmentation, and artificial barriers (e.g. roads, fuel breaks) leads to vegetation and fire regime changes.⁶⁶ For example, it has been suggested

that long-term exclusion of fire from forests has contributed to the very high intensity and severity of recent wildfires^{70,75} (although this is not accepted by all in all ecosystems^{76,77}). Changes to historical trends in fire suppression and ignition is likely to increase in the future as populations increase and land conversion continues.

As with the biological and climatic drivers of fire, the socioeconomic drivers vary across regions and with time, and may interact with other drivers not controlled by humans.⁷⁸ Fire weather and fuel availability affect the timing and impact of different sources of anthropogenic ignitions (e.g. cigarettes, welding sparks, campfires, and arson).^{73,79,80} Fuel reduction burns have been shown to reduce the severity of wildfires in many regions (e.g. Ref 81), and demands to increase prescribed management burning to reduce fire risk are likely in fire-prone areas as fire frequency rises under climate change. However, under warmer conditions the fire season is projected to occur earlier in the year, and last longer,^{82–86} so quotas for increased prescribed burning may be constrained by a narrowing window of opportunity with suitable weather conditions for controlled burning. Resources available for such management will also be stretched as greater areas require treatment.^{19,87} In many regions prescribed burning is limited by the negative effects of smoke-related particulate matter on human health.^{88–91} Additionally, controlled burning has been shown to be ineffective at reducing fire spread or severity under extreme weather conditions,^{92,93} which are projected to increase with climate change.⁹⁴ Nor is controlled burning always effective at reducing the area burned by unplanned fires.^{93,95–97} An increase in the frequency of prescribed burning may also increase flammability in some vegetation types, a human-induced positive feedback effect.^{63,98,99} In subalpine and alpine forests of south-eastern Australia, for example, Zylstra¹⁰⁰ demonstrated that frequent burning (up to a 14-year cycle) led to changes in forest structure that more than doubled the average size of fires, which spread faster and were more difficult to suppress. Other management options to reduce fuel loads, such as grazing or mechanical removal, may therefore become more important in the future.

Deforestation and increased burning in ‘fire frontiers’ such as high-biomass tropical rainforests, which would not historically have supported fire,⁶⁸ may exacerbate climate change, firstly by releasing carbon stocks, but also by inhibiting regional rainfall through the production of tropospheric smoke layers^{101,102} and the reduction of evaporation,¹⁰³ in turn encouraging more fires.^{104,105} Similarly,

combustion of the massive stores of carbon in both tropical and boreal organic forest soils represents a substantial risk to amplifying atmospheric CO₂ concentrations.¹⁰⁶

Climate Drivers

Several recent reviews provide detailed overviews of the climate drivers of fire (e.g. Ref 1,107). Here we highlight the interactions and feedbacks that exist with the biological and human dimensions that pose challenges in projecting future fire regimes.

Feedbacks, both positive and negative, also exist between macro climate and large-scale fires.¹⁰ Positive feedbacks include the CO₂ emitted,¹⁰⁵ increased lightning caused by smoke contributions to convection,¹⁰⁸ and changes to surface albedo.¹⁰⁹ Changes to albedo can occur within burn perimeters following a single intense fire,¹¹⁰ and as the result of more gradual vegetation change with increased fire frequency in response to drier conditions (e.g. the conversion of boreal forest to tundra¹⁰⁹), but will differ across vegetation types and regionally due to interactions with other drivers.¹¹¹ Carbon and energy exchange is affected immediately after fire, with the release of carbon stores and when productivity and CO₂ sequestration rates are reduced. On longer time scales, the exchange is affected through impacts on soils, drainage, decomposition and vegetation composition.^{106,112,113}

In addition to CO₂, fires emit aerosol particles, which are one of the largest sources of change in the earth's radiation budget.¹¹⁴ Ash and soot from fires affect the global radiation budget directly by scattering and absorbing radiation (the albedo effect), and indirectly by serving as nuclei for cloud formation.^{111,115} Aerosols therefore have a cooling effect on the troposphere,¹¹⁶ a negative feedback that is further strengthened by the increased albedo and biophysical cooling associated with regrowth after high intensity fires.¹⁰⁹ Although improvements have been made in new generations of global climate model (GCM), the effect of smoke aerosols on clouds and the earth's radiation balance remains one of the larger uncertainties in projections of future climate and estimates of anthropogenic effects on climate.¹¹⁷

Ignitions are the ultimate barrier to prediction of future fire. Non-anthropogenic lightning activity appears to have increased with recent warming,¹¹⁸ and, assuming the observed relationship between surface temperatures and lightning activity holds into the future,¹ it is projected to increase further with continuing climate change.^{119–121} It has been estimated, for example, that there may be 10% more lightning

for every 1°C of warming.¹²² However, whether a strike results in a fire event requires many factors to coincide, including the type of lightning event (dry vs wet lightning; positive vs negative lightning strokes), vegetation type, and fuel moisture and condition at the time of the strike, determined by antecedent drought, fuel availability and weather.^{1,123}

Multiscale Interactions

Fire research in the past has tended to concentrate on one spatial or temporal scale at a time,¹²⁴ while the important interactions and feedbacks occur across scales, from the scale of a leaf to global and atmospheric levels, and seconds to centuries^{1,107} (Table 1, Figure 1). Much of our understanding of the interactions between fire, climate and vegetation is based on experimental data at scales that are inappropriate for understanding fire regimes. For example, flammability experiments at the leaf scale have limited relevance to fire behavior at the landscape scale, which is determined by the arrangement, size distribution and ratio of living to dead components of the fuel load and fuel moisture.¹²⁷ Similarly, short-term (from seconds to weeks) physiological responses to elevated CO₂ and temperature at the leaf level are well understood,²¹ but there are fewer data on longer-term CO₂ acclimation responses, which can reverse the increase in photosynthesis and growth seen in short-term studies.¹²⁸ While short-term experiments may overestimate the direct effects of climate change because they do not consider acclimation, they may also underestimate community effects, particularly in ecosystems that respond slowly.¹²⁹ The Free Air Enrichment Experiments (FACE) contributed important information about long-term, ecosystem-level responses to CO₂,^{15,21,130} but there are few data on vegetation responses to CO₂ at larger spatial scales, so there is high uncertainty about how CO₂ enrichment could affect fuel production and amplify or counteract climate variability. Likewise, beyond small plots such as Harvard Forest (<http://harvardforest.fas.harvard.edu/research/LTER>), there have been no studies to investigate the response of forest ecosystems to warming, or changes to precipitation, over the timescale of decades.¹³¹ Scaling up from physiological experiments at small spatial and temporal scales therefore remains a major challenge.¹³¹

While modeling and macro ecological inferences may identify some generalizations about fire–climate interactions at the global scale, they do not always hold at the regional or local scales. For example, plant productivity, and therefore fuel production, is strongly linked to temperature and

TABLE 1 | The Properties and Drivers of Fire Regimes Characterizing the Temporal and Spatial Patterns and Impacts of Fire in a Region (Adapted from Falk et al.¹²⁴).

Property	Drivers			
	Climate/Weather	Biological	Terrain	Social
<i>Spatial characteristics</i>				
Extent—size and spatial homogeneity of burning	Climatic influences on vegetation type, fuel accumulation, and condition Daily and seasonal weather conditions (temperature, humidity, wind) determining fire spread	Fuel type, structure, flammability, vertical continuity, landscape connectivity	Physical barriers to fire spread (e.g. water, gullies)	Suppression capability (accessibility); proximity to valued assets
Intensity—amount and rate of surface fuel consumption	Seasonal weather conditions determining fuel moisture; daily fire weather	Fuel type, structure, flammability, and connectivity (landscape and vertical)	Slope and aspect effects on fuel moisture and fire behavior	Pattern of management burning
Heterogeneity—pattern of burning	Atmospheric instability, wind	Patchiness of flammable fuels across the landscape	Topographic influence on wind (roughness, slope)	Location of built environment; ignition patterns
Severity—impact of fire on biotic and abiotic ecosystem properties	Daily fire weather	Fuel volume, condition, connectivity	Slope and aspect effects on fuel moisture and fire behavior	Suppression capability
<i>Temporal characteristics</i>				
Frequency—number of fires per unit time in an area	Teleconnections, drought, dry lightning frequency and intensity, fire weather	Fuel type and accumulation, regeneration after fire		Frequency of management burns, other human ignitions
Seasonality—timing of fires	Length of fire season	Community composition and structure, phenology (e.g. timing of leaf fall, greenup)	Slope and aspect effects on soil moisture	Timing of management burns, other human ignitions
Duration—length of burn period	Length of fire season	Fuel structure, continuity		Suppression capability

precipitation at the global scale.¹³² However, at the regional scale, diverse socioeconomic drivers (e.g. fire suppression and land use and land cover change) result in complex patterns in fire activity.¹³³ Furthermore, local site factors affect biomass and fuel accumulation, with steep slopes and coarser soils generally being less productive than flatter and finer-textured soils.¹³⁴ Similarly, empirical models of fire activity at different temporal scales provide different understanding of fire–climate–vegetation relationships. For example, models using annually updated climate and land-cover variables characterize the relationship differently to models based on climatological means.¹³⁵ Annual models are able to

capture short-term variation in climate whereas averaged models define broad climate envelopes within which flammable vegetation and fire-conductive climate conditions overlap.

Given the above spatiotemporal constraints on models it follows that the accuracy and precision with which the drivers of fire can be projected under future conditions is also scale dependent (Figure 2). At the continental and global scales, the statistical distribution of key climate variables (precipitation, temperature, wind) is known, and spatial data exist to describe broad vegetation types and ecosystem productivity, so it is possible to model the ‘niche’ of fire.⁶⁸ However at landscape and regional scales

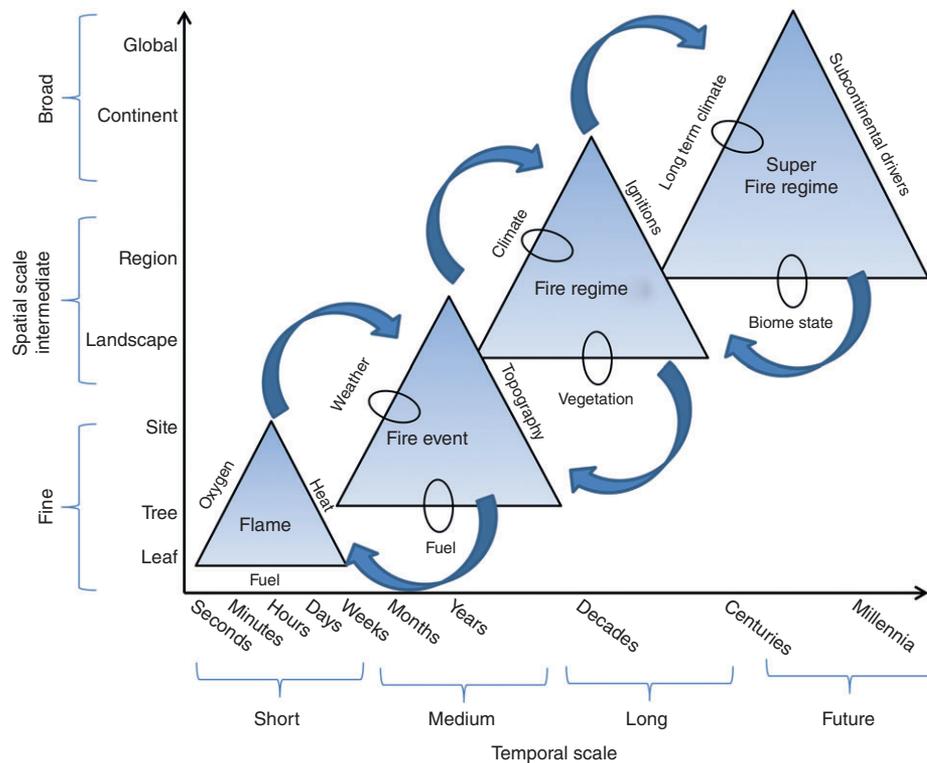


FIGURE 1 | The drivers of fire across multiple temporal and spatial scales. This is an adaptation of the diagram first presented by Moritz et al.,¹²⁵ in which the fire triangle concept was extended to incorporate the feedbacks between fire drivers (small loops) and processes (arrows) at different scales. Whitlock et al.¹²⁶ added the super-fire regime triangle to include the long-temporal perspective supported by paleo-ecological studies. The dominant drivers at each scale are represented by the side of each triangle.

predictability often declines¹³⁶ because accurate mapping of vegetation and fire history (and hence fuel loading), soils and climate is generally lacking. This reduces the ability to capture the influence of natural variability in these drivers. One exception is that recent land management (forestry, agriculture, urbanization) is often available at these intermediate spatial scales, although this does not improve predictability if the impact of management decisions is not monitored. Productivity and vegetation structure can be precisely mapped using surrogate indices based on satellite data, although accuracy is compromised because understorey biomass and structure are not resolved in these measurements. Key microclimatic variables that often help maintain abrupt vegetation boundaries (e.g. wind, precipitation, temperature, and humidity) are not well represented in forecasts or climate models, but with appropriate investment of human and scientific resources very accurate measurements at a single point are possible if the research question warranted that level of detail.¹³⁷ This is also the case for other drivers such as CO₂, biomass, vegetation type and structure, and soil. Although regions with a high incidence of lightning and human ignitions are broadly known,¹³⁸ prediction of ignition

remains a barrier to accurate predictive models of fire occurrence. The importance of anthropogenic ignitions relative to natural ignitions differs around the world,^{139,140} as does our understanding of the factors driving ignitions and our ability to predict them.

Similarly, the ability to project the drivers of fire varies across temporal scales. Fire activity and behavior of an ignited fire can be reasonably well predicted over the scale of days across the landscape using short-term weather forecasts and fire behavior models correctly parameterized for dominant vegetation types. In contrast, estimates of future levels of CO₂ and temperature can only be broadly bounded by scenarios of future emissions. Long-term climate projections are not designed to provide predictions of future conditions, but probabilistic statements of what the future climate could look like if certain conditions are met (see Box 1). Projections of change to fire activity in the near-term are simpler than longer-term projections of changes to fire regimes, because the long term will be determined by global greenhouse gas mitigation and may include non-linear fire regime shifts and unpredictable adaptive response of fire managers. For other drivers, such as wind and precipitation, the accuracy of projections quickly

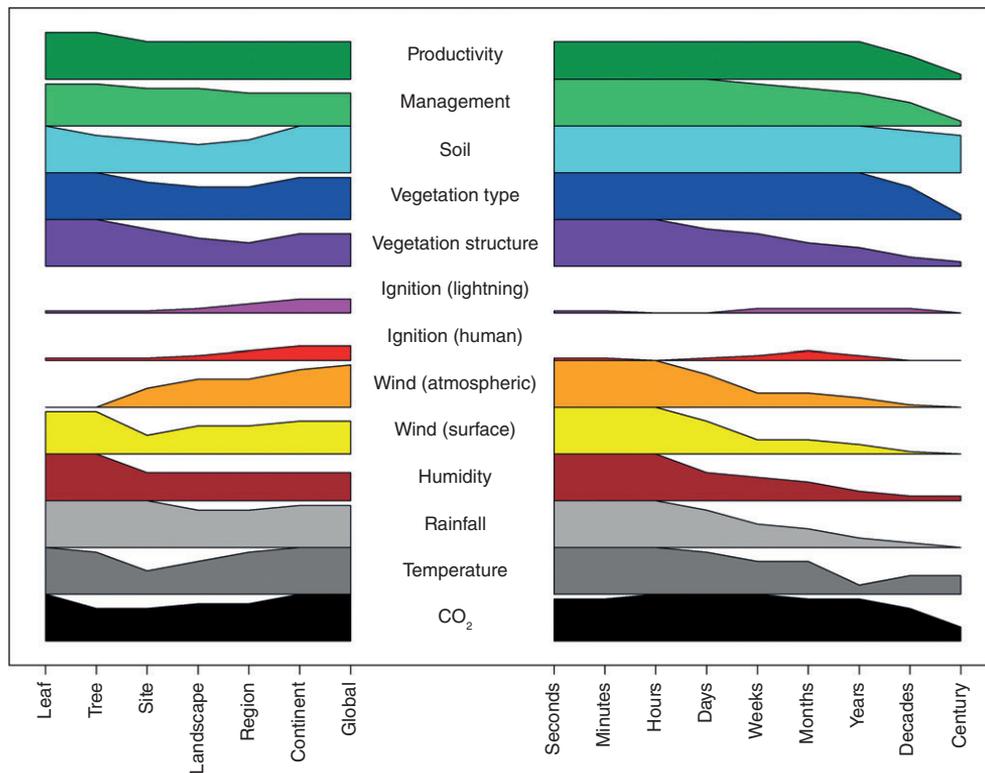


FIGURE 2 | A qualitative assessment of the certainty associated with projections of the drivers of fire across temporal and spatial scales. Thicker wedges indicate greater accuracy in measurements or projections of the driver at each scale. Scores are relative and unit-less. Spatial scale was scored on the ability to predict the variable under current conditions, while temporal scale was scored for one point in space, assuming best available knowledge. Further details are provided in Supporting Information.

degrade over time, either because the underlying physical mechanisms are not fully understood, or the mechanisms operate at a much finer resolution than that of general circulation models.¹⁴¹ Land cover and associated fire activity can be predicted relatively accurately in the short term, but become less predictable at longer time scales due to the influence of social and political demands, which could shift in response to changes in area burnt and perceptions of fire risk to unburnt areas (discussed in *Conceptual Models*). Soil type is relatively static up to the scale of decades, so accurate predictions of soil moisture flux and eco-hydrological dynamics are possible, although landscape scale fires can have dramatic impacts on catchments, resulting in substantial shifts in hydrology and wide scale erosion and soil loss.¹⁴² Sudden changes in soil can also occur when fires consume peatlands¹⁴³ or generate debris flows.¹⁴⁴ At time scales beyond decades, vegetation structure, condition and even type are unpredictable because of the interactions and feedbacks discussed above.

Overall, there are substantial gaps in our ability to project the biophysical drivers of fire, even when each driver is considered in isolation (as in Figure 2).

The ‘cascade of uncertainties’ from the uncertainty associated with future emissions, carbon-cycle modeling and climate modeling¹⁴⁵ drives an even larger range of uncertain climate impacts, which is further compounded by interactions between the drivers of fire across scales of time and space.

APPROACHES RELEVANT TO UNDERSTANDING FUTURE FIRE ACTIVITY

There are three main approaches that can be used to inform our thinking about fire activity under future climate conditions. They were not designed to answer the same questions about fire activity or fire regimes, and are applicable at different scales, but each approach contributes information relevant to the challenge of projecting future fire activity.

Conceptual Models

Several conceptual models have been used to describe fire activity under current climate conditions, and

BOX 1

PREDICTION VERSUS PROJECTION

The challenges in understanding the complex and heterogeneous interactions between vegetation, fire, and climate require clarity in research objectives and an understanding of the available tools, climate models and projections. The most basic approach is to describe systems based on analyses of existing spatial and temporal data, to illuminate potential mechanisms. These mechanisms form the basis of models attempting to *predict* or *project* fire activity under a given climate or plausible future climates.

Fire activity *predictions* seek to describe a very complex response to specific changes in climatic conditions in specific areas, by a particular period in time. For example, fire managers may want to know the changing return interval of large wildfires on the urban fringe so they can best allocate scarce resources to protect lives and property. Climate predictions are generally only available for short-term forecasts (from 30 days to 2 years). They are initialized with observations, and attempt to produce an estimate of the actual evolution of the climate in the future. By contrast, climate *projections* are not predictions of future conditions, but probabilistic statements of what the future climate could look like if certain conditions are met. Their intention is not to make accurate predictions regarding the future state of the climate system at any given point in time, but to represent the range of plausible possible futures climates under a given set of scenarios of climate forcings and model-derived estimates of climate sensitivity (the temperature change resulting from increases in CO₂).¹⁴⁶

provide a basis for thinking about future fire. All acknowledge the importance of climate and weather, operating at a range of temporal scales, in determining fire activity mediated through fuel effects.

The fire regime triangle reflects the three dominant factors influencing fire in different regions of the world.¹⁴⁷ These are the vegetation characteristics, fire weather climatology, and ignition patterns, all of which vary in importance spatially and temporally. This model identifies gradients in fire probabilities that are controlled by long-term environmental norms in addition to the spatial variation in probabilities

driven by inter-annual fluctuations in environmental conditions (climate vs weather).

The intermediate-fire-productivity model, also known as the varying constraints hypothesis,¹⁴⁸ suggests that fire activity peaks at intermediate levels of aridity and productivity, reflecting the changing roles of fuel availability and drought as fire drivers along the productivity gradient.^{132,149,150} In moist, productive regions there is an abundance of fuel, and fire activity is determined by the frequency of dry conditions, while in dry, unproductive regions fire activity is limited by fuel availability. Examples of the former are the Mediterranean-type ecosystems of California in the United States, the Mediterranean Basin of southern Europe and North Africa, the Western Cape region of South Africa and southwest and south Australia. Desert regions around the world belong to the latter, fuel limited type, while the savannahs of northern Australia and Africa represent an intermediate type in which high productivity and very dry conditions alternate between wet and dry seasons.

The four switch model¹⁵¹ integrates many of the processes from the previous concepts, but adds greater understanding of the temporal dimension. It describes fire activity in terms of four factors that must be fulfilled simultaneously (switched 'on') for fire to occur. There must be fuel available (biomass); it must be dry enough to burn (availability to burn); weather conditions must be conducive to fire spread (fire weather), and there must be an ignition source (ignition). The four switches operate at very different temporal scales. The fuel switches develop over years to centuries, the weather switch operates over weeks to months and the ignition switch occurs in seconds.¹⁵²

These conceptual models have contributed to our understanding that fire regimes will change in step with climate change and provide a framework for understanding the mechanisms of change in fire regimes at a global scale. All models suggest that climate change will affect fire activity differently in different biomes or ecosystems, so that fire may increase in some systems and decrease in others. For example, an increase in the frequency of droughts with climate change might increase fire activity in productive forest environments, but reduce fire activity in dry ecosystems where plant growth may be limited and fuel loads reduced.¹³² Identifying the factor limiting fire in different ecosystems is a step forward because climate change will affect the limiting factors in different ways.

However, since these conceptual models were not designed to answer questions about fire activity

under future climate conditions, they have some limitations when applied to this question. One constraint is that they deal with only one component determining fire regimes, the frequency of fire, and ignore other components such as the seasonality, intensity, and severity of fire.¹⁵² Although fire frequency tends to be correlated with other characteristics of fire regimes, leading to relatively few combinations of broad fire regime types (or pyromes) globally,⁹ relying solely on them risks underestimating widely differing ecological responses to climate change. Additionally, since equilibrium in the climate-vegetation-fire relationship is an underlying assumption of these models, they are unable to resolve the transient dynamics involved in ecological change. Finally, because feedbacks between fire, vegetation, climate, and socioeconomic drivers are not incorporated, they cannot predict the location, the timing or the impact of changes in fire regime, and are unable to consider the possibility of non-linear responses such as biome shifts into alternative stable states.⁵

Empirical Models

Empirical models attempt to build statistical models of fire based on fire activity and the prevailing climate conditions. Based on the assumption that the relationship between fire activity and climate remains unchanged into the future, they can be used to project into future climate conditions. Empirical models have been used to relate historical climate and fire activity inferred from paleoecological records of charcoal sediments, fire-scarred trees, and tree growth rings.^{153–155} Such studies have identified shifts in the drivers of the global fire regime over time (from precipitation in preindustrial times, to anthropogenic drivers during the Industrial Revolution, to temperature under future climate conditions), and project the development of an unprecedentedly fire-prone global environment in the future.¹⁵⁶

Empirical modeling approaches have been used to document the role of weather and climate on fire activity (e.g. Ref 157–160), validate the importance of productivity (e.g. Ref 68,147), and identify other environmental and social factors determining fire activity (e.g. Ref 161–163). Importantly, they have highlighted the substantial changes in fire activity in some regions that can result from relatively small changes in climatic drivers of fire, such as annual precipitation (e.g. Ref 164).

However, empirical models are often limited by the short observational records and limited temporal resolution available from observations, so they are

unable to characterize fire activity in systems with very long fire return intervals. They can only identify patterns with those environmental and climatic variables included in the analyses, and they are unable to capture the potential for the relationships and interactions between key drivers to fundamentally change under future climate conditions. As with the conceptual models considered above, the ability of statistical models to predict climate change impacts on fire activity is fundamentally limited by the simplification required to reduce the complexity of fire regimes to a single variable such as fire frequency.¹⁵²

Additionally, correlative models based on mean annual conditions will never capture the extreme events that are associated with the large, high intensity wildfires in biomass rich forests that have severe impacts on ecological and human communities, such as those in south-eastern Australia and California. While the models could be improved by using the extremes of the distribution such as the 99th percentile of fire danger indices,¹⁵² the extremes are often not well simulated in projections of future climate.^{165–167} Extreme fire weather is associated with specific synoptic-scale meteorological conditions and broader-scale oscillations,^{168,169} which can be represented in dynamic climate models,^{170,171} but are not captured by many commonly used climate projections, such as statistically downscaled products.^{172,173} Similarly, extreme winds, which can drive fires under otherwise moderate weather conditions and create heavy fuel loads, are not currently well represented in climate models.¹⁷⁴

Process Models

Process models attempt to quantify the understandings provided by conceptual and empirical models, and can incorporate projections of future climate to predict fire activity across landscapes and time.

Fire Behavior Models

Wildfire behavior models are generally used to inform operational fire management, by predicting the behavior of fire in response to changes in topography and fuel under particular weather conditions.¹⁷⁵ Examples include the Coupled Atmosphere-Wildland Fire-Environment (CAWFE),¹⁷⁶ FARSITE-Fire Area Simulator,¹⁷⁷ and PHOENIX RapidFire.¹⁷⁸ They require accurate data about topography, vegetation and fuel, in addition to weather predictions. Since they are designed to predict fire behavior at the landscape scale over the course of several days, they are not applicable to long-term projections of future fire activity. However, output from behavior models

could be used to validate or adjust longer-term projections of fire activity.¹⁷⁹

Landscape Fire Succession Models

Landscape fire succession models have been developed to simulate the interactions between fire and vegetation, by quantifying fuel accumulation and transitions between vegetation states or successional stages. These models have been used to investigate the relative importance of climate, weather and fuel characteristics on fire dynamics at the landscape scale.¹⁸⁰ Examples include FireBGCv2,¹⁸¹ FIRESCAPE,^{182,183} LAMOS-FATEHS,⁸⁷ EMBYR,¹⁸⁴ and LANDSUM.¹⁸⁵

This approach has demonstrated that the interaction between succession and fire alter landscape composition and structure enough to influence coarse-scale simulations, and these changes are amplified under future climate warming.¹⁸⁰ Detailed representations of vegetation succession are therefore necessary to realistically simulate interactions between fire and vegetation under future climate conditions.

However, the general application of landscape fire succession models is limited because their parameterization requires extensive empirical data (e.g. fuel accumulation and fire spread in particular forest types). They are therefore not readily transferable across different vegetation types (e.g. grassland vs temperate forest) or hemispheres (although there are exceptions¹⁸⁶), and it is not possible to scale predictions of fire activity up to continental or global scales.

Dynamic Global Vegetation Models

Dynamic global vegetation models (DGVMs) simulate the long-term response of vegetation to climate processes at a global scale. Processes such as photosynthesis, competition, disturbance and mortality are modeled. Many DGVMs now include fire sub-models, in addition to the vegetation, carbon and water models (e.g. Ref 187–190). The latest generation of models (earth system models) also incorporate feedbacks between atmospheric and land processes so that changes in vegetation, carbon and hydrological cycles affect the climate.

DGVMs have been used to simulate global vegetation in the absence of fire, contributing to our understanding of the evolution of fire regimes and current vegetation patterns.¹⁹¹ By evaluating the mismatch between climate potential and actual vegetation distribution, such experiments have highlighted the importance of fire as a global control of vegetation structure. Coupled with GCMs, DGVMs are the

only way currently available to achieve a globally consistent analysis of future fire activity.

However, to achieve global applicability, DGVMs have to use simplified representations of landscapes, vegetation, and fire. Currently, most DGVMs describe vegetation in terms of broad functional types and physiognomic groups, rather than as individual plant species or vegetation communities.^{192,193} This limits the ability of these models to simulate the responses of communities at regional scales, so that even the most advanced models fail to represent the seasonal and geographic distribution of fire activity globally.¹⁹⁴ Future improvements are likely, as demonstrated by Scheiter and Higgins,¹⁹⁵ who developed an individual-based model that simulates a heterogeneous tree population, with the biomass, carbon status, phenology and fire response of each tree being tracked over time.

There are several additional factors limiting the ability of DGVMs to accurately project vegetation dynamics and fire activity, particularly in intensively human-managed landscapes.^{180,192} DGVMs do not dynamically simulate anthropogenic disturbance or land management decisions.^{196,197} Some models assume that vegetation composition and structure are static, and only simulate climate effects on biogeochemistry and ecophysiology.^{198,199} Others, such as state- and- transition and equilibrium biogeographical models, are based on the assumption that vegetation will change instantaneously when climate thresholds are crossed (e.g. Ref 200,201). Importantly, they are not initialized with current vegetation, which would enable the effects of past fire activity to be incorporated, and they lack realistic rates of vegetation growth and replacement affecting successional change (e.g. time lags to capture tree longevity).¹⁹² Addressing these deficiencies requires information about vegetation at a fine spatial scale, which is lacking for most of the world.

Integrated Fire-vegetation Models

Integrated fire-vegetation models (IFVMs) are similar to DGVMs, in that they attempt to model the interacting effects of climate and other drivers on fuel availability and fire regimes. However, they differ slightly in terms of their focus. IFVMs integrate fire and vegetation models to study shifts in fire regimes resulting from changing conditions, while DGVMs model changing vegetation dynamics.¹⁷⁹ When coupled with GCMs, IFVMs are powerful tools for understanding future climate interactions with vegetation dynamics and fire, although the same limitations in the parameterisation of mechanisms apply. Examples include

Global FIRE Model (GlobFIRM)²⁰² and The Large-fire Simulator (FSim).²⁰³

FUTURE RESEARCH DIRECTIONS

The conceptual, empirical and process models discussed here all help direct thinking about feedbacks between vegetation, climate and fire, but quantifying these feedbacks demands better integration of the different model approaches²⁰⁴ (Figure 3). Without better consideration of the underlying processes, existing empirical models will never be able to discriminate cause from effect, while process models could be improved with greater experimental validation,²⁰⁵ particularly exploring feedbacks amongst system components. Improved empirical and process models provide the architecture for more nuanced conceptual models, which in combination with narratives of future societies can highlight research areas requiring refinement and quantification. Research is required to refine each of the approaches, but the development of plausible scenarios of future fire activity depends on the integration and synthesis of all approaches to inform dynamic experiments and improve simulations of future responses.

The concept of the pyrome is useful for describing patterns in current fire regimes,⁹ but projecting

potential changes to future fire regimes requires knowledge of the underlying mechanisms controlling fire at the biome level. Further historical reconstructions, longitudinal studies, and long-term monitoring should focus on filling in the knowledge gaps that exist in different biomes around the world. The state of knowledge remains highly skewed, with research being focused on ecosystems that are currently fire-prone, such as savannahs in Australia and Southern Africa, or the temperate forests of Australia and California and the rainforest of the Amazonia. In contrast, there is little knowledge about ecosystems such as the temperate grasslands of Central Asia and dry forests of southeast Asia, and those systems with a very close coupling between humans and fire, such as the rainforests of Asia. These gaps prevent comparative analyses which could identify testable hypotheses to direct future research.

More appropriate scale-dependent research questions are required to fill in the gaps that remain between the broad continental patterns and these regional or biome specific responses.¹³⁶ Different patterns, relationships, and mechanisms will be identified at different scales. If research questions are not applied at the appropriate scale to address specific objectives, artifacts of scale are likely to obscure actual patterns and processes. This is particularly important in studies of biological responses, where

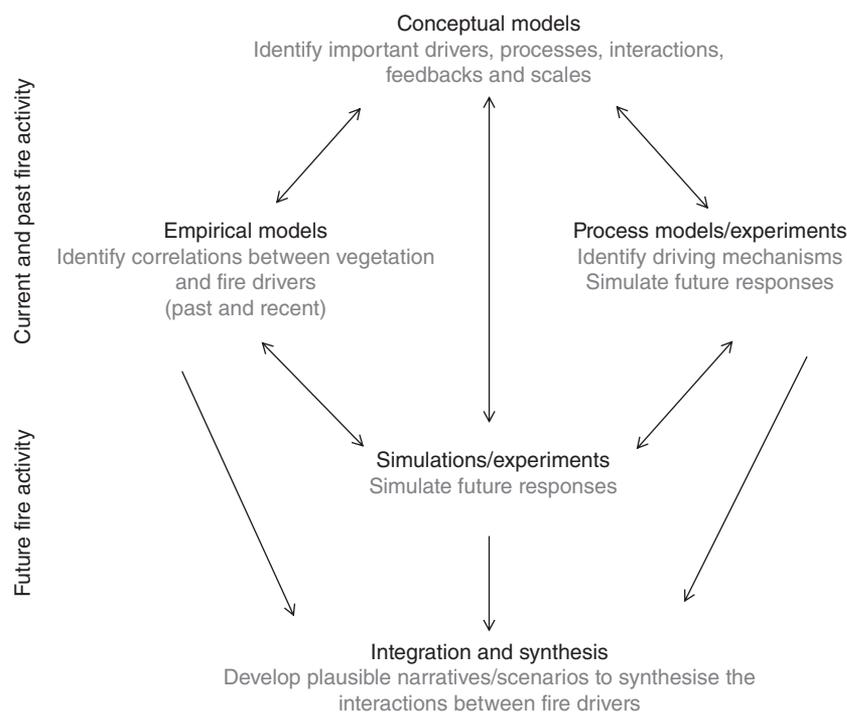


FIGURE 3 | The key approaches relevant to understanding fire danger under climate change (Adapted from Bowman et al.²⁰⁴).

interactions and feedbacks can appear to decouple responses from climate drivers, or introduce temporal lags. The identification of 'domains of scale,'²⁰⁶ within which patterns or responses are similar, or scale in a predictable manner, would improve the ability to generalize across systems.

A better understanding of fire regimes across multiple scales would also improve predictions of fire activity.^{124,207} Analyses performed at multiple spatial and temporal scales are necessary to identify the relative importance of the drivers of fire and identify times and places when broad-scale processes may be more or less important than fine-scale processes.^{208,209} This would highlight cross-scale interactions which may lead to non-linear responses, such as occurs when catastrophic weather conditions over-ride the importance of fuel condition.²⁰⁷ Related to this is the need for a better appreciation of the role that inter-annual and internal variability (e.g. ENSO, Pacific Decadal Oscillation) may play in determining fire regimes and activity,²¹⁰ particularly in regions such as Australia and Africa with large inter-annual climate variability.⁸⁶

Satellite-based datasets are increasingly being used to inform empirical models, and show great potential to improve the models and our understanding of long-term vegetation change, landscape fire feedbacks on climate change and fire processes. The LANDSAT earth observation satellite program has operated for four decades now, and recent advances in computational power have enabled significant advances in cataloging long-term global vegetation and land use change.²¹¹ Vegetation structural characteristics such as cover and life form are also being mapped at increasing resolution,²¹² and technologies such as space borne LIDAR are providing global vegetation forest height fields.²¹³ Climate feedback drivers from landscape fire, such as aerosol emissions, are being captured in more detail from satellites,²¹⁴ and new geostationary satellites with a high temporal resolution, such as GOES-R and Himawari-8, are allowing us to gain information on intra-fire dynamics and intensity²¹⁵ in different vegetation types, as well as lightning strike density.²¹⁶ Improved global surveillance at high resolution will reduce the uncertainty that remains around the drivers of fire at the landscape, regional and continental scales (Figure 2), and will enable the spatial variation and temporal patterns, including switches to fire season, to be integrated into dynamic models.²¹⁷

Dynamic modeling experiments will facilitate more thorough investigations of fire-vegetation feedbacks and interactions, but their success will depend on the inclusion of more complex biological,

ecological, and social relationships in DGVMs.²¹⁸ The incorporation of current vegetation, improvements in plant functional types and the representation of vegetation growth and mortality is essential. This may be achieved by linking to other models, such as landscape succession models. For example, Yospin et al.¹⁹² developed a climate-sensitive vegetation state-and-transition simulation model (CV-STSM). States were characterized based on assessments of both current and projected future vegetation from a DGVM. The model was integrated with an agent-based model of land use decisions and a mechanistic model of fire behavior and spread. They concluded that DGVMs alone will not be able to provide realistic projections of vegetation dynamics and disturbance. However, by combining DGVMs with state-and-transition models incorporating management decisions and land use change the interactions between disturbance and climate-change effects on vegetation can be simulated at a scale relevant to management.

Projections of future fire activity are only possible within a scenario framework, because fire activity is not solely a climate phenomenon. Models of fire activity based only on climate drivers are likely to be gross oversimplifications, and this will become more so as the influence of human drivers increases over time.¹⁹⁷ Recent DGVMs have started to incorporate decision-making for land use change scenarios,²¹⁹ but research is required to identify the socioeconomic and political mechanisms driving changes in fire policy.¹⁹⁷ Only by including the biological, atmospheric, and socioeconomic drivers of fire, and their interactions and feedbacks across spatial and temporal scales will we improve our understanding of fire under changing climate conditions. Global pyrogeography, the study of the spatial distribution of fire across large scales, has been suggested as one way to synthesize the biological, physical, and social science relevant to understanding the drivers of fire and define fire regimes.⁵ The development of plausible scenarios should be informed by comparative analyses of contrasting approaches to fire management, land use changes and future greenhouse gas emissions to help improve fire management and carbon storage.

CONCLUSIONS

Conceptual, empirical, and process models have contributed to our understanding of the interactions and feedbacks between vegetation, fuel, and fire regimes, and provide a useful basis to consider future fire

activity under climate change. These approaches, informed by greatly improved satellite data, have identified patterns and some of the mechanisms and processes driving fire regimes across temporal and spatial scales. Collectively, they suggest that climate change will affect fire activity differently in different biomes. However, there are many aspects of fire

regimes, across the globe and at regional and landscape scales, which cannot be projected into the future using currently available tools. Until they are better represented in earth system models and projections of climate change, fire will remain a major barrier to our understanding of the future of the Earth system.

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