Received: 3 April 2019 | Accepted: 6 February 2020
DOI: 10.1111/1365-2745.13403

ESSAY REVIEW

Journal of Ecology
BRITISH ECOLOGICAL SOCIETY

Fire as a fundamental ecological process: Research advances and frontiers

Kendra K. McLauchlan[1] | Philip E. Higuera[2] | Jessica Miesel[3] | Brendan M. Rogers[4] | Jennifer Schweitzer[5] | Jacquelyn K. Shuman[6] | Alan J. Tepley[2] | J. Morgan Varner[7] | Thomas T. Veblen[8] | Solny A. Adalsteinsson[9] | Jennifer K. Balch[8] | Patrick Baker[10] | Enric Batllori[11] | Erica Bigio[12] | Paulo Brando[13] | Megan Cattau[14] | Melissa L. Chipman[15] | Janice Coen[6] | Raelene Crandall[16] | Lori Daniels[17] | Neal Enright[18] | Wendy S. Gross[19] | Brian J. Harvey[20] | Jeff A. Hatten[21] | Sharon Hermann[22] | Rebecca E. Hewitt[23] | Leda N. Kobziar[24] | Jennifer B. Landesmann[25] | Michael M. Loranty[26] | S. Yoshi Maezumi[27] | Linda Mearns[6] | Max Moritz[28] | Jonathan A. Myers[9] | Juli G. Pausas[29] | Adam F. A. Pellegrini[30] | William J. Platt[31] | Jennifer Roozeboom[1] | Hugh Safford[32] | Fernanda Santos[33] | Robert M. Scheller[34] | Rosemary L. Sherriff[35] | Kevin G. Smith[36] | Melinda D. Smith[37] | Adam C. Watts[38]

[1]Department of Geography and Geospatial Sciences, Kansas State University, Manhattan, KS, USA; [2]Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT, USA; [3]Department of Plant, Soil and Microbial Sciences, Michigan State University, East Lansing, MI, USA; [4]Woods Hole Research Center, Falmouth, MA, USA; [5]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN, USA; [6]National Center for Atmospheric Research, Boulder, CO, USA; [7]Tall Timbers Research Station and Land Conservancy, Tallahassee, FL, USA; [8]Department of Geography, University of Colorado, Boulder, CO, USA; [9]Tyson Research Center, Department of Biology, Washington University in St. Louis, St. Louis, MO, USA; [10]School of Ecosystem and Forest Sciences, University of Melbourne, Melbourne, Vic., Australia; [11]Center for Ecological Research and Forestry Applications, Bellaterra, Spain; [12]Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV, USA; [13]Department of Earth System Science, University of California, Irvine, CA, USA; [14]Human-Environment Systems, Boise State University, Boise, ID, USA; [15]Department of Earth Sciences, Syracuse University, Syracuse, NY, USA; [16]School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA; [17]Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC, USA; [18]Conservation and Environment, Murdoch University, Perth, WA, Australia; [19]National Centers for Environmental Information, Asheville, NC, USA; [20]School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA; [21]Department of Forest Engineering, Resources and Management, Oregon State University, Corvallis, OR, USA; [22]Department of Biological Sciences, Auburn University, Auburn, AL, USA; [23]Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ, USA; [24]Department of Natural Resources and Society, University of Idaho, Moscow, ID, USA; [25]INIBIOMA, Universidad Nacional del Comahue, CONICET, Neuquen, Argentina; [26]Department of Geography, Colgate University, Hamilton, NY, USA; [27]Ecosystem and Landscape Dynamics, University of Amsterdam, Amsterdam, the Netherlands; [28]Bren School of Environmental Science and Management, University of California, Santa Barbara, CA, USA; [29]CIDE-CSIC, Valencia, Spain; [30]Department of Earth System Science, Stanford University, Stanford, CA, USA; [31]Division of Systematics, Ecology and Evolution, Louisiana State University, Baton Rouge, LA, USA; [32]USDA Forest Service Pacific Southwest Region, Vallejo, CA, USA; [33]School of Natural Sciences, University of California-Merced, Merced, CA, USA; [34]Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, USA; [35]Department of Geography, Environment and Spatial Analysis, Humboldt State University, Arcata, CA, USA; [36]Department of Biology, Davidson College, Davidson, NC, USA; [37]Department of Biology, Colorado State University, Fort Collins, CO, USA and [38]Division of Atmospheric Sciences, Desert Research Institute, Reno, NV, USA

Correspondence
Kendra K. McLauchlan
Email: mclauch@ksu.edu

Funding information
Division of Environmental Biology, Grant/Award Number: 1743681

Handling Editor: Giselda Durigan

Abstract

1. Fire is a powerful ecological and evolutionary force that regulates organismal traits, population sizes, species interactions, community composition, carbon and nutrient cycling and ecosystem function. It also presents a rapidly growing societal challenge, due to both increasingly destructive wildfires and fire exclusion

---

The authors of this paper comprise the Future of Fire Consortium.

in fire-dependent ecosystems. As an ecological process, fire integrates complex feedbacks among biological, social and geophysical processes, requiring coordination across several fields and scales of study.

2. Here, we describe the diversity of ways in which fire operates as a fundamental ecological and evolutionary process on Earth. We explore research priorities in six categories of fire ecology: (a) characteristics of fire regimes, (b) changing fire regimes, (c) fire effects on above-ground ecology, (d) fire effects on below-ground ecology, (e) fire behaviour and (f) fire ecology modelling.
3. We identify three emergent themes: the need to study fire across temporal scales, to assess the mechanisms underlying a variety of ecological feedbacks involving fire and to improve representation of fire in a range of modelling contexts.
4. *Synthesis*: As fire regimes and our relationships with fire continue to change, prioritizing these research areas will facilitate understanding of the ecological causes and consequences of future fires and rethinking fire management alternatives.

KEYWORDS
climate, Earth System models, fire regime, fuels, plant traits, prescribed fire, vegetation, wildfire

1 | INTRODUCTION

Fire is an Earth system process that has operated for many millions of years. The current context of fire ecology studies (Archibald et al., 2018; Bond, Woodward, & Midgley, 2005; Bowman et al., 2009; Krawchuk, Moritz, Parisien, Dorn, & Hayhoe, 2009; Pausas, Keeley, & Schwilk, 2017; van der Werf et al., 2006) reflects a remarkable paradigm shift—from earlier concepts of fire as a destructive and irreversible force to the current concepts of fire as an inherent and fundamental process influencing most terrestrial ecosystems on Earth (He & Lamont, 2018; Pausas & Bond, 2019). Fire ecologists now view fires as dynamic ecological forces that have evolutionary consequences and are fundamentally shaped by human actions. The goal of fire ecology is to understand the diversity of ways in which fire affects organisms and ecosystems on Earth (Figure 1).

Fire ecologists have constructed an increasingly nuanced, sophisticated and mechanistic understanding of the variable nature of fire as part of the ecological system. Fire is now recognized as a recurrent process, resulting in fire regimes that have direct ecological effects and act as selective forces by shaping species traits throughout the histories of entire lineages (He, Lamont, & Pausas, 2019; Simon et al., 2009). Moreover, fire regimes are important at multiple levels of biological organization, influencing populations, communities and ecosystems.

There is an amazing diversity of fire regimes on Earth. The geographic distribution of fire has been mapped based on current global fire activity (Andela et al., 2019; Krawchuk et al., 2009) and classified into geographically distinct fire regimes called pyromes (Archibald, Lehmann, Gomez-Dans, & Bradstock, 2013). Further, the concept of pyrodiversity—the spatial and temporal heterogeneity of fire regimes—has been examined in ecological contexts such as functional biodiversity and food webs (Bowman et al., 2016). However, a number of questions remain about the causes and ecological consequences of variation in fire regimes. The resulting magnitude and diversity of ongoing fire ecology research is challenging to integrate, given the many different lines of inquiry based on the concept of fire as a central ecological process.

Two notable features of recent fire activity frame fire ecology research. First, many fires are planned by people (see 'prescribed fire' in Box 1) due to the importance of both maintaining fire-adapted systems and the long history of using fire as a management tool (Ryan, Knapp, & Varner, 2013). People also exclude fires from fire-adapted systems, with ecological consequences such as the disappearance of tropical and temperate savannas (Fill, Platt, Welch, Waldron, & Mousseau, 2015; Overbeck et al., 2015). Second, land use and ongoing climate change are altering characteristics of individual fires and changing fire regimes, in some cases pushing them outside the historical range of variability in terms of frequency, size, seasonality or severity (Abatzoglou & Williams, 2016; Balch et al., 2018; Kelly et al., 2013; Miller et al., 2019; Walker et al., 2018). Many recent fires have had negative consequences for natural ecosystems and humans (Balch et al., 2018; Stevens-Rumann et al., 2018). There is a pressing need to project future fire activity under varying scenarios of climate change and land management strategies (Bowman, Murphy, Williamson, & Cochrane, 2014).

Our central goal in this paper is to advance knowledge of fire ecology. As the magnitude of fire ecology research increases, it becomes increasingly important to identify priorities in understanding

FIGURE 1 Selected examples of diversity of fire activity on Earth. Note that although these represent single fire events, the cumulative properties of fire events over time characterize a fire regime. (a) lightning-ignited wildfire in the boreal forest, Alaska, USA, photo credit: Philip Higuera (b) prescribed fire in tallgrass prairie in the Flint Hills of Kanas, USA, photo credit: Kendra McLauchlan (c) prescribed fire in temperate oak savanna in Minnesota, USA, photo credit: Susan Barrott (d) post-fire landscape in the Mediterranean biome of Catalonia, Spain, photo credit: Enric Batllori (e) prescribed fire in tropical forest in Brazil, photo credit: Paulo Brando (f) post-fire landscape in coniferous forest in Montana, USA, photo credit: Kendra McLauchlan (g) prescribed fire in mesic pine savanna in Florida, USA, photo credit: Raelene Crandall (h) lightning-ignited wildfire in the tundra, Alaska, USA, photo credit: Philip Higuera

the ecological and evolutionary implications of changing fire activity. Here, we attempt to synthesize the major areas of fire ecology research. We consider six priority areas, identified through an open online survey distributed broadly to the fire ecology research community but focused in the US (see Supplemental Information). We conducted bottom-up coding and qualitative text analysis of responses to the question: 'What are the biggest unmet scientific challenges currently in fire research?' Qualitative analysis grouped common text themes from survey responses into six priority categories. Members of the Future of Fire Consortium further refined the content of these six priority categories during a two-day workshop. We briefly summarize the state of knowledge in each category and propose avenues for progress in our understanding of fire as a fundamental ecological process. Our overall perspective, reflecting the composition of the consortium members, focuses on biophysical and ecological aspects of fire. We also recognize humans as central components of fire regimes, as described effectively in recent work (Maezumi et al., 2018; Roos, Zedeno, Hollenback, & Erlick, 2018). Ultimately, any review based on survey data and expert opinion will produce inevitable gaps in scope and emphasis. However, the value of such a process is to find patterns not evident from any single viewpoint or discipline.

2 | FIRE REGIME AS AN ECOLOGICAL FACTOR

Fire regimes are important because they help characterize and classify the diversity of fire and its ecological impacts into a simplified set of categories (Agee, 1993). This variation in fire activity and fire effects, over space and time, fundamentally shapes the structure, composition and dynamics of biotic communities across most of Earth's terrestrial ecosystems. Simplifying the diversity of fire activity into fire regimes is as fundamental to fire ecology as simplifying

BOX 1 Definitions of selected terms used in the text

Principal sources: National Wildfire Coordinating Group glossary (www.nwcg.gov/glossary/a-z), (Agee, 1993; Keeley, 2009; Pausas et al., 2017; van Wagtendonk, 2018).

Available fuel: The portion of the total fuel that would actually burn under various environmental conditions. Fuel availability is largely influenced by fuel moisture content.

Burn severity: *Synonym of fire severity.* Burn severity and fire severity refer to the magnitude of effect that fire has on the environment. This can be measured in many ways, using ground-based metrics or remotely sensed data (see Table S1). 'Soil burn severity' refers primarily to fire effects on soil properties (e.g. soil structure, soil and soil surface organics, changes in erodibility) and below-ground plant parts. 'Vegetation burn severity' refers to injury to and mortality of above-ground vegetation.

Crown fire: Fire that occurs in the vegetation canopy. The occurrence of crown fire usually depends on heat released from burning in surface fuels, but under some combinations of conditions (e.g. extreme wind, high connectivity between surface and canopy fuels, high canopy density and/or continuity, extremely dry live fuels) fire can propagate itself through the vegetation canopy independently of surface fuels.

Fire behaviour: The manner in which a fire reacts to the influences of fuel, weather and topography; quantified via rate of spread (m/s), residence time (s), intensity (kW/m), flame lengths (m) and combustion phase (e.g. smoldering, flaming).

Fire climate: Composite pattern of weather elements over time that affect fire behaviour in a given region. Like climate, fire climate is defined over multiple decades and over regional spatial scales.

Fire ecology: The study of the relationship between fire and populations, communities and ecosystems.

Fire intensity: the energy released by a fire per unit time per unit area.

Fire regime: A generalized description of the typical characteristics determined from multiple fires (e.g. intensity, frequency, size, extent, type, seasonality) and their ecological impacts (e.g. severity); fire regimes are often defined for a dominant vegetation or ecosystem type, and inherently include variability over space and time.

Fire severity: *See burn severity.*

Fire weather: Weather conditions that influence fire ignition, fuel conditions and fire behaviour, including wind, atmospheric temperature, stability, humidity, and ignition factors like lightning.

Fuel: Any combustible material including live and dead biomass. Petroleum products and buildings can be additional fuels that influence fire behaviour and effects in the wildland-urban interface.

Fuel load: The amount of fuel present expressed quantitatively in terms of dry weight of fuel per unit area (kg/m^2). See also available fuel.

Prescribed fire: Any wildland fire intentionally ignited by management actions in accordance with applicable laws, policies and regulations to meet specific objectives.

Wildfire: An unplanned wildland fire including those caused by lightning, unauthorized human causes, escaped prescribed fires and all other wildland fires where the management objective is fire containment.

the diversity of plant assemblages into communities is to plant ecology.

2.1 | Characterizing past fire regimes

Fire regimes are described with a number of metrics, including fire frequency (point-specific mean return intervals or area-based fire rotation periods), size, seasonality, intensity (the rate of energy release), severity (the direct impacts of fire), type (ground, surface, crown, mixed) and mode of combustion (flaming or smoldering; Keeley, Bond, Bradstock, Pausas, & Rundel, 2012). Past fire activity is interpreted from historical sources such as observational records and maps of area burned (Morgan, Losey, & Trout, 2014), and from palaeoecological proxy archives such as fire scars in tree-rings, tree age structures, charcoal particles preserved in sediments and organic compounds preserved in ice cores (Conedera et al., 2009; Figure 2). Many datasets derived from these sources are publicly available through international databases such as the Global Charcoal Database and NOAA's International Multiproxy Paleofire Database (Gross, Morrill, & Wahl, 2018; Marlon et al., 2016; Power et al., 2008). A key remaining challenge to fire ecology is characterizing and interpreting the high spatial and temporal variability in the characteristics of fire regimes within and among biomes (Figure 1; Table 1).

Few observational datasets or palaeoecological archives of past fire are spatially contiguous. In remote and non-forested regions, palaeoecological data are particularly sparse. In cold tundra and arid grassland ecosystems (with low above-ground productivity), little charcoal is produced from fires and few, if any, trees exist. Tree-ring fire histories are predominantly from temperate forested ecosystems with surface fire regimes. Where high intensity fires kill most trees or where trees do not form annual growth rings

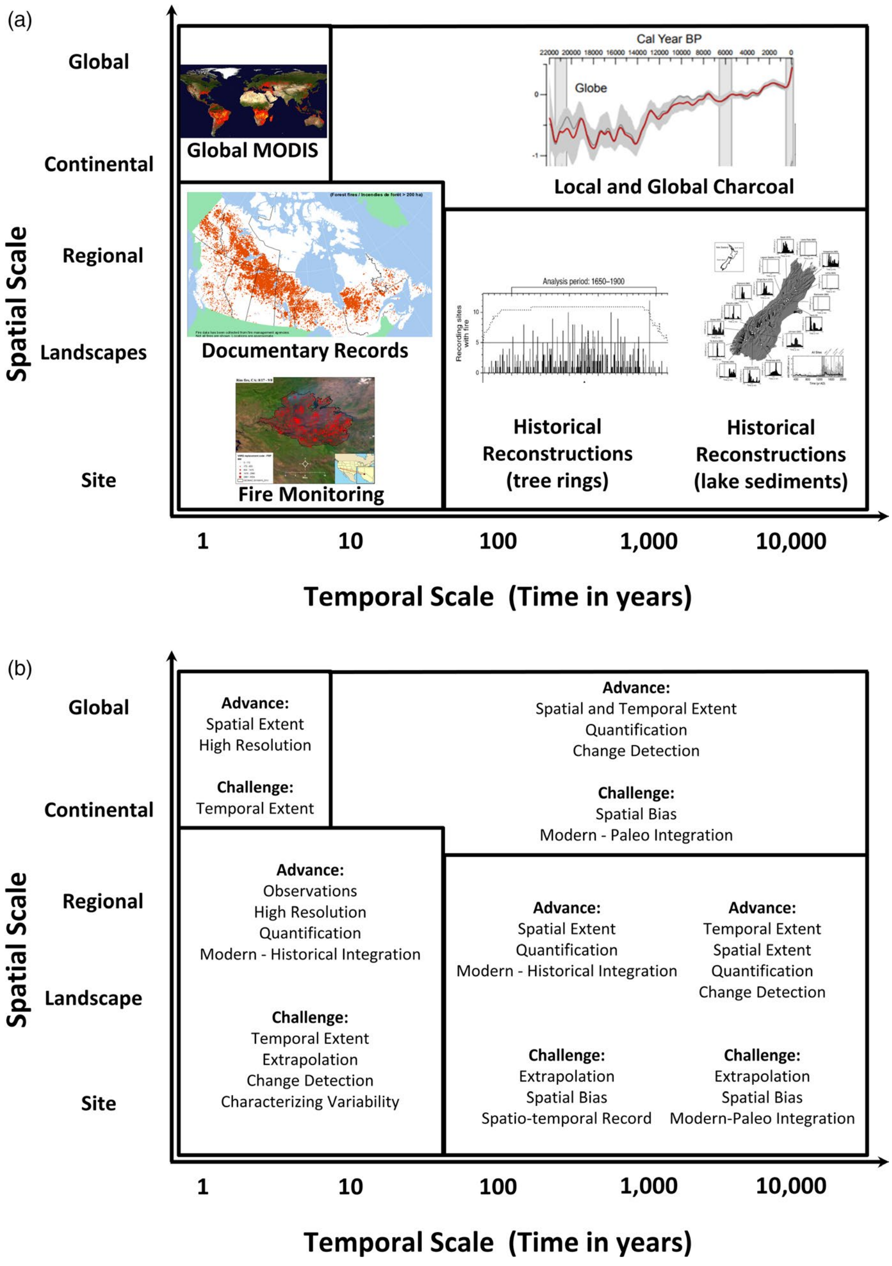

FIGURE 2 Methods, advances and remaining challenges in characterizing fire regimes and fire regime change. Advances over the past decade include Earth observing satellites and the development of palaeoecological records spanning continental to global scales. While each method has remaining challenges, the main limitation for detecting changing fire regimes is linking insights gained from different methods. (a) Citations: 'Local and Global Charcoal' (Marlon et al., 2016), 'Historical reconstruction (tree rings)' (Heyerdahl, Morgan, & Riser, 2008) 'Historical reconstruction (lake sediments)' (McWethy et al., 2010). (b) A key challenge for sedimentary charcoal records is translating into variables used in contemporary fire ecology: burned area, fire intensity, fire severity and emissions

(i.e. tropical forests and savannas), tree-ring records are very sparse or absent (but see Baker & Bunyavejchewin, 2017). In addition to the need for increased spatial coverage, key time periods in the past, such as the Medieval Climate Anomaly (950–1250 CE), may provide important analogues to modern and predicted scenarios of changing fire activity (Kelly et al., 2013; Pierce, Meyer, & Jull, 2004). Moreover, although fire history records provide valuable data on fire occurrence and frequency, new proxies need to be developed to reconstruct additional characteristics of fire regimes, such as fire severity, fire size and fire temperature (Dunnette et al., 2014; Gosling, Cornelissen, & McMichael, 2019; Leys, Commerford, & McLauchlan, 2017). The detection and quantification of variation in fire regimes is the first step to understanding and predicting their sensitivity to environmental change and the associated ecological consequences.

2.2 | Characterizing current fire regimes

Advances in the temporal and spatial resolution of imagery from Earth observation satellites have led to unprecedented descriptions of recent fire activity at the global scale (Figure 2). These methods utilize satellite observations of either fire activity or pre- and post-fire imagery, with varying levels of field observations for ground verification. Daily fire detection has provided new insights into the seasonality of burning (Giglio, Csiszar, & Justice, 2006; Roy, Boschetti, Justice, & Ju, 2008), and the influence of fire-season length on fire size and total burned area (Andela et al., 2019). The global extent of satellite-based products enables measurement of fire activity from remote regions where little data were previously available, advancing the study of fire ecology at global scales.

TABLE 1 Key challenges in fire ecology within each of the six research priority areas

Research priority area	Key challenge in fire ecology
1. Regimes	Characterizing fire regime components beyond area burned and fire frequency, in the past and present
1. Regimes	Increasing the spatial and temporal coverage of fire history records
1. Regimes	Linking satellite-derived products of actively burning areas to the diversity of fire regimes
2. Changing regimes	Integrating fire-adapted plant traits into global fire models
2. Changing regimes	Predicting fire probability in both fuel- and climate-limited ecosystems under future climate conditions
2. Changing regimes	Including the many influences of humans in global assessments and projections of fire activity
3. Above-ground	Understanding post-fire community assembly processes and how they interact with fire regime characteristics (especially severity)
3. Above-ground	Documenting the plasticity of fire-related traits at the community level
3. Above-ground	Accounting for fire-induced vegetation change feedbacks with the global climate system through albedo, ash, carbon cycle and smoke
4. Below-ground	Separating the direct effects of fire from the indirect effects of fire on soil properties and microbial composition and function
4. Below-ground	Quantifying the interactive effects of compound disturbances on soil properties
4. Below-ground	Incorporating variation in soil responses (at surface and sub-surface) to fire behaviour and fire severity
5. Fire behaviour	Linking measurements of fuels to resultant fire behaviour and effects across spatial scales
5. Fire behaviour	Measuring and characterizing below-ground fuel sources and fire behaviour
6. Models	Understanding the impact of spatial and temporal patterns of human-caused ignitions and management
6. Models	Studying interactions and feedbacks among multiple disturbances (including multiple fire events)

Remote sensing of fires has improved ecological understanding of several phenomena. For example, Archibald et al. (2013) used MODIS and GFED (van der Werf et al., 2017) products over the span of a decade to classify global fire characteristics based on five key elements (size, frequency, intensity, season and spatial extent). To link fire characteristics with ecosystem functions, Pausas and Ribeiro (2017) used MODIS hotspots to relate global fire patterns to productivity and diversity. Like any tool, these global products have detection biases and limitations, especially in their ability to detect small fires, such as those from agricultural burning, or low-intensity fires (fires with low rates of energy release). The satellite records are also limited by their temporal extent, spanning only the past several decades (i.e. since the 1980s). This motivates a critical research need to link the remote-sensing data with palaeoecological records to better understand how fire regimes have changed over time.

Fire severity has received considerable attention from ecologists because of the direct links to plant mortality and changes in soil properties. Ecologists have a variety of tools for assessing fire severity, including both remote-sensing and field-based methods (Table S1). The Monitoring Trends in Burn Severity (MTBS) program in the United States (Eidenshink et al., 2007) has facilitated wide access to data on fire perimeters and fire severity at 30-m resolution for all 'large' fires (>*c*. 400 ha in the Western US and >*c*. 200 ha in the Eastern US) that have burned since Landsat 5 was launched in 1984. MTBS-like approaches can now be applied globally (Parks, Holsinger, Voss, Loehman, & Robinson, 2018). Severity metrics derived from MODIS data have been compared within and among regions to define essential fire regime characteristics (Rogers, Soja, Goulden, & Randerson, 2015; Singleton, Thode, Meador, & Iniguez, 2019). Other metrics have been used to model fire impacts on key variables such as carbon emissions (Rogers et al., 2014; Walker et al., 2018). Together, these datasets have revealed much greater heterogeneity in fire effects than previously characterized (Cansler & McKenzie, 2012; Collins et al., 2017). Accurately applying these methods across regionally and globally diverse fire regimes remains a substantial challenge, because existing satellite-based products such as MODIS detect actively burning areas, and assessment of individual fires or fire behaviour is still in development. Overcoming this challenge is a key research need, because the underlying heterogeneity in fire activity is a critical source of ecological diversity within and across landscapes, regions and biomes.

2.3 | Characterizing fire regime changes

Detecting changes in fire regimes remains a pressing challenge for ecologists. The ability to characterize fire regimes has been based on construction of probabilistic estimates of fire regime characteristics (McCarthy, Gill, & Bradstock, 2001). These probabilistic distributions are then compared to recent fire events to assess the likelihood of a shift to a different fire regime (Bigio, Swetnam, & Baisan, 2016; Chipman et al., 2015; Kelly et al., 2013). Changes in fire regimes can be detected given a relatively long time period or spatially dense networks of samples (Taylor, Trouet, Skinner, & Stephens, 2016), with some of the clearest examples of change reflecting shifts in human-dominated fire regimes (McWethy et al., 2010). Beyond changes in fire frequency and area burned, other changing components of fire regimes have been identified in recent years, including changing spatial patterns of fire severity (Harvey, Donato, & Turner, 2016b; Miller, Skinner, Safford, Knapp, & Ramirez, 2012; Steel, Koontz, & Safford, 2018) and the lengthening of wildfire seasons (Jolly et al., 2015). These different aspects of fire regime can have unique ecological impacts on plant populations and communities, by affecting mortality, establishment, survival and reproduction.

3 | INTERACTIONS AMONG ECOLOGY-, CLIMATE- AND HUMAN-DRIVEN CHANGES IN FIRE REGIMES

What causes fire regimes to change over space and time? Understanding the multiple ecological interactions in fire regimes is a complex challenge. Nonetheless, three fundamental limits to burning—available fuel, appropriate climate conditions and ignitions—have consistently been identified as important controls of fire activity across multiple spatial and temporal scales (Krawchuk et al., 2009).

3.1 | Vegetation as a driver of fire regimes: Co-evolution of fire and biota

Fire has been a dominant ecological and evolutionary force on Earth since plants colonized the land about 400 Mya (Judson, 2017; Pausas & Keeley, 2009). In an evolutionary context, the fire regime is an important force of natural selection in plants and other organisms (Simon et al., 2009). However, strong feedbacks between plants and fire also mean that plants directly influence fire regimes (Beckage, Platt, & Gross, 2009; Nowacki & Abrams, 2008; Platt, Ellair, Huffman, Potts, & Beckage, 2016). While there has been increasing recognition that 'coevolution' of plants and fire regimes drives many ecological processes (Archibald et al., 2018), it is still unclear to what extent such co-evolutionary relationships have influenced landscapes and biomes (Pausas & Bond, 2019).

There is enormous potential to understand when and where fire acts as a macroevolutionary process by studying fire-related plant traits. Fire-adaptive traits (Keeley, Pausas, Rundel, Bond, & Bradstock, 2011) include those for post-fire recruitment (serotiny; fire-stimulated germination), resprouting (Pausas, Lamont, Paula, Appezzato-da-Gloria, & Fidelis, 2018) and either fire resistance (thick bark) or fire promotion (resin content and branch retention; Keeley et al., 2012). Phylogenetic tools can help identify when and how fire-related traits evolved, such as the origin of cone serotiny 100 Mya in pines (He, Pausas, Belcher, Schwilk, & Lamont, 2012), epicormic resprouting 60 Mya in eucalypts (Crisp, Burrows, Cook, Thornhill, & Bowman, 2011) and branch abscission in Palaeozoic conifers (Looy, 2013).

Plant communities also alter fire regimes, often through a self-reinforcing cycle that selects for particular traits and species to survive within a given fire regime (Rogers et al., 2015). For example, invasive plant species have the potential to alter fire regimes when they modify the flammability of an ecosystem (Balch, Bradley, D'Antonio, & Gomez-Dans, 2013; Paritsis et al., 2018). Similarly, changes in the spatial distribution of plant traits across a landscape can affect fuel continuity and therefore fire probability and spread. Ultimately, changes in fire regimes resulting from altered plant assemblages have the potential to generate abrupt fire regime shifts and to move ecological systems outside their historical evolutionary arena (Fill et al., 2015; Kane, Varner, Metz, & Mantgem, 2017). One major research challenge is to integrate global databases of fire-adapted traits into global fire and vegetation models for projecting future changes.

3.2 | The role of climate and climate-fuel interactions

Climate affects fire regimes across temporal scales ranging from short-term fire weather to millennial-scale climate conditions. In many arid and semi-arid ecosystems, climatic conditions during the fire season are usually favourable for burning, but low fuel loads or a lack of fuel continuity limit fire occurrence and spread. In these fuel-limited systems, widespread fire activity requires periods of increased antecedent precipitation that increase productivity and connectivity of fine fuels (Grau & Veblen, 2000; Swetnam & Betancourt, 1998). In contrast, flammability-limited systems, such as closed canopy forests, typically have high fuel loads, but require an extended period of drought to create conditions favourable to burning. Notably, many ecosystems represent some mixture of fuel- or flammability-limited fire regimes, termed 'hybrid' systems by McKenzie and Littell (2017). A fourth category is 'ignition-limited' systems, where dry fuels are abundant but lacking non-human ignition sources, such as lowland sclerophyllous shrublands in California (Steel, Safford, & Viers, 2015) and Mediterranean shrublands in Chile (Keeley et al., 2012).

A key research frontier is understanding how changing climate variables (temperature, precipitation, changes in sequences of extreme wet and dry conditions and the likelihood of ignition) should alter controlling aspects of fire regimes. There is high variability in fire-climate relationships within and across ecosystems, and fire-climate relationships have shifted over time (Kitzberger, Veblen, & Villalba, 1997; Sherriff & Veblen, 2008). Some of this variability is due to differences in species composition, vegetation structure and climate within a region (Gartner, Veblen, Sherriff, & Schoennagel, 2012; Heyerdahl, Brubaker, & Agee, 2001; Taylor & Skinner, 2003). Over time, changes in species composition may shift how the climate limits fire activity (Boer et al., 2016). In those systems where fuel is abundant but generally too moist to burn, changes toward a warmer, drier climate are expected to decrease fuel moisture content and increase fire activity (McKenzie & Littell, 2017).

3.3 | Humans contribute to and are affected by changing fire regimes

Humans play fundamental roles in shaping fire regimes world-wide, and have done so for millennia (Bowman et al., 2011; Guarinello de Oliveira Portes, Safford, & Behling, 2018; Kobziar, Godwin, Taylor, & Watts, 2015; McWethy et al., 2013). The mechanisms by which humans alter fire regimes include: (a) changing the frequency, timing and spatial distribution of ignition sources, (b) changing fuel structure, composition and loading through land use and land cover change, (c) suppressing fire and (d) contributing greenhouse gases to the atmosphere, which drives climate warming. In many regions, humans account for the majority of ignitions and burned area, replacing lightning as the primary ignition source (Achard, Eva, Mollicone, & Beuchle, 2008; Lasslop & Kloster, 2017). On continental to global scales, humans expand the fire season, facilitating burning during cooler and wetter conditions outside the historical wildfire season (Balch et al., 2013; Le Page et al., 2017). Land uses fundamentally change fuel composition and structure, which can either increase or decrease fire occurrence (Brando et al., 2014; Chergui, Fahd, Santos, & Pausas, 2018; Pausas & Fernandez-Munoz, 2012). Fire suppression prevents fire from spreading, and fire suppression can cause accumulation of fuels that increases the likelihood of fire ignition, fire spread and crown fire activity (Parks, Holsinger, Miller, & Nelson, 2015). In addition, fire suppression may facilitate invasion by species from non-pyrogenic habitats, ultimately threatening fire-adapted ecosystems (e.g. Fill et al., 2015).

Finally, humans alter fire regimes through anthropogenic climate change. Across much of the globe, climate conditions are becoming increasingly conducive for fire. The length of the fire-weather season (days with fire danger metrics above their median values) has increased by nearly 20% from 1970 to 2013 (Jolly et al., 2015). An example is in the western United States, where the fire-season length has increased by 34% (from 166 to 222 days), ultimately leading to increased annual area burned (Westerling, 2016). Globally, anthropogenic climate change has emerged as a significant driver of increased fire danger, independent of natural climate variability (Abatzoglou, Williams, & Barbero, 2019). These factors have relevance to ecological interactions as humans introduce and remove fire from landscapes (Moritz et al., 2014). A major research challenge is to incorporate all the influences of humans into global assessments and projections, given the inherent complexity and differing regional socio-economic contexts (Table 1).

4 | EFFECTS OF FIRE ON ABOVE-GROUND ECOLOGICAL PROCESSES

Studies of above-ground fire effects traditionally emphasized plant mortality and regeneration. Yet, fire affects a broader range of above-ground ecological processes, with consequences at spatial scales ranging from establishment of individual plants to global climate. Additional research is needed to understand the feedback mechanisms involved in increasing fire activity, as well as the timing and persistence of plant population traits and community processes after fires.

4.1 | Fire-vegetation feedbacks

Post-fire vegetation successional trajectories depend on numerous factors, including fire size and effects, pre- and post-fire climate, recent fire history and plant life-history traits related to survival and recolonization (Davis, Higuera, & Sala, 2018; Johnstone et al., 2016). Plant traits interact with fire severity to influence post-fire regrowth, reproduction, dispersal, germination and establishment. Fires in grasslands and in many Mediterranean shrublands, for example, tend to perpetuate the existing plant community because the dominant species resprout from protected basal meristems (Keeley & Rundel, 2005). Forest fires, by contrast, can lead to a variety of post-fire successional pathways, depending not only on fire severity but also on the adaptations (Pausas, 2015) and spatial configurations of surviving trees, and canopy and soil seed banks (Figure 3). Predicting future post-fire vegetation composition is difficult because landscape fragmentation, changing climate, non-native species, herbivory, variable propagule availability and interacting disturbances can alter successional trajectories from those in the past (Batllori et al., 2018; Blackhall et al., 2017). Models can be effective for investigating these dynamics (Crandall & Knight, 2015; Scheller & Swanson, 2015) but many of the underlying mechanisms remain poorly understood. Thus, caution is needed when considering modelling results.

The expanding field of fire-vegetation feedbacks emphasizes the interactive nature of plants and fire (Batllori, Ackerly, & Moritz, 2015; Beckage, Gross, & Platt, 2011; Tepley et al., 2018; Figure 3). Vegetation structure, microclimate and plant flammability vary along post-fire succession sequences, and these characteristics interact with climate and weather to influence fire regimes and the persistence of different vegetation types (Pausas et al., 2017; Platt et al., 2016; Varner, Kane, Kreye, & Engber, 2015). Positive feedbacks, whereby frequent burning maintains flammable plant communities, can perpetuate grasslands and savannas in regions climatically suitable for forests (Dantas, Batalha, & Pausas, 2013; Harms, Gagnon, Passmore, Myers, & Platt, 2017; Hoffmann et al., 2012). Positive feedbacks can also maintain non-flammable forests (e.g. tropical forests and Southern Hemisphere beech forests), where shading by the dense forest canopy that develops over long fire-free intervals maintains a cool, moist microclimate and disrupts the continuity of flammable surface fuels such as grasses. Extremely dry, windy conditions can weaken these feedbacks, enabling fires to spread into otherwise non-flammable forests. Burning then shifts the ecosystem to a more flammable, non-forest state (Pausas & Bond, 2020), which is perpetuated through a positive feedback with fire (Paritsis, Veblen, & Holz, 2015; Tepley, Veblen, Perry, Stewart, & Naficy, 2016).

Some ecosystems demonstrate negative fire-vegetation feedbacks, whereby fire temporarily reduces fuel loading or flammability, which decreases the probability of repeat burning for a period of years to several decades (Figure 3). Such feedbacks are evident in boreal forests and several types of temperate coniferous forest (Heon, Arseneault, & Parisien, 2014; Parks et al., 2015). Differences in the direction and strength of fire-vegetation feedbacks, and their interactions with the trajectories and rates of post-fire vegetation recovery, strongly influence how different landscapes will respond to increasing fire activity as the climate warms (Figure 3). Further, in many systems, feedbacks can switch from negative to positive due

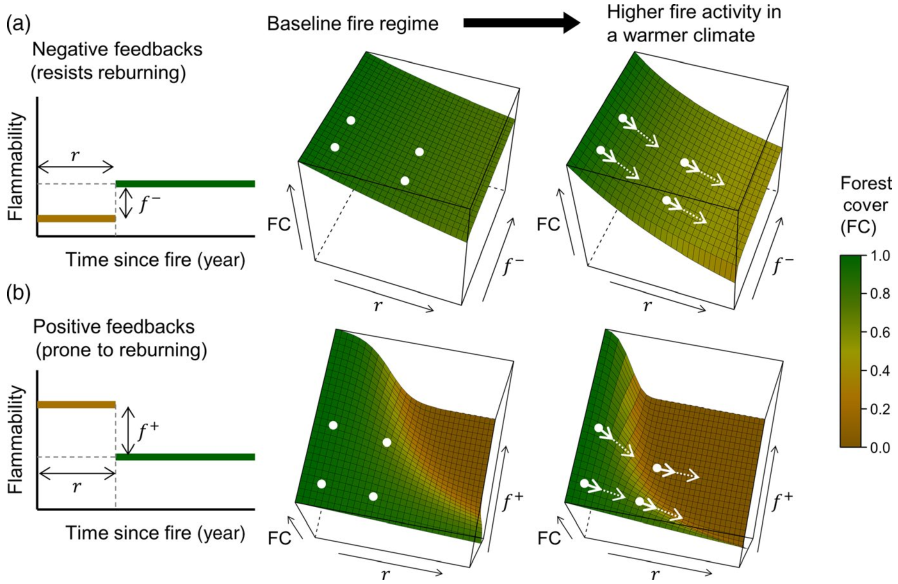

FIGURE 3 Feedbacks between fire and vegetation interact with post-fire forest recovery rates to mediate responses to altered fire regimes in landscapes that currently support forest cover. High-severity fire alters fuel and microclimate, making sites either more (positive feedback) or less (negative feedback) likely to reburn soon after a severe fire. The direction and strength of the feedbacks (f^- and f^+) interact with the time to forest recovery (*r*) after high-severity fire to determine how the proportion of a landscape that supports forest cover (FC) varies as fire activity increases. Negative feedbacks (a) reduce the probability of reburning, limiting the amount of forest lost as the climate become more conducive to fire. Positive feedbacks (b) produce a threshold, where small increases in either fire activity or the time to forest recovery after severe fire can shift the system from forest to non-forest cover. White dots on the left response surfaces represent hypothetical baseline conditions in different forest regions. Climate change and increased wildfire activity alter the shape of the response surfaces. At the same time, the x-axis positions of the regions shift (white arrows) as forest recovery slows under a more arid environment with larger patches of high-severity fire. Short and long arrows represent regional differences in sensitivity to the slowing of forest recovery (after Tepley et al., 2018)

to post-fire changes in vegetation or fuel accumulation over unusually long fire-free intervals (Harvey, Donato, & Turner, 2016a).

4.2 | Climate-vegetation feedbacks

Interactions between above-ground vegetation and climate at local to global scales are key to understanding the ecosystem consequences of changing fire activity (Archibald et al., 2018). At a local scale, recent investigations into the interactions between climate variables (especially drought) and seedling recruitment have highlighted decreases, or failures, in post-fire tree regeneration (Stevens-Rumann & Morgan, 2019). Local mechanisms, such as reductions in tree seedling recruitment, growth and survival under warmer conditions may drive fundamental changes in ecosystems (Enright, Fontaine, Bowman, Bradstock, & Williams, 2015) but the timing and persistence of these transitions are largely unknown.

Understanding of the mechanisms and degree to which fire-induced vegetation change can alter regional climate also needs to be further advanced (Beringer et al., 2015; Liu, Ballantyne, & Cooper, 2019). At the global scale, increasing fire activity can reduce ecosystem carbon storage (De Faria et al., 2017). The resulting increase in atmospheric carbon dioxide concentrations accelerates climate warming, potentially driving further increases in wildfire activity. In addition to carbon cycle feedbacks, changes in surface energy partitioning, including changes in surface albedo, have important influences on regional climate (Rogers, Randerson, & Bonan, 2013), and aerosols emitted during fire combustion could have large impacts on regional and global climate as well (Chakrabarty et al., 2016). A comprehensive understanding of how changing fire activity may influence global and regional climate is still lacking.

4.3 | Fire and above-ground biodiversity

Fire is known to affect plant species diversity (He et al., 2019), and the effects can be grouped into a few general patterns. First, many ecosystems exhibit declining plant species diversity with increasing time since fire (Swanson et al., 2011). Second, there may be an optimum range of fire regime characteristics that sustains the highest diversity. The optimum appears to depend on the fire-evolutionary history of the ecosystem and species traits (Kelly & Brotons, 2017). Thus, an absence of fire can reduce plant diversity in certain ecosystems (Abreu et al., 2017; Parr, Lehmann, Bond, Hoffmann, & Andersen, 2014). Third, the spatial and temporal heterogeneity of fire regimes can either increase or decrease biodiversity, but existing examples are ecosystem-dependent (Martin & Sapsis, 1992; Parr & Andersen, 2006), and the influence of fires on biodiversity may depend on trophic levels (Davies, Eggleton, Rensburg, & Parr, 2012; Maravalhas & Vasconcelos, 2014). Another important factor for fire and biodiversity is the spatial arrangement of fire refugia—locations that experience longer fire-free intervals or tend to burn with lower severity than the broader landscape in which they are embedded (Crandall & Platt, 2012; Landesmann & Morales, 2018; Meddens et al., 2018). Refugia may sustain local populations of fire-sensitive species within large burned areas, increasing post-fire habitat diversity. Meta-analyses of community diversity, informed by evolutionary history and historical fire regimes, are needed to further advance insight into the relationships between fire and above-ground biodiversity.

Studies about fire and biodiversity have traditionally focused on vascular plants. Other organisms, from decomposers to higher trophic levels, are only starting to be considered (Geary, Doherty, Nimmo, Tulloch, & Ritchie, 2019; Mikita-Barbato, Kelly, & Tate, 2015; Ponisio et al., 2016). For example, fire indirectly influences ungulate populations and avian communities through its effects on habitat quality, including forage and nesting opportunities (Hutto, 2008; Rupp et al., 2006; Smucker, Hutto, & Steele, 2005). It is also clear that herbivory interacts with fire activity (Blackhall et al., 2017; Fuhlendorf, Engle, Kerby, & Hamilton, 2009). However, the effect of fire on other plant–animal interactions (pollination, dispersal, seed predation) is less known (Lazarina et al., 2017). There is also an increasing recognition that fire may have evolutionary consequences in animals (Pausas & Parr, 2018). Future biodiversity studies could more explicitly examine the effects of fire across a broader range of biotic interactions and trophic levels. Further, there is a need to expand the focus from fire frequency and sometimes severity, to address how a broader range of fire regime attributes affect biodiversity (Miller et al., 2019).

4.4 | Fire influences plant community assembly

Fire regime characteristics, along with their variability, influence how plants are assembled into communities (Harms et al., 2017; Myers & Harms, 2011). Fire excludes individuals from communities by selectively filtering traits of individuals from the regional species pool (Verdu & Pausas, 2007). When fire-intolerant species are selectively filtered, fire homogenizes species composition among sites (Pausas & Verdu, 2008) and increases phenotypic (and often phylogenetic) clustering in communities (Forrestel, Donoghue, & Smith, 2014). However, even where fire regimes have long remained similar across sites, other contextual factors such as soil type and landscape patterns can exert considerable influence on beta diversity, nestedness and community assemblages (Freeman, Kobziar, Leone, & Williges, 2019). More locally, biotic interactions within and among plant species can further influence changes in deterministic assembly with time since fire and produce changes in fire regimes (Landesmann, Gowda, & Kitzberger, 2016; Tepley, Thompson, Epstein, & Anderson-Teixeira, 2017). In contrast, fire may contribute to stochastic community assembly by influencing random colonization or extinction processes that increase ecological drift. For example, when fire decreases the total number of individuals in communities (community size), it may increase local extinctions due to demographic stochasticity, and increase variation in species composition among sites (Myers, Chase, Crandall, & Jimenez, 2015). Post-fire community assembly will also depend on dispersal abilities of species within the regional species pool as well as rates of dispersal among local communities. Understanding this balance of deterministic and stochastic processes is likely to be as important in fire ecology as it has been in other subfields of ecology (Vellend, 2010).

Fire-related plant traits are important both for basic ecological and evolutionary understanding of the role of fire in plant communities, and for improving models that use simplified plant functional types (see Section 6). For example, whereas dynamic global vegetation models (DGVMs) conventionally used static plant traits and emphasized resource competition as the primary driver of species composition, these models are now being modified to make plant traits an emergent evolutionary process (Scheiter, Langan, & Higgins, 2013). Caution must be taken when using plant traits related to fire for modelling at the global scale, as correlations with other dynamic traits are contingent on biogeographic history, and thus may be ecosystem-dependent. The plasticity of fire-related traits at the community level is virtually unknown, and it is important to identify potential limits to adaptation.

5 | FIRE SETS ECOLOGICAL GROUND RULES THROUGH SOILS

The effect of fire on soils is inherently coupled with changes above-ground (Wardle, Jonsson, Mayor, & Metcalfe, 2016). However, responses to fire below-ground may differ than those above-ground because soils contain a relatively large pool of carbon, nutrients and organisms that are at least partially buffered from combustion and mortality during fire events. While plant traits for extensive below-ground biomass and resprouting are important features of fire-adapted communities (Maurin et al., 2014), we focus this section on soil and soil biota.

5.1 | Fire effects on soil physical, chemical and biological properties

Fire alters multiple physical, chemical and biological properties of soil, such as texture, aggregation, pH, nutrient content and microbial community composition. The magnitude of fire effects on soils depends on above-ground fire behaviour (Massman, 2012), organic horizon depth and moisture content (Hartford & Frandsen, 1992) and the physical properties of mineral soil (Giovannini, Lucchesi, & Giachetti, 1988). Fire directly impacts the upper organic horizons *via* pyrolysis and combustion reactions, including physical loss of the organic horizon, and the underlying mineral soil by conductive and advective heating during a fire (Araya, Fogel, & Berhe, 2017; Certini, 2005; Neary, Ryan, & DeBano, 2008). Fire may also contribute to soil formation (Certini, 2014).

Similar to above-ground fire severity characteristics described earlier, fire severity in soils can be characterized based on change to or loss of the organic horizon, and change to mineral soil physical characteristics. Fire can thus change soil structure (reducing porosity), carbon and nutrient pools and fluxes (reducing concentrations and turnover), soil organic matter composition and biochemistry (increasing pyrogenic carbon and polyphenols) and the composition (decreasing richness, altering community structure) and activity rates (decreasing decomposition) of soil biota (Adkins, Sanderman, & Miesel, 2019; Gutknecht, Henry, & Balser, 2010; Miesel, Hockaday, Kolka, & Townsend, 2015). Because combustion results in losses of carbon and nitrogen, but not other elements such as phosphorus (Bodi et al., 2014; Butler, Elser, Lewis, Mackey, & Chen, 2018), intense or repeated fires can alter nutrient concentrations and stoichiometry when compared with unburned sites (Ludwig et al., 2018; Pellegrini et al., 2018). These changes to soils have profound impacts on plant growth, community composition and ecosystem processes (da Silva & Batalha, 2008).

Fire effects on the soil microbial community (heterotrophs and symbionts) increase with fire severity (Whitman et al., 2019) which can alter plant recovery and microbially mediated ecosystem processes after fire events. Overall, fire decreases bacterial biomass and diversity, fungal species richness and mycorrhizal colonization, although responses of fungal species can be ephemeral (Dove & Hart, 2017). Responses of microbial biomass and diversity can persist for a decade or more, depending on the ecosystem, fire severity and organic horizon loss (Dooley & Treseder, 2012; Pressler, Moore, & Cotrufo, 2018). Despite these general trends, the limited information on key covariates such as soil pH makes it difficult to determine the mechanisms regulating the responses of soil microbial communities after fire (Pingree & Kobziar, 2019) or effects on subsequent microbial function.

5.2 | Effects of compound disturbances on soil properties

Interactions between fire and other disturbances such as drought, wind damage, beetle outbreaks and landslides can have important effects on soil structure and chemistry and subsequent ecological interactions. For example, in ecosystems underlain with permafrost, wildfires can accelerate permafrost thaw and ground subsidence (Gibson et al., 2018), resulting in altered soil hydrology and subsequent likelihood of fire. Additionally, high rates of erosion following post-disturbance vegetation mortality can increase losses of soil organic matter after a fire (Pierson, Robichaud, Rhoades, & Brown, 2019). Thus, interaction effects between fires and other disturbances should be considered as these interactions may amplify or dampen changes to soil properties after fire. Given that global change projections indicate increased frequency of fire and other disturbances, additional work is needed to classify the additive or interactive effects of compound disturbance (Bradford et al., 2012). The existence of numerous experiments manipulating fire frequency (Godwin, Kobziar, & Robertson, 2017; Guinto, Xu, House, & Saffigna, 2001; Holdo, Mack, & Arnold, 2012) provides the opportunity to impose additional disturbances—such as reduced precipitation—to study the combined responses of soil properties such as soil aggregation, pH, nutrient pools, respiration rates and microbial community composition.

5.3 | Ecological consequences of temporal and spatial variation in soil properties influenced by fire

The temporal responses of soil to fire depend on the variable considered. For example, shifts in microbial biomass and composition occur on sub-annual to decadal time-scales (Dooley & Treseder, 2012) whereas the effect of charcoal formation on soil carbon storage occurs over centennial to millennial time-scales (He et al., 2016). Moreover, the effects of fire on soil carbon dynamics vary across biomes, with soil carbon stocks commonly recovering within a year following fire in temperate grasslands, over decades to centuries in boreal forests and potentially never recovering in some peatlands (Harden et al., 2000). In tropical grasslands, savannas and forests, repeated burning can also deplete total soil carbon and nutrients, but usually only at high frequencies and over decadal time-scales (Liu, Chen, Wang, Hughes, & Lewis, 2015; Pellegrini, Hedin, Staver, & Govender, 2015). These declines may or may not have deleterious impacts on ecosystem productivity (Tierney, 2019).

Fire effects on mineral soils usually emerge over the course of decades due to the mechanism of changes in plant biomass inputs balanced with the turnover time of soil, in contrast to the immediate and direct effects of a single fire on the organic horizon. Consequently, the coupling between above-and below-ground processes may be altered under changing fire regimes. Furthermore, interactions among pre-fire soil properties, fire severity and post-fire vegetation recovery influence the magnitude of change in soil nutrient pools over time after fire, relative to pre-fire conditions (Godwin et al., 2017; Kranabetter et al., 2016). This post-fire variation in soil properties can have important consequences for microbial communities and plant–microbe interactions (Kardol, Deyn, Laliberte, Mariotte, & Hawkes, 2013).

Soils are heterogeneous across both the soil surface and with soil depth. Combined with the inherent heterogeneity of fire, spatial variability in soil properties can be important for determining post-fire changes in nutrients at the landscape scale that can alter whole ecosystems (Homann, Bormann, & Boyle, 2001). However, it is unclear how heterogeneity in fire behaviour determines heterogeneity in soil responses over time, in large part because of the limited studies that investigate fire severity gradients (Adkins et al., 2019; Garcia-Oliva et al., 2018; Hewitt, Hollingsworth, Chapin, & Taylor, 2016; Kolka et al., 2017; Whitman et al., 2019). Most of our understanding of how fire severity influences soil responses is based on the comparison between wildfire and prescribed fire with the assumption that wildfires are more severe than prescribed fires (Nave, Vance, Swanston, & Curtis, 2011). Moreover, 90% of studies focus only on the upper 30 cm of the soil profile (Richter & Billings, 2015), thus the influences of fire on soil processes throughout the profile remain poorly characterized.

6 | FIRE BEHAVIOUR DIRECTS ECOLOGICAL OUTCOMES

Living and dead plant fuels play a prominent role in fire ecology because they help determine fire behaviour and fire effects from below-ground to the upper atmosphere. Fuels are also the most readily manipulated factor influencing fire behaviour, making them a focal point of fire management. The type and amount of fuels consumed during a fire are key links in feedbacks between fire and climate.

6.1 | Characterizing fuels

A leaf-to-globe approach is necessary to characterize fuels (See 'fuels' in Box 1 and Figure 4). Moving from small to large scales, fuel characteristics include those of individual plants (e.g. leaf anatomy, chemistry and water content), whole-plant morphology, vegetation composition and structure and ecosystem productivity. Each of these characteristics can be translated into data relevant to relationships between fuels and fire characteristics; these terms include the ratio of fuel surface area to volume, fuel particle size and density, moisture and chemical content, total and available fuel mass and spatial arrangement. These fuel characteristics are used to parameterize fuel models (see below). However, research relating fuel characteristics to determinants of fire behaviour and effects is not as advanced as other trait-centred investigations (see previous sections).

At the global scale, developments in remote-sensing methods have enabled major advances in fuels measurement. For example, measurement of aerial fuels has been revolutionized with LiDAR methods that remotely capture canopy, crown, leaf shape and spatial arrangement, and provide estimates of fuel mass (Andersen, McGaughey, & Reutebuch, 2005). Below the canopy, surface fuels can be characterized with precise 3D ground-based terrestrial laser scanning (TLS; Loudermilk, Hiers, & O'Brien, 2017). Recent efforts to bridge these techniques with dynamic fuel moisture (so-called 4-D fuels) and fire behaviour models significantly advance the ability to understand fuel combustion processes. Because below-ground fuels are driven by fine-scale topography, hydrology, tree stand age and species composition, they are currently difficult to quantify at large scales.

6.2 | Fire behaviour links fuels with fire effects

Two different modes of combustion—flaming and smoldering—occur during a fire but ecological processes are not necessarily related to combustion mode. Rather, they depend on a combination of fire intensity, duration of exposure and the transfer of that energy to objects in the environment. Estimating fire intensity from field-based observations is difficult and requires either infrared sequences (Clark, Radke, Coen, & Middleton, 1999) or direct measurements of heat flux (Butler et al., 2016). Fire radiative power can be detected from the thermal bands of satellite sensors, but these are either limited by temporal frequency (a few detections per day from MODIS and VIIRS) or spatial resolution (at coarser satellite scales). The relationship between fire behaviour and fire effects has been improved by quantification of fire intensity, at least above-ground (Hiers, O'Brien, Mitchell, Grego, & Loudermilk, 2009).

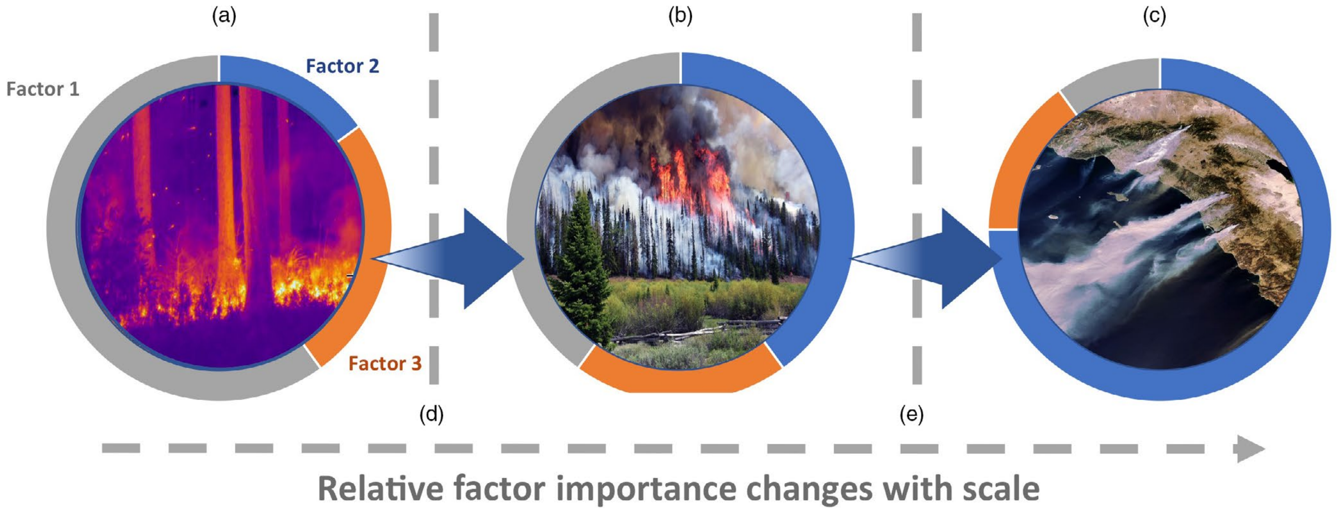

FIGURE 4 The relative role of factors driving fire behaviour and effects varies with spatial scale. Several factors (shown as different colours) determine the relationship between fire behaviour and fire's ecological effects. For example, for tree mortality, factors could include leaf moisture content, ecosystem productivity and forest structure and composition as Factors 1, 2 and 3 respectively. The relative importance of these factors (percent of ring with a given colour) changes across spatial and temporal scales. These scales range from fires acting on individual organisms (a), to stands (b), to large landscapes (c). We posit that thresholds of spatial and/or temporal scales exist at which the relative influence of these factors shifts substantially (d, e)

New approaches to measure thermal properties, dubbed fire metrology (Kremens, Smith, & Dickinson, 2010), link plant injuries to post-fire recovery of ecosystems. For example, at the level of a leaf, fire behaviour is affected by the micrometeorological conditions of the boundary layer (Dickinson & Johnson, 2001). Heat fluxes can be measured at very fine scales using thermography at sub-centimetre and sub-second scales (Figure 4; O'Brien et al., 2016), which allows detailed knowledge about heat transfer and tree injury (Sparks et al., 2017). Measures of heat flux at scales relevant to plant, soil and microbial processes enable mechanistic understanding of ecological change (Butler & Dickinson, 2010). Below-ground fire behaviour has been advanced by a small number of observational, experimental and model-based approaches (Huang & Rein, 2015; Massman, 2012). However, the field of below-ground fire behaviour is much less developed when compared to the more-readily observed above-ground processes.

6.3 | Fire behaviour integrates climate and fuels

The longer-term ecological outcomes of fire often depend on the relationship between above-ground and below-ground fuels. Below-ground properties and processes critically influence above-ground fuel recovery (*via* vegetation regeneration, seed germination and soil nutrients and symbionts), physiological status, moisture content and decomposition rates. Under climate warming, below-ground fuels (thermokarst soils, drought-exposed organic horizons and peat soils) are increasingly available for combustion during fires. Roots act as one of the many connections between above-ground and below-ground fire behaviour and its subsequent impacts (Hood, Smith, & Cluck, 2010). Recent work has advanced from observations of fire effects on above-ground indicators such as tree mortality to quantifying below-ground fire behaviour (Varner et al., 2009). Below-ground fire intensity and heating duration affects soil physical, chemical and biological properties and processes (see Section 4), yet the conditions that determine thermal severity remain poorly understood.

The relationship between fire behaviour and fuels dictates the quantity and quality of combustion products. The physical and chemical products of fuel consumption —including smoke, aerosols and volatilized gases— influence the translocation of carbon, nutrients and living organisms, and affect human health (Bowman & Johnston, 2014; Kobziar et al., 2018). Several aspects of smoke and particulate emissions are understudied from an ecological standpoint, including smoke transport of living microorganisms (Kobziar et al., 2018) and the promotion of germination and plant growth by smoke. Smoke alters UV profiles, obscures sunlight, provides substrates for water and ice condensation, and deposits particulates on plants and the environment. These processes occur both within burn perimeters (Bell, Stephens, & Moritz, 2013) and beyond *via* atmospheric transport. Aerosol radiative forcing is also a major uncertainty in our understanding of the net effects of fire on Earth's climate (Landry, Matthews, & Ramankutty, 2015). The ecological effects of smoke over multiple spatial and temporal scales should be more fully characterized (Table 1).

7 | MODELLING FIRE ACTIVITY

Fire models accomplish several unique goals essential to answering ecological questions, including (a) characterizing fire and its effects at large spatial extents, (b) testing scenarios and hypotheses regarding the interactions described in previous sections and (c) projecting fire behaviour and effects into the future. Numerous fire models are currently in use and under development (Table S2).

7.1 | Fire ignition in models

Revolutions in data collection and availability have improved our ability to model fire processes. For example, the availability and reporting of ignitions (both natural and anthropogenic) have vastly improved. Within the US there are detailed data on the location, date and ignition source for most fires (Short, 2014). Globally, there are data on lightning strikes and human-ignition proxies, such as distance to roads, transportation corridors and railroad tracks (Andela et al., 2017; Loboda, 2009; Morton, Page, DeFries, Collatz, & Hurtt, 2013). Many fire models now explicitly include ignitions and their sources (Hantson, Lasslop, Kloster, & Chuvieco, 2015; Lasslop, Thonicke, & Kloster, 2014; Li, Levis, & Ward, 2013; Mangeon et al., 2016; Scheller, Kretchun, Hawbaker, & Henne, 2019; Yue et al., 2014). However, there remain challenges associated with capturing impacts of land use (Andela et al., 2017; Schoennagel et al., 2017), the expansion of the wildland-urban interface (Radeloff et al., 2018) and the natural variability associated with lightning ignitions and ignition efficiency (the proportion of lightning strikes that generate ignitions; Romps, Seeley, Vollaro, & Molinari, 2014).

7.2 | Fire behaviour models

Modelling fire behaviour began with the work of (Rothermel, 1972) and (Van Wagner, 1973) and has improved over time (Table S2), including coupling with dynamic vegetation and/or Earth System models spanning a wide range of spatial and temporal scales. Further, coupled weather-fire models now capture the unfolding of complex landscape-scale events over a period of days (Coen, Stavros, & Fites-Kaufman, 2018), while global models continue to improve their representation of fire frequency, burned area and seasonality across years to decades (Forkel et al., 2019; Hantson et al., 2016). The representation of dynamic policy and management actions, and the evolving wildland-urban interface, requires concerted interdisciplinary efforts with social scientists (Kline et al., 2017). An ongoing challenge for global fire modelling is scaling up existing fire behaviour models from point scales to grid cells tens to hundreds of kilometres in size, without downplaying the importance of spatial heterogeneity and spatially interactive processes occurring within those large grid cells.

7.3 | Fire effects models

Fire effects models represent combustion, intensity and severity *via* physically based models and vegetation characteristics (e.g. bark thickness, resprouting, serotiny). As models improve their representation of vegetation such as with the incorporation of plant physiology, growth, and size-structure (Fisher et al., 2018) and trait-based modelling (Fisher et al., 2015), simulation of fire mortality also improves.

Dependent on the duration, magnitude and depth of heat transfer, fire can alter soil in ways that influence vegetation recovery (Brando, Oliveria-Santos, Rocha, Cury, & Coe, 2016; Johnstone, Hollingsworth, Chapin, & Mack, 2010), the structure of invertebrate and microbial communities (Hewitt et al., 2016) and availability of nutrients (Karam, Weisberg, Scheller, Johnson, & Miller, 2013). The representation of interactions between fire and below-ground processes must be improved within models to properly project landscape and biome changes (Foster et al., 2019; Pausas et al., 2018). The forefront of fire effects model development is to include interactions with other disturbances (drought, harvesting, insect outbreaks, wind-throw; Kane et al., 2017; Scheller et al., 2018), with human behaviour (suppression, human ignitions), and more refined representation of fire behaviour and effects, including the feedbacks among fire, vegetation and climate described in Section 3.

8 | EMERGENT THEMES FOR FIRE ECOLOGY

Across the six identified research areas in fire ecology from the research community—characteristics of fire regimes, changing fire regimes, fire effects on above-ground ecology, fire effects on below-ground ecology, fire behaviour and fire ecology modelling—three common themes emerge.

8.1 | Understanding the ecological consequences of fire through time

A wide array of time-scales is necessary for understanding fire processes, from measures of fire behaviour during seconds to minutes, to multi-millennial records of fire history. However, most research tends to study fire processes on a single time-scale, exposing a large untapped potential to link across time-scales. There is a particular opportunity to understand how fire regimes change over multi-decadal to centennial and millennial time-scales. Fundamental knowledge of ecosystem ecology could then be increased through mechanistic links between fire regimes and fire effects. Our current understanding of fire regimes is based on well-developed approaches for reconstructing fire history—particularly fire return interval—through dendrochronology and palaeoecology. Expanding on these methods to produce metrics used to study contemporary fire ecology, including area burned, fire severity and seasonality, would further advance our understanding of fire regimes. Better integration of fire histories into models would also lead to insights regarding the ecological and evolutionary consequences of changing fire regimes. Finally, archaeological and palaeoecological research can provide important information about the human dimension of fire regimes over the long-term, and this integration is likely to provide key insights for living with fire in the future.

8.2 | Characterizing feedbacks and nonlinearities

Despite the long recognition of fire as an important ecological process, the mechanisms underlying the interactions and feedbacks of fire with other ecological processes are only beginning to be explored in a systematic way. Determining the generality of such feedbacks, especially in systems with a long evolutionary relationship with fire, would greatly deepen our understanding of fire's role on Earth while enabling better projections of future fire effects.

To better project where positive or negative feedbacks between vegetation and fire will occur, we suggest four research priorities. First, continue to study the individual components of the primary drivers of fire activity and the relatively simple pairwise feedbacks between components, including human influences. Second, diversify the types of fire regimes studied, especially those where fire behaviour is highly variable in space and time (grasslands, savannas, Mediterranean systems). Third, expand the study of feedbacks to include not only vegetation, but also higher trophic levels and below-ground components of fire-frequented ecosystems, especially those that influence fuel composition and dynamics. Fourth, use the power of models to explore feedbacks that are difficult to observe because they either develop slowly or are difficult to interpret without controlling for other influencing factors in the field.

8.3 | Harnessing the data revolution and using models to explore the diversity of fire on Earth

The many data sources described in this manuscript provide unique and complementary views of fire on Earth, offering ecologists an incredible opportunity to draw new insights about how fire is changing. Over a dozen satellites and space-borne sensors are collecting information about fire events and their effects in real time (e.g. Landsat, MODIS, Sentinel, VIIRS, Planet, DigitalGlobe's Worldview Collection, GEDI, ECOSTRESS, and others), climate and Earth System models are operating on a variety of spatial scales and databases are providing unprecedented detail about fuels and ignitions. Ongoing data efforts include further development and better integration of palaeorecords and government incident reports addressing spatial heterogeneity, and incorporation of new sources of information about fire—from social media to drones. However, there is still a long way to go to develop better data infrastructure, to improve curation of data in a standardized format that includes controlled vocabularies that describe what was measured (Gross et al., 2018), to increase transparency, reusability and interoperability of data products across political and disciplinary boundaries and to apply new data analysis techniques such as machine learning to discover important large-scale patterns about fire behaviour, fire regimes and ecological outcomes.

There is significant intellectual momentum building in the area of fire models, with several parallel but largely disconnected efforts under way. The diversity of modelling approaches reflects the spatio-temporal issues described earlier, the diversity of fire regimes on Earth, and the individual goals of the disparate modelling communities, which range from detailed landscape models to Earth System Models. One urgent fire modelling need is to better understand the fuel-fire-atmospheric conditions that generate extreme fire behaviours that exceed the predictive ability of our current fire models. An additional modelling need is the explicit incorporation of human interactions with fire, which will be required to project the consequences of future fires. To advance this area, we need a more accurate parameterization of how people create and alter fire regimes, from changes in spatial and temporal patterns of ignitions to alteration of fuel type and continuity, coupled with past and future land use and land cover scenarios, and global data layers that provide a mechanistic understanding of human decision-making processes.

9 | CONCLUSIONS

Fire is a fundamental component of most terrestrial ecosystems on Earth. In many cases fire is key to understanding population, community and ecosystem ecology. Theories of how fire interacts with evolutionary processes are just beginning to develop and, although currently focused largely on plants, these theories are poised to advance rapidly in the animal and microbial realms. The fire ecology research community has made immense progress in recent years to understand the many aspects of fire and fire regimes, including the number, timing, changes and ultimate effect of fires on the Earth system. Here, we offer guidance to continue the important mission of understanding the fundamental role of fire in a diverse array of ecological systems.

ACKNOWLEDGEMENTS

This manuscript is a product of discussions at the Future of Fire workshop held in November 2017 in Boulder, Colorado, USA. Support was provided by NSF-DEB-1743681 to K.K.M. and A.J.T. We thank Shalin Hai-Jew for helpful discussion of the survey and qualitative methods.

AUTHORS' CONTRIBUTIONS

K.K.M., P.E.H., J.M., B.M.R., J.S., J.K.S., A.J.T., J.M.V. and T.T.V. conceived, designed and implemented the process that led to the manuscript. K.K.M. led completion of the first draft and revision of the manuscript. All authors—K.K.M., P.E.H., J.M., B.M.R., J.S., J.K.S., A.J.T., J.M.V., T.T.V., S.A.A., J.K.B., P.B., E.B., E.B., P.B., M.C., M.L.C., J.C., R.C., L.D., N.E., W.S.G., B.J.H., J.A.H., S.H., R.E.H., L.N.K., J.B.L., M.M.L., S.Y.M., L.M., M.M., J.A.M., J.G.P., A.F.A.P., W.J.P., J.R., H.S., F.S., R.M.S., R.L.S., K.G.S., M.D.S. and A.C.W. produced text and/or figures for the manuscript, contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Survey responses to the question that provided the six priority areas are available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.2280gb5nm (McLauchlan et al., 2020).

ORCID

Kendra K. McLauchlan https://orcid.org/0000-0002-6612-1097
Philip E. Higuera https://orcid.org/0000-0001-5396-9956
Jessica Miesel https://orcid.org/0000-0001-7446-464X
Brendan M. Rogers https://orcid.org/0000-0001-6711-8466
Jennifer Schweitzer https://orcid.org/0000-0003-4890-7632
Jacquelyn K. Shuman https://orcid.org/0000-0003-2588-2161
Alan J. Tepley https://orcid.org/0000-0002-5701-9613
J. Morgan Varner https://orcid.org/0000-0003-3781-5839
Thomas T. Veblen https://orcid.org/0000-0002-3037-640X
Solny A. Adalsteinsson https://orcid.org/0000-0003-4945-7266
Jennifer K. Balch https://orcid.org/0000-0002-3983-7970
Patrick Baker https://orcid.org/0000-0002-6560-7124
Enric Batllori https://orcid.org/0000-0002-2130-0489
Paulo Brando https://orcid.org/0000-0001-8952-7025
Megan Cattau https://orcid.org/0000-0003-2164-3809
Melissa L. Chipman https://orcid.org/0000-0002-6872-8829
Janice Coen https://orcid.org/0000-0003-3927-989X
Raelene Crandall https://orcid.org/0000-0002-0229-5418
Lori Daniels https://orcid.org/0000-0002-5015-8311
Neal Enright https://orcid.org/0000-0003-2979-4505
Wendy S. Gross https://orcid.org/0000-0002-4468-8666
Brian J. Harvey https://orcid.org/0000-0002-5902-4862
Jeff A. Hatten https://orcid.org/0000-0002-1685-6351
Sharon Hermann https://orcid.org/0000-0002-7572-2265
Rebecca E. Hewitt https://orcid.org/0000-0002-6668-8472
Leda N. Kobziar https://orcid.org/0000-0002-5882-8498
Jennifer B. Landesmann https://orcid.org/0000-0002-2009-0731
Michael M. Loranty https://orcid.org/0000-0001-8851-7386
S. Yoshi Maezumi https://orcid.org/0000-0002-4333-1972
Linda Mearns https://orcid.org/0000-0002-2875-5830
Max Moritz https://orcid.org/0000-0002-8995-8893
Jonathan A. Myers https://orcid.org/0000-0002-2058-8468
Juli G. Pausas https://orcid.org/0000-0003-3533-5786
Adam F. A. Pellegrini https://orcid.org/0000-0003-0418-4129
William J. Platt https://orcid.org/0000-0003-0837-8115
Fernanda Santos https://orcid.org/0000-0001-9155-5623
Robert M. Scheller https://orcid.org/0000-0002-7507-4499
Rosemary L. Sherriff https://orcid.org/0000-0003-1639-203X
Kevin G. Smith https://orcid.org/0000-0001-9691-9625
Melinda D. Smith https://orcid.org/0000-0003-4920-6985
Adam C. Watts https://orcid.org/0000-0002-7313-9906

REFERENCES

Abatzoglou, J. T., & Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 11770–11775. https://doi.org/10.1073/pnas.1607171113

Abatzoglou, J. T., Williams, A. P., & Barbero, R. (2019). Global emergence of anthropogenic climate change in fire weather indices. *Geophysical Research Letters*, *46*, 326–336. https://doi.org/10.1029/2018GL080959

Abreu, R. C. R., Hoffmann, W. A., Vasconcelos, H. L., Pilon, N. A., Rossatto, D. R., & Durigan, G. (2017). The biodiversity cost of carbon sequestration in tropical savanna. *Science Advances*, *3*. https://doi.org/10.1126/sciadv.1701284

Achard, F., Eva, H. D., Mollicone, D., & Beuchle, R. (2008). The effect of climate anomalies and human ignition factor on wildfires in Russian boreal forests. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *363*, 2331–2339. https://doi.org/10.1098/rstb.2007.2203

Adkins, J., Sanderman, J., & Miesel, J. (2019). Soil carbon pools and fluxes vary across a burn severity gradient three years after wildfire in Sierra Nevada mixed-conifer forest. *Geoderma*, *333*, 10–22. https://doi.org/10.1016/j.geoderma.2018.07.009

Agee, J. K. (1993). *Fire ecology of Pacific Northwest forests*. Washington, DC: Island Press.

Andela, N., Morton, D. C., Giglio, L., Chen, Y., van der Werf, G. R., Kasibhatla, P. S., … Randerson, J. T. (2017). A human-driven decline in global burned area. *Science*, *356*, 1356–1361. https://doi.org/10.1126/science.aal4108

Andela, N., Morton, D. C., Giglio, L., Paugam, R., Chen, Y., Hantson, S., … Randerson, J. T. (2019). The Global Fire Atlas of individual fire size, duration, speed and direction. *Earth System Science Data*, *11*, 529–552. https://doi.org/10.5194/essd-11-529-2019

Andersen, H. E., McGaughey, R. J., & Reutebuch, S. E. (2005). Estimating forest canopy fuel parameters using LIDAR data. *Remote Sensing of the Environment*, *9*, 441–449. https://doi.org/10.1016/j.rse.2004.10.013

Araya, S. N., Fogel, M. L., & Berhe, A. A. (2017). Thermal alteration of soil organic matter properties: A systematic study to infer response of Sierra Nevada climosequence soils to forest fires. *Soil*, *3*, 14.

Archibald, S., Lehmann, C. E. R., Belcher, C. M., Bond, W. J., Bradstock, R. A., Daniau, A. L., … Zanne, A. E. (2018). Biological and geophysical feedbacks with fire in the Earth system. *Environmental Research Letters*, *13*. https://doi.org/10.1088/1748-9326/aa9ead

Archibald, S., Lehmann, C. E. R., Gomez-Dans, J. L., & Bradstock, R. A. (2013). Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 6442–6447. https://doi.org/10.1073/pnas.1211466110

Baker, P. J., & Bunyavejchewin, S. (2017). Complex historical disturbance regimes shape forest dynamics across a seasonal tropical landscape in western Thailand. In M. M. Amoroso, L. D. Daniels, P. J. Baker, & J. J. Camarero (Eds.), *Dendroecology: Tree-ring analyses applied to ecological studies* (pp. 75–96). Cham, Switzerland: Springer International Publishing.

Balch, J. K., Bradley, B. A., D'Antonio, C. M., & Gomez-Dans, J. (2013). Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology*, *19*, 173–183. https://doi.org/10.1111/gcb.12046

Balch, J., Schoennagel, T., Williams, A., Abatzoglou, J., Cattau, M., Mietkiewicz, N., & St. Denis, L. (2018). Switching on the big burn of 2017. *Fire*, *1*, 17. https://doi.org/10.3390/fire1010017

Batllori, E., Ackerly, D. D., & Moritz, M. A. (2015). A minimal model of fire-vegetation feedbacks and disturbance stochasticity generates alternative stable states in grassland-shrubland-woodland systems. *Environmental Research Letters*, *10*. https://doi.org/10.1088/1748-9326/10/3/034018

Batllori, E., De Cáceres, M., Brotons, L., Ackerly, D. D., Moritz, M. A., & Lloret, F. (2018). Compound fire-drought regimes promote ecosystem transitions in Mediterranean ecosystems. *Journal of Ecology*, *107*, 1187–1198. https://doi.org/10.1111/1365-2745.13115

Beckage, B., Gross, L. J., & Platt, W. J. (2011). Grass feedbacks on fire stabilize savannas. *Ecological Modelling*, *222*, 2227–2233. https://doi.org/10.1016/j.ecolmodel.2011.01.015

Beckage, B., Platt, W. J., & Gross, L. J. (2009). Vegetation, fire, and feedbacks: A disturbance-mediated model of savannas. *The American Naturalist*, *174*, 805–818. https://doi.org/10.1086/648458

Bell, T. L., Stephens, S. L., & Moritz, M. A. (2013). Short-term physiological effects of smoke on grapevine leaves. *International Journal of Wildland Fire*, *22*, 933–946. https://doi.org/10.1071/WF12140

Beringer, J., Hutley, L. B., Abramson, D., Arndt, S. K., Briggs, P., Bristow, M., … Uotila, P. (2015). Fire in Australian savannas: From leaf to landscape. *Global Change Biology*, *21*, 62–81. https://doi.org/10.1111/gcb.12686

Bigio, E. R., Swetnam, T. W., & Baisan, C. H. (2016). Local-scale and regional climate controls on historical fire regimes in the San Juan Mountains, Colorado. *Forest Ecology and Management*, *360*, 311–322. https://doi.org/10.1016/j.foreco.2015.10.041

Blackhall, M., Raffaele, E., Paritsis, J., Tiribelli, F., Morales, J. M., Kitzberger, T., … Veblen, T. T. (2017). Effects of biological legacies and herbivory on fuels and flammability traits: A long-term experimental study of alternative stable states. *Journal of Ecology*, *105*, 1309–1322. https://doi.org/10.1111/1365-2745.12796

Bodi, M. B., Martin, D. A., Balfour, V. N., Santin, C., Doerr, S. H., Pereira, P., … Mataix-Solera, J. (2014). Wildland fire ash: Production, composition and eco-hydro-geomorphic effects. *Earth-Science Reviews*, *138*, 503.

Boer, M. M., Bowman, D. M. J. S., Murphy, B. P., Cary, G. J., Cochrane, M. A., Fensham, R. J., … Bradstock, R. A. (2016). Future changes in climatic water balance determine potential for transformational shifts in Australian fire regimes. *Environmental Research Letters*, *11*. https://doi.org/10.1088/1748-9326/11/6/065002

Bond, W. J., Woodward, F. I., & Midgley, G. F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, *165*, 525–537. https://doi.org/10.1111/j.1469-8137.2004.01252.x

Bowman, D., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., … Pyne, S. J. (2009). Fire in the Earth system. *Science*, *324*, 481–484. https://doi.org/10.1126/science.1163886

Bowman, D., Balch, J., Artaxo, P., Bond, W. J., Cochrane, M. A., D'Antonio, C. M., … Swetnam, T. W. (2011). The human dimension of fire regimes on Earth. *Journal of Biogeography*, *38*, 2223–2236. https://doi.org/10.1111/j.1365-2699.2011.02595.x

Bowman, D., & Johnston, F. (2014). Bushfires, human health economics, and pyrogeography. *Geographical Research*, *52*, 340–343. https://doi.org/10.1111/1745-5871.12065

Bowman, D., Murphy, B. P., Williamson, G. J., & Cochrane, M. A. (2014). Pyrogeographic models, feedbacks and the future of global fire regimes. *Global Ecology and Biogeography*, *23*, 821–824. https://doi.org/10.1111/geb.12180

Bowman, D., Perry, G. L., Higgins, S. I., Johnson, C. N., Fuhlendorf, S. D., & Murphy, B. P. (2016). Pyrodiversity is the coupling of biodiversity and fire regimes in food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *5*, 371. https://doi.org/10.1098/rstb.2015.0169

Bradford, J. B., Fraver, S., Milo, A. M., D'Amato, A. W., Palik, B., & Shinneman, D. J. (2012). Effects of multiple interacting disturbances and salvage logging on forest carbon stocks. *Forest Ecology and Management*, *267*, 209–214. https://doi.org/10.1016/j.foreco.2011.12.010

Brando, P. M., Balch, J. K., Nepstad, D. C., Morton, D. C., Putz, F. E., Coe, M. T., … Soares-Filho, B. S. (2014). Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 6347–6352. https://doi.org/10.1073/pnas.1305499111

Brando, P. M., Oliveria-Santos, C., Rocha, W., Cury, R., & Coe, M. T. (2016). Effects of experimental fuel additions on fire intensity and severity: Unexpected carbon resilience of a neotropical forest. *Global Change Biology*, *22*, 2516–2525. https://doi.org/10.1111/gcb.13172

Butler, B. W., & Dickinson, M. B. (2010). Tree injury and mortality in fires: Developing process-based models. *Fire Ecology*, *6*, 55–79. https://doi.org/10.4996/fireecology.0601055

Butler, B., Teske, C., Jimenez, D., O'Brien, J., Sopko, P., Wold, C., … Loudermilk, E. (2016). Observations of energy transport and rate of spreads from low-intensity fires in longleaf pine habitat – RxCADRE 2012. *International Journal of Wildland Fire*, *25*, 76–89. https://doi.org/10.1071/WF14154

Butler, O. M., Elser, J. J., Lewis, T., Mackey, B., & Chen, C. (2018). The phosphorus-rich signature of fire in the soil-plant system: A global meta-analysis. *Ecology Letters*, *21*, 335–344. https://doi.org/10.1111/ele.12896

Cansler, C. A., & McKenzie, D. (2012). How robust are burn severity indices when applied in a new region? Evaluation of alternate field-based and remote-sensing methods. *Remote Sensing*, *4*, 456. https://doi.org/10.3390/rs4020456

Certini, G. (2005). Effects of fire on properties of forest soils: A review. *Oecologia*, *143*, 1–10. https://doi.org/10.1007/s00442-004-1788-8

Certini, G. (2014). Fire as a soil-forming factor. *Ambio*, *43*, 191–195. https://doi.org/10.1007/s13280-013-0418-2

Chakrabarty, R. K., Gyawali, M., Yatavelli, R. L. N., Pandey, A., Watts, A. C., Knue, J., … Moosmuller, H. (2016). Brown carbon aerosols from burning of boreal peatlands: Microphysical properties, emission factors, and implications for direct radiative forcing. *Atmospheric Chemistry and Physics*, *16*, 3033–3040. https://doi.org/10.5194/acp-16-3033-2016

Chergui, B., Fahd, S., Santos, X., & Pausas, J. G. (2018). Socioeconomic factors drive fire-regime variability in the Mediterranean Basin. *Ecosystems*, *21*, 619–628. https://doi.org/10.1007/s10021-017-0172-6

Chipman, M. L., Hudspith, V., Higuera, P. E., Duffy, P. A., Kelly, R., Oswald, W. W., & Hu, F. S. (2015). Spatiotemporal patterns of tundra fires: Late-quaternary charcoal records from Alaska. *Biogeosciences*, *12*, 4017–4027. https://doi.org/10.5194/bg-12-4017-2015

Clark, T. L., Radke, L., Coen, J., & Middleton, D. (1999). Analysis of small scale convective dynamics in a crown fire using infrared video camera imagery. *Journal of Applied Meteorology*, *38*, 1401–1420. https://doi.org/10.1175/1520-0450(1999)038<1401:AOSSCD>2.0.CO;2

Coen, J. L., Stavros, E. N., & Fites-Kaufman, J. A. (2018). Deconstructing the king megafire. *Ecological Applications*, *28*, 1565–1580. https://doi.org/10.1002/eap.1752

Collins, B., Stevens, J., Miller, J., Stephens, S., Brown, P., & North, M. (2017). Alternative characterization of forest fire regimes: Incorporating spatial patterns. *Landscape Ecology*, *32*, 1543–1552. https://doi.org/10.1007/s10980-017-0528-5

Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A. F., & Krebs, P. (2009). Reconstructing past fire regimes: Methods, applications, and relevance to fire management and conservation. *Quaternary Science Reviews*, *28*, 555–576. https://doi.org/10.1016/j.quascirev.2008.11.005

Crandall, R., & Knight, T. M. (2015). Positive frequency dependence undermines the success of restoration using historical disturbance regimes. *Ecology Letters*, *18*, 883–891. https://doi.org/10.1111/ele.12473

Crandall, R. M., & Platt, W. J. (2012). Habitat and fire heterogeneity explain the co-occurrence of congeneric resprouter and reseeder *Hypericum* spp. along a Florida pine savanna ecocline. *Plant Ecology*, *213*, 1643–1654. https://doi.org/10.1007/s11258-012-0119-0

Crisp, M. D., Burrows, G. E., Cook, L. G., Thornhill, A. H., & Bowman, D. M. J. S. (2011). Flammable biomes dominated by eucalypts originated at the Cretaceous-Palaeogene boundary. *Nature Communications*, *2*. https://doi.org/10.1038/ncomms1191

da Silva, D. M., & Batalha, M. A. (2008). Soil–vegetation relationships in cerrados under different fire frequencies. *Plant and Soil*, *311*, 87–96. https://doi.org/10.1007/s11104-008-9660-y

Dantas, V. D. L., Batalha, M. A., & Pausas, J. G. (2013). Fire drives functional thresholds on the savanna–forest transition. *Ecology*, *94*, 2454–2463. https://doi.org/10.1890/12-1629.1

Davies, A. B., Eggleton, P., van Rensburg, B. J., & Parr, C. L. (2012). The pyrodiversity-biodiversity hypothesis: A test with savanna termite assemblages. *Journal of Applied Ecology*, *49*, 422–430. https://doi.org/10.1111/j.1365-2664.2012.02107.x

Davis, K. T., Higuera, P. E., & Sala, A. (2018). Anticipating fire-mediated impacts of climate change using a demographic framework. *Functional Ecology*, *32*, 1729–1745. https://doi.org/10.1111/1365-2435.13132

De Faria, B. L., Brando, P. M., Macedo, M. N., Panday, P. K., Soares, B. S., & Coe, M. T. (2017). Current and future patterns of fire-induced forest degradation in Amazonia. *Environmental Research Letters*, *12*. https://doi.org/10.1088/1748-9326/aa69ce

Dickinson, M. B., & Johnson, E. A. (2001). Fire effects on trees. In E. A. Johnson & K. Miyanishi (Eds.), *Forest fires: Behavior and ecological effects* (pp. 477–525). Cambridge, MA: Academic Press.

Dooley, S. R., & Treseder, K. K. (2012). The effect of fire on microbial biomass: A meta-analysis of field studies. *Biogeochemistry*, *109*, 49–61. https://doi.org/10.1007/s10533-011-9633-8

Dove, N. C., & Hart, S. C. (2017). Fire reduces fungal species richness and in situ mycorrhizal colonization: A meta-analysis. *Fire Ecology*, *13*, 37–65. https://doi.org/10.4996/fireecology.130237746

Dunnette, P. V., Higuera, P. E., McLauchlan, K. K., Derr, K. M., Briles, C. E., & Keefe, M. H. (2014). Biogeochemical impacts of wildfires over four millennia in a Rocky Mountain subalpine watershed. *New Phytologist*, *203*, 900–912. https://doi.org/10.1111/nph.12828

Eidenshink, J., Schwind, B., Brewer, K., Zhu, Z., Quayle, B., & Howard, S. (2007). A project for monitoring trends in burn severity. *Fire Ecology*, *3*, 19. https://doi.org/10.4996/fireecology.0301003

Enright, N. J., Fontaine, J. B., Bowman, D. M. J. S., Bradstock, R. A., & Williams, R. J. (2015). Interval squeeze: Altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment*, *13*, 265–272. https://doi.org/10.1890/140231

Fill, J. M., Platt, W. J., Welch, S. M., Waldron, J. L., & Mousseau, T. A. (2015). Updating models for restoration and management of fiery ecosystems. *Forest Ecology and Management*, *356*, 54–63. https://doi.org/10.1016/j.foreco.2015.07.021

Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C., Farrior, C. E., … Moorcroft, P. R. (2018). Vegetation demographics in Earth System Models: A review of progress and priorities. *Global Change Biology*, *24*, 35–54. https://doi.org/10.1111/gcb.13910

Fisher, R. A., Muszala, S., Verteinstein, M., Lawrence, P., Xu, C., McDowell, N. G., … Bonan, G. (2015). Taking off the training wheels: The properties of a dynamic vegetation model without climate envelopes, CLM4.5(ED). *Geoscientific Model Development*, *8*, 3593–3619. https://doi.org/10.5194/gmd-8-3593-2015

Forkel, M., Andela, N., Harrison, S. P., Lasslop, G., van Marle, M., Chuvieco, E., … Arneth, A. (2019). Emergent relationships with respect to burned area in global satellite observations and fire-enabled vegetation models. *Biogeosciences*, *16*, 57–76. https://doi.org/10.5194/bg-16-57-2019

Forrestel, E. J., Donoghue, M. J., & Smith, M. D. (2014). Convergent phylogenetic and functional responses to altered fire regimes in mesic savanna grasslands of North America and South Africa. *New Phytologist*, *203*, 1000–1011. https://doi.org/10.1111/nph.12846

Foster, A., Armstrong, A., Shuman, J., Shugart, H., Rogers, B., Mack, M., … Ranson, J. (2019). Importance of tree- and species-level interactions with wildfire, climate, and soils in interior Alaska: Implications for forest change under a warming climate. *Ecological Modelling*, *409*, 108765. https://doi.org/10.1016/j.ecolmodel.2019.108765

Freeman, J. E., Kobziar, L. N., Leone, E. H., & Williges, K. (2019). Drivers of plant functional group richness and beta diversity in fire-dependent pine savannas. *Diversity and Distributions*, *25*, 1024–1044. https://doi.org/10.1111/ddi.12926

Fuhlendorf, S. D., Engle, D. M., Kerby, J., & Hamilton, R. (2009). Pyric herbivory: Rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology*, *23*, 588–598. https://doi.org/10.1111/j.1523-1739.2008.01139.x

Garcia-Oliva, F., Merino, A., Fonturbel, M. T., Omil, B., Fernandez, C., & Vega, J. A. (2018). Severe wildfire hinders renewal of soil P pools by thermal mineralization of organic P in forest soil: Analysis by sequential extraction and P-31 NMR spectroscopy. *Geoderma*, *309*, 32–40.

Gartner, M. H., Veblen, T. T., Sherriff, R. L., & Schoennagel, T. L. (2012). Proximity to grasslands influences fire frequency and sensitivity to climate variability in ponderosa pine forests of the Colorado Front Range. *International Journal of Wildland Fire*, *21*, 562–571. https://doi.org/10.1071/WF10103

Geary, W. L., Doherty, T. S., Nimmo, D. G., Tulloch, A. I., & Ritchie, E. G. (2019). Predator responses to fire: A global systematic review and meta-analysis. *Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.13153

Gibson, C. M., Chasmer, L. E., Thompson, D. K., Quinton, W. L., Flannigan, M. D., & Olefeldt, D. (2018). Wildfire as a major driver of recent permafrost thaw in boreal peatlands. *Nature Communications*, *9*. https://doi.org/10.1038/s41467-018-05457-1

Giglio, L., Csiszar, I., & Justice, C. O. (2006). Global distribution and seasonality of active fires as observed with the terra and aqua moderate resolution imaging spectroradiometer (MODIS) sensors. *Journal of Geophysical Research-Biogeosciences*, *111*. https://doi.org/10.1029/2005JG000142

Giovannini, G., Lucchesi, S., & Giachetti, M. (1988). Effect of heating on some physical and chemical parameters related to soil aggregation and erodibility. *Soil Science*, *146*, 255–261. https://doi.org/10.1097/00010694-198810000-00006

Godwin, D. R., Kobziar, L. N., & Robertson, K. M. (2017). Effects of fire frequency and soil temperature on soil CO_2 efflux rates in old-field pine-grassland forests. *Forests*, *8*. https://doi.org/10.3390/f8080274

Gosling, W. D., Cornelissen, H. L., & McMichael, C. N. H. (2019). Reconstructing past fire temperatures from ancient charcoal material. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *520*, 128–137. https://doi.org/10.1016/j.palaeo.2019.01.029

Grau, H. R., & Veblen, T. T. (2000). Rainfall variability, fire and vegetation dynamics in neotropical montane ecosystems in north-western Argentina. *Journal of Biogeography*, *27*, 1107–1121. https://doi.org/10.1046/j.1365-2699.2000.00488.x

Gross, W., Morrill, C., & Wahl, E. (2018). New advances at NOAA's World data service for paleoclimatology – Promoting the FAIR principles. *Past Global Change Magazine*, *26*(2), 58. https://doi.org/10.22498/pages.26.2.58

Guarinello de Oliveira Portes, M. C., Safford, H., & Behling, H. (2018). Humans and climate as designers of the landscape in Serra da Bocaina National Park, southeastern Brazil, over the last seven centuries. *Anthropocene*, *24*, 61–71. https://doi.org/10.1016/j.ancene.2018.11.004

Guinto, D. F., Xu, Z. H., House, A. P. N., & Saffigna, P. G. (2001). Soil chemical properties and forest floor nutrients under repeated prescribed-burning in eucalypt forests of south-east Queensland, Australia. *New Zealand Journal of Forestry Science*, *31*, 170–187.

Gutknecht, J. L. M., Henry, H. A. L., & Balser, T. C. (2010). Inter-annual variation in soil extra-cellular enzyme activity in response to simulated global change and fire disturbance. *Pedobiologia*, *53*, 283–293. https://doi.org/10.1016/j.pedobi.2010.02.001

Hantson, S., Arneth, A., Harrison, S. P., Kelley, D. I., Prentice, I. C., Rabin, S. S., … Yue, C. (2016). The status and challenge of global fire modelling. *Biogeosciences*, *13*, 3359–3375. https://doi.org/10.5194/bg-13-3359-2016

Hantson, S., Lasslop, G., Kloster, S., & Chuvieco, E. (2015). Anthropogenic effects on global mean fire size. *International Journal of Wildland Fire*, *24*, 589–596. https://doi.org/10.1071/WF14208

Harden, J. W., Trumbore, S. E., Stocks, B. J., Hirsch, A., Gower, S. T., O'Neill, K. P., & Kasischke, E. S. (2000). The role of fire in the boreal carbon budget. *Global Change Biology*, *6*, 174–184. https://doi.org/10.1046/j.1365-2486.2000.06019.x

Harms, K. E., Gagnon, P. R., Passmore, H. A., Myers, J. A., & Platt, W. J. (2017). Groundcover community assembly in high-diversity pine savannas: Seed arrival and fire-generated environmental filtering. *Ecosphere*, *8*. https://doi.org/10.1002/ecs2.1716

Hartford, R. A., & Frandsen, W. H. (1992). When it's hot, it's hot … or maybe it's not! (surface flaming may not portend extensive soil heating). *International Journal of Wildland Fire*, *2*, 6. https://doi.org/10.1071/WF9920139

Harvey, B. J., Donato, D. C., & Turner, M. G. (2016a). Burn me twice, shame on who? Interactions between successive forest fires across a temperate mountain region. *Ecology*, *97*, 2272–2282. https://doi.org/10.1002/ecy.1439

Harvey, B. J., Donato, D. C., & Turner, M. G. (2016b). Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984–2010). *Landscape Ecology*, *31*, 2367–2383. https://doi.org/10.1007/s10980-016-0408-4

He, T., & Lamont, B. B. (2018). Baptism by fire: The pivotal role of ancient conflagrations in evolution of the Earth's flora. *National Science Review*, *5*, 237–254. https://doi.org/10.1093/nsr/nwx041

He, T., Lamont, B. B., & Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity. *Biological Reviews*, *94*, 1983–2010. https://doi.org/10.1111/brv.12544

He, T., Pausas, J. G., Belcher, C. M., Schwilk, D. W., & Lamont, B. B. (2012). Fire-adapted traits of Pinus arose in the fiery Cretaceous. *New Phytologist*, *194*, 751–759.

He, Y., Trumbore, S. E., Torn, M. S., Harden, J. W., Vaughn, L. J. S., Allison, S. D., & Randerson, J. T. (2016). Radiocarbon constraints imply reduced carbon uptake by soils during the 21st century. *Science*, *353*, 1419–1424. https://doi.org/10.1126/science.aad4273

Heon, J., Arseneault, D., & Parisien, M.-A. (2014). Resistance of the boreal forest to high burn rates. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 13888–13893. https://doi.org/10.1073/pnas.1409316111

Hewitt, R. E., Hollingsworth, T. N., Chapin, F. S., & Taylor, D. L. (2016). Fire-severity effects on plant-fungal interactions after a novel tundra wildfire disturbance: Implications for arctic shrub and tree migration. *BMC Ecology*, *16*. https://doi.org/10.1186/s12898-016-0075-y

Heyerdahl, E. K., Brubaker, L. B., & Agee, J. K. (2001). Spatial controls of historical fire regimes: A multiscale example from the interior west, USA. *Ecology*, *82*, 660–678. https://doi.org/10.1890/0012-9658(2001)082[0660:SCOHFR]2.0.CO;2

Heyerdahl, E. K., Morgan, P., & Riser, J. P. II (2008). Multi-season climate synchronized historical fires in dry forests (1650–1900), northern Rockies, USA. *Ecology*, *89*, 705–716. https://doi.org/10.1890/06-2047.1

Hiers, J. K., O'Brien, J. J., Mitchell, R. J., Grego, J. M., & Loudermilk, E. L. (2009). The wildland fuel cell concept: An approach to characterize fine-scale variation in fuels and fire in frequently burned longleaf pine forests. *International Journal of Wildland Fire*, *18*, 315–325. https://doi.org/10.1071/WF08084

Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C. R., Lau, O. L., … Franco, A. C. (2012). Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters*, *15*, 759–768. https://doi.org/10.1111/j.1461-0248.2012.01789.x

Holdo, R. M., Mack, M. C., & Arnold, S. G. (2012). Tree canopies explain fire effects on soil nitrogen, phosphorus and carbon in a savanna ecosystem. *Journal of Vegetation Science*, *23*, 352–360. https://doi.org/10.1111/j.1654-1103.2011.01357.x

Homann, P. S., Bormann, B. T., & Boyle, J. R. (2001). Detecting treatment differences in soil carbon and nitrogen resulting from forest manipulations. *Soil Science Society of America Journal*, *65*, 463–469. https://doi.org/10.2136/sssaj2001.652463x

Hood, S. M., Smith, S. L., & Cluck, D. R. (2010). Predicting mortality for five California conifers following wildfire. *Forest Ecology and Management*, *260*, 750–762. https://doi.org/10.1016/j.foreco.2010.05.033

Huang, X., & Rein, G. (2015). Computational study of critical moisture and depth of burn in peat fires. *International Journal of Wildland Fire*, *24*, 798–808. https://doi.org/10.1071/WF14178

Hutto, R. L. (2008). The ecological importance of severe wildfires: Some like it hot. *Ecological Applications*, *18*, 1827–1834. https://doi.org/10.1890/08-0895.1

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., … Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, *14*, 369–378. https://doi.org/10.1002/fee.1311

Johnstone, J. F., Hollingsworth, T. N., Chapin, F. S. III, & Mack, M. C. (2010). Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, *16*, 1281–1295. https://doi.org/10.1111/j.1365-2486.2009.02051.x

Jolly, W. M., Cochrane, M. A., Freeborn, P. H., Holden, Z. A., Brown, T. J., Williamson, G. J., & Bowman, D. M. J. S. (2015). Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, *6*. https://doi.org/10.1038/ncomms8537

Judson, O. P. (2017). The energy expansions of evolution. *Nature Ecology & Evolution*, *1*. https://doi.org/10.1038/s41559-017-0138

Kane, J. M., Varner, J. M., Metz, M. R., & van Mantgem, P. J. (2017). Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western US Forests. *Forest Ecology and Management*, *405*, 188–199. https://doi.org/10.1016/j.foreco.2017.09.037

Karam, S. L., Weisberg, P. J., Scheller, R. M., Johnson, D. W., & Miller, W. W. (2013). Development and evaluation of a nutrient cycling extension for the LANDIS-II landscape simulation model. *Ecological Modelling*, *250*, 45–57. https://doi.org/10.1016/j.ecolmodel.2012.10.016

Kardol, P., De Deyn, G. B., Laliberte, E., Mariotte, P., & Hawkes, C. V. (2013). Biotic plant-soil feedbacks across temporal scales. *Journal of Ecology*, *101*, 309–315. https://doi.org/10.1111/1365-2745.12046

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire*, *18*, 116–126. https://doi.org/10.1071/WF07049

Keeley, J. E., Bond, W. J., Bradstock, R. A., Pausas, J. G., & Rundel, P. W. (2012). *Fire in mediterranean ecosystems: Ecology, evolution and management*. New York, NY: Cambridge University Press.

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, *16*, 406–411. https://doi.org/10.1016/j.tplants.2011.04.002

Keeley, J. E., & Rundel, P. W. (2005). Fire and the Miocene expansion of C-4 grasslands. *Ecology Letters*, *8*, 683–690. https://doi.org/10.1111/j.1461-0248.2005.00767.x

Kelly, L. T., & Brotons, L. (2017). Using fire to promote biodiversity. *Science*, *355*, 1264–1265. https://doi.org/10.1126/science.aam7672

Kelly, R., Chipman, M. L., Higuera, P. E., Stefanova, I., Brubaker, L. B., & Hu, F. S. (2013). Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 13055–13060. https://doi.org/10.1073/pnas.1305069110

Kitzberger, T., Veblen, T. T., & Villalba, R. (1997). Climatic influences on fire regimes along a rain forest to xeric woodland gradient in northern Patagonia, Argentina. *Journal of Biogeography*, *24*, 35–47. https://doi.org/10.1111/j.1365-2699.1997.tb00048.x

Kline, J. D., White, E. M., Fischer, A. P., Steen-Adams, M. M., Charnley, S., Olsen, C. S., … Bailey, J. D. (2017). Integrating social science into empirical models of coupled human and natural systems. *Ecology and Society*, *22*. https://doi.org/10.5751/ES-09329-220325

Kobziar, L., Godwin, D., Taylor, L., & Watts, A. (2015). Perspectives on trends, effectiveness, and impediments to prescribed burning in the southern U.S. *Forests*, *6*, 561. https://doi.org/10.3390/f6030561

Kobziar, L. N., Pingree, M. R. A., Larson, H., Dreaden, T. J., Green, S., & Smith, J. A. (2018). Pyroaerobiology: The aerosolization and transport of viable microbial life by wildland fire. *Ecosphere*, *9*. https://doi.org/10.1002/ecs2.2507

Kolka, R. K., Sturtevant, B. R., Miesel, J. R., Singh, A., Wolter, P. T., Fraver, S., … Townsend, P. A. (2017). Emissions of forest floor and mineral soil carbon, nitrogen and mercury pools and relationships with fire severity for the Pagami Creek Fire in the Boreal Forest of northern Minnesota. *International Journal of Wildland Fire*, *26*, 296–305. https://doi.org/10.1071/WF16128

Kranabetter, J. M., McLauchlan, K. K., Enders, S. K., Fraterrigo, J. M., Higuera, P. E., Morris, J. L., … Perakis, S. (2016). A framework to assess biogeochemical response to ecosystem disturbance using nutrient partitioning ratios. *Ecosystems*, *19*, 387–395. https://doi.org/10.1007/s10021-015-9934-1

Krawchuk, M. A., Moritz, M. A., Parisien, M.-A., Van Dorn, J., & Hayhoe, K. (2009). Global pyrogeography: The current and future distribution of wildfire. *PLoS ONE*, *4*. https://doi.org/10.1371/journal.pone.0005102

Kremens, R. L., Smith, A. M. S., & Dickinson, M. B. (2010). Fire Metrology: Current and future directions in physics-based measurements. *Fire Ecology*, *6*, 13–35. https://doi.org/10.4996/fireecology.0601013

Landesmann, J. B., Gowda, J. H., & Kitzberger, T. (2016). Temporal shifts in the interaction between woody resprouters and an obligate seeder tree during a post-fire succession in Patagonia. *Journal of Vegetation Science*, *27*, 1198–1208. https://doi.org/10.1111/jvs.12430

Landesmann, J. B., & Morales, J. M. (2018). The importance of fire refugia in the recolonization of a fire-sensitive conifer in northern Patagonia. *Plant Ecology*, *219*, 455–466. https://doi.org/10.1007/s11258-018-0808-4

Landry, J.-S., Matthews, H. D., & Ramankutty, N. (2015). A global assessment of the carbon cycle and temperature responses to major changes in future fire regime. *Climatic Change*, *133*, 179–192. https://doi.org/10.1007/s10584-015-1461-8

Lasslop, G., & Kloster, S. (2017). Human impact on wildfires varies between regions and with vegetation productivity. *Environmental Research Letters*, *12*, 115011.

Lasslop, G., Thonicke, K., & Kloster, S. (2014). SPITFIRE within the MPI Earth system model: Model development and evaluation. *Journal of Advances in Modeling Earth Systems*, *6*, 740–755. https://doi.org/10.1002/2013MS000284

Lazarina, M., Sgardelis, S. P., Tscheulin, T., Devalez, J., Mizerakis, V., Kallimanis, A. S., … Petanidou, T. (2017). The effect of fire history in shaping diversity patterns of flower-visiting insects in post-fire Mediterranean pine forests. *Biodiversity and Conservation*, *26*, 115–131. https://doi.org/10.1007/s10531-016-1228-1

Le Page, Y., Morton, D., Hartin, C., Bond-Lamberty, B., Cardoso Pereira, J. M., Hurtt, G., & Asrar, G. (2017). Synergy between land use and climate change increases future fire risk in Amazon forests. *Earth System Dynamics*, *8*, 1237–1246. https://doi.org/10.5194/esd-8-1237-2017

Leys, B. A., Commerford, J. L., & McLauchlan, K. K. (2017). Reconstructing grassland fire history using sedimentary charcoal: Considering count, size and shape. *PLoS ONE*, *12*. https://doi.org/10.1371/journal.pone.0176445

Li, F., Levis, S., & Ward, D. S. (2013). Quantifying the role of fire in the Earth system – Part 1: Improved global fire modeling in the Community Earth System Model (CESM1). *Biogeosciences*, *10*, 2293–2314.

Liu, X., Chen, C., Wang, W., Hughes, J. M., & Lewis, T. (2015). Response of soil denitrifying communities to long-term prescribed burning in two Australian sclerophyll forests. *Geomicrobiology Journal*, *32*, 577–584. https://doi.org/10.1080/01490451.2014.908981

Liu, Z., Ballantyne, A. P., & Cooper, L. A. (2019). Biophysical feedback of global forest fires on surface temperature. *Nature Communications*, *10*. https://doi.org/10.1038/s41467-018-08237-z

Loboda, T. V. (2009). Modeling fire danger in data-poor regions: A case study from the Russian Far East. *International Journal of Wildland Fire*, *18*, 19–35. https://doi.org/10.1071/WF07094

Looy, C. V. (2013). Natural history of a plant trait: Branch-system abscission in Paleozoic conifers and its environmental, autecological, and ecosystem implications in a fire-prone world. *Paleobiology*, *39*, 235–252. https://doi.org/10.1666/12030

Loudermilk, L. E., Hiers, J. K., & O'Brien, J. J. (2017). The role of fuels for understanding fire behavior and fire effects. In L. K. Kirkman & S. B. Jack (Eds.), *Ecological restoration and management of longleaf pine forests* (1st ed., pp. 107–122). Boca Raton, FL: CRC Press.

Ludwig, S. M., Alexander, H. D., Kielland, K., Mann, P. J., Natali, S. M., & Ruess, R. W. (2018). Fire severity effects on soil carbon and nutrients and microbial processes in a Siberian larch forest. *Global Change Biology*, *24*, 5841–5852. https://doi.org/10.1111/gcb.14455

Maezumi, S. Y., Robinson, M., de Souza, J., Urrego, D. H., Schaan, D., Alves, D., & Iriarte, J. (2018). New insights from Pre-Columbian land use and fire management in Amazonian dark earth forests. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00111

Mangeon, S., Voulgarakis, A., Gilham, R., Harper, A., Sitch, S., & Folberth, G. (2016). INFERNO: A fire and emissions scheme for the UK Met Office's Unified Model. *Geoscientific Model Development*, *9*. https://doi.org/10.5194/gmd-9-2685-2016

Maravalhas, J., & Vasconcelos, H. L. (2014). Revisiting the pyrodiversity-biodiversity hypothesis: Long-term fire regimes and the structure of ant communities in a Neotropical savanna hotspot. *Journal of Applied Ecology*, *51*, 1661–1668. https://doi.org/10.1111/1365-2664.12338

Marlon, J. R., Kelly, R., Daniau, A.-L., Vanniere, B., Power, M. J., Bartlein, P., … Zhihai, T. (2016). Reconstructions of biomass burning from sediment-charcoal records to improve data-model comparisons. *Biogeosciences*, *13*, 3225–3244. https://doi.org/10.5194/bg-13-3225-2016

Martin, R. E., & Sapsis, D. B. (1992). Fires as agents of biodiversity: Pyrodiversity promotes biodiversity. In R. Harris, D. Erman, & H. Kerner (Eds.), *Proceedings of the conference on biodiversity of northwest California ecosystems* (pp. 150–157). Berkeley, CA: Cooperative Extension, University of California.

Massman, W. J. (2012). Modeling soil heating and moisture transport under extreme conditions: Forest fires and slash pile burns. *Water Resources Research*, *48*. https://doi.org/10.1029/2011WR011710

Maurin, O., Davies, T. J., Burrows, J. E., Daru, B. H., Yessoufou, K., Muasya, A. M., … Bond, W. J. (2014). Savanna fire and the origins of the 'underground forests' of Africa. *New Phytologist*, *204*, 201–214. https://doi.org/10.1111/nph.12936

McCarthy, M. A., Gill, A. M., & Bradstock, R. A. (2001). Theoretical fire-interval distributions. *International Journal of Wildland Fire*, *10*, 73–77. https://doi.org/10.1071/WF01013

McKenzie, D., & Littell, J. S. (2017). Climate change and the eco-hydrology of fire: Will area burned increase in a warming western USA? *Ecological Applications*, *27*, 26–36. https://doi.org/10.1002/eap.1420

McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., … Watts, A. C. (2020). Data from: Fire as a fundamental ecological process: Research advances and frontiers. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.2280gb5nm

McWethy, D. B., Higuera, P. E., Whitlock, C., Veblen, T. T., Bowman, D. M. J. S., Cary, G. J., … Tepley, A. J. (2013). A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes. *Global Ecology and Biogeography*, *22*, 900–912. https://doi.org/10.1111/geb.12038

McWethy, D. B., Whitlock, C., Wilmshurst, J. M., McGlone, M. S., Fromont, M., Li, X., … Cook, E. R. (2010). Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(50), 21343–21348. https://doi.org/10.1073/pnas.1011801107

Meddens, A. J. H., Kolden, C. A., Lutz, J. A., Smith, A. M. S., Cansler, C. A., Abatzoglou, J. T., … Krawchuk, M. A. (2018). Fire refugia: What are they, and why do they matter for global change? *BioScience*, *68*, 944–954. https://doi.org/10.1093/biosci/biy103

Miesel, J. R., Hockaday, W. C., Kolka, R. K., & Townsend, P. A. (2015). Soil organic matter composition and quality across fire severity gradients in coniferous and deciduous forests of the southern boreal region. *Journal of Geophysical Research-Biogeosciences*, *120*, 1124–1141. https://doi.org/10.1002/2015JG002959

Mikita-Barbato, R. A., Kelly, J. J., & Tate, R. L. (2015). Wildfire effects on the properties and microbial community structure of organic horizon soils in the New Jersey Pinelands. *Soil Biology & Biochemistry*, *86*, 67–76. https://doi.org/10.1016/j.soilbio.2015.03.021

Miller, J. D., Skinner, C. N., Safford, H. D., Knapp, E. E., & Ramirez, C. M. (2012). Trends and causes of severity, size, and number of fires in northwestern California, USA. *Ecological Applications*, *22*, 184–203. https://doi.org/10.1890/10-2108.1

Miller, R. G., Tangney, R., Enright, N. J., Fontaine, J. B., Merritt, D. J., Ooi, M. K. J., … Miller, B. P. (2019). Mechanisms of fire seasonality effects on plant populations. *Trends in Ecology & Evolution*, *34*, 1104–1117. https://doi.org/10.1016/j.tree.2019.07.009

Morgan, C., Losey, A., & Trout, L. (2014). Late-Holocene paleoclimate and treeline fluctuation in Wyoming's Wind River Range, USA. *Holocene*, *24*, 209–219. https://doi.org/10.1177/0959683613516817

Moritz, M. A., Batllori, E., Bradstock, R. A., Gill, A. M., Handmer, J., Hessburg, P. F., … Syphard, A. D. (2014). Learning to coexist with wildfire. *Nature*, *515*, 58–66. https://doi.org/10.1038/nature13946

Morton, D. C., Le Page, Y., DeFries, R., Collatz, G. J., & Hurtt, G. C. (2013). Understorey fire frequency and the fate of burned forests in southern Amazonia. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *368*. https://doi.org/10.1098/rstb.2012.0163

Myers, J. A., Chase, J. M., Crandall, R. M., & Jimenez, I. (2015). Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *Journal of Ecology*, *103*, 1291–1299. https://doi.org/10.1111/1365-2745.12436

Myers, J. A., & Harms, K. E. (2011). Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology*, *92*, 676–686. https://doi.org/10.1890/10-1001.1

Nave, L. E., Vance, E. D., Swanston, C. W., & Curtis, P. S. (2011). Fire effects on temperate forest soil C and N storage. *Ecological Applications*, *21*, 1189–1201. https://doi.org/10.1890/10-0660.1

Neary, D. G., Ryan, K. C., & DeBano, L. F. (2008). *Wildland fire in ecosystems: Effects of fire on soils and water*. General Technical Report RMRS-GTR-42-vol. 4. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT.

Nowacki, G. J., & Abrams, M. D. (2008). The demise of fire and "Mesophication" of forests in the eastern United States. *BioScience*, *58*, 123–138. https://doi.org/10.1641/B580207

O'Brien, J. J., Loudermilk, E. L., Hornsby, B., Hudak, A. T., Bright, B. C., Dickinson, M. B., … Ottmar, R. D. (2016). High-resolution infrared thermography for capturing wildland fire behaviour – RxCADRE 2012. *International Journal of Wildland Fire*, *25*, 62–75. https://doi.org/10.1071/WF14165

Overbeck, G. E., Velez-Martin, E., Scarano, F. R., Lewinsohn, T. M., Fonseca, C. R., Meyer, S. T., … Pillar, V. D. (2015). Conservation in Brazil needs to include non-forest ecosystems. *Diversity and Distributions*, *21*, 1455–1460. https://doi.org/10.1111/ddi.12380

Paritsis, J., Landesmann, J. B., Kitzberger, T., Tiribelli, F., Sasal, Y., Quintero, C., … Nunez, M. A. (2018). Pine plantations and invasion alter fuel structure and potential fire behavior in a Patagonian forest-steppe ecotone. *Forests*, *9*. https://doi.org/10.3390/f9030117

Paritsis, J., Veblen, T. T., & Holz, A. (2015). Positive fire feedbacks contribute to shifts from *Nothofagus pumilio* forests to fire-prone shrublands in Patagonia. *Journal of Vegetation Science*, *26*, 89–101.

Parks, S. A., Holsinger, L. M., Miller, C., & Nelson, C. R. (2015). Wildland fire as a self-regulating mechanism: The role of previous burns and weather in limiting fire progression. *Ecological Applications*, *25*, 1478–1492. https://doi.org/10.1890/14-1430.1

Parks, S. A., Holsinger, L. M., Voss, M. A., Loehman, R. A., & Robinson, N. P. (2018). Mean composite fire severity metrics computed with Google Earth Engine offer improved accuracy and expanded mapping potential. *Remote Sensing*, *10*, 879. https://doi.org/10.3390/rs10060879

Parr, C. L., & Andersen, A. N. (2006). Patch mosaic burning for biodiversity conservation: A critique of the pyrodiversity paradigm. *Conservation Biology*, *20*, 1610–1619. https://doi.org/10.1111/j.1523-1739.2006.00492.x

Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A., & Andersen, A. N. (2014). Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology & Evolution*, *29*, 205–213. https://doi.org/10.1016/j.tree.2014.02.004

Pausas, J. G. (2015). Evolutionary fire ecology: Lessons learned from pines. *Trends in Plant Science*, *20*, 318–324. https://doi.org/10.1016/j.tplants.2015.03.001

Pausas, J. G., & Bond, W. J. (2019). Humboldt and the reinvention of nature. *Journal of Ecology*, *107*(3), 1031–1037.

Pausas, J. G., & Bond, W. J. (2020). Alternative biome states in terrestrial ecosystems. *Trends in Plant Science*, *25*(3), 250–263. https://doi.org/10.1016/j.tplants.2019.11.003

Pausas, J. G., & Fernandez-Munoz, S. (2012). Fire regime changes in the Western Mediterranean Basin: From fuel-limited to drought-driven fire regime. *Climatic Change*, *110*, 215–226. https://doi.org/10.1007/s10584-011-0060-6

Pausas, J. G., & Keeley, J. E. (2009). A burning story: The role of fire in the history of life. *BioScience*, *59*, 593–601. https://doi.org/10.1525/bio.2009.59.7.10

Pausas, J. G., Keeley, J. E., & Schwilk, D. W. (2017). Flammability as an ecological and evolutionary driver. *Journal of Ecology*, *105*, 289–297. https://doi.org/10.1111/1365-2745.12691

Pausas, J. G., Lamont, B. B., Paula, S., Appezzato-da-Gloria, B., & Fidelis, A. (2018). Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist*, *217*, 1435–1448. https://doi.org/10.1111/nph.14982

Pausas, J. G., & Parr, C. L. (2018). Towards an understanding of the evolutionary role of fire in animals. *Evolutionary Ecology*, *32*, 113–125. https://doi.org/10.1007/s10682-018-9927-6

Pausas, J. G., & Ribeiro, E. (2017). Fire and plant diversity at the global scale. *Global Ecology and Biogeography*, *26*, 889–897. https://doi.org/10.1111/geb.12596

Pausas, J. G., & Verdu, M. (2008). Fire reduces morphospace occupation in plant communities. *Ecology*, *89*, 2181–2186. https://doi.org/10.1890/07-1737.1

Pellegrini, A. F. A., Ahlstrom, A., Hobbie, S. E., Reich, P. B., Nieradzik, L. P., Staver, A. C., … Jackson, R. B. (2018). Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature*, *553*, 194–198. https://doi.org/10.1038/nature24668

Pellegrini, A. F. A., Hedin, L. O., Staver, A. C., & Govender, N. (2015). Fire alters ecosystem carbon and nutrients but not plant nutrient stoichiometry or composition in tropical savanna. *Ecology*, *96*, 1275–1285. https://doi.org/10.1890/14-1158.1

Pierce, J. L., Meyer, G. A., & Jull, A. J. T. (2004). Fire-induced erosion and millennial-scale climate change in northern ponderosa pine forests. *Nature*, *432*, 87–90. https://doi.org/10.1038/nature03058

Pierson, D. N., Robichaud, P. R., Rhoades, C. C., & Brown, R. E. (2019). Soil carbon and nitrogen eroded after severe wildfire and erosion mitigation treatments. *International Journal of Wildland Fire*, *28*, 814–821. https://doi.org/10.1071/WF18193

Pingree, M. R. A., & Kobziar, L. N. (2019). The myth of the biological threshold: A review of biological responses to soil heating associated with wildland fire. *Forest Ecology and Management*, *432*, 1022–1029. https://doi.org/10.1016/j.foreco.2018.10.032

Platt, W. J., Ellair, D. P., Huffman, J. M., Potts, S. E., & Beckage, B. (2016). Pyrogenic fuels produced by savanna trees can engineer humid savannas. *Ecological Monographs*, *86*, 352–372. https://doi.org/10.1002/ecm.1224

Ponisio, L. C., Wilkin, K., M'Gonigle, L. K., Kulhanek, K., Cook, L., Thorp, R., … Kremen, C. (2016). Pyrodiversity begets plant-pollinator community diversity. *Global Change Biology*, *22*, 1794–1808. https://doi.org/10.1111/gcb.13236

Power, M. J., Marlon, J., Ortiz, N., Bartlein, P. J., Harrison, S. P., Mayle, F. E., … Zhang, J. H. (2008). Changes in fire regimes since the Last Glacial Maximum: An assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics*, *30*, 887–907. https://doi.org/10.1007/s00382-007-0334-x

Pressler, Y., Moore, J. C., & Cotrufo, M. F. (2018). Belowground community responses to fire: Meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. *Oikos*, *128*, 309–327. https://doi.org/10.1111/oik.05738

Radeloff, V. C., Helmers, D. P., Kramer, H. A., Mockrin, M. H., Alexandre, P. M., Bar-Massada, A., … Stewart, S. I. (2018). Rapid growth of the US wildland-urban interface raises wildfire risk. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 3314–3319. https://doi.org/10.1073/pnas.1718850115

Richter, D. D., & Billings, S. A. (2015). 'One physical system': Tansley's ecosystem as Earth's critical zone. *New Phytologist*, *206*, 900–912. https://doi.org/10.1111/nph.13338

Rogers, B. M., Randerson, J. T., & Bonan, G. B. (2013). High-latitude cooling associated with landscape changes from North American boreal forest fires. *Biogeosciences*, *10*, 699–718. https://doi.org/10.5194/bg-10-699-2013

Rogers, B. M., Soja, A. J., Goulden, M. L., & Randerson, J. T. (2015). Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience*, *8*, 228–234. https://doi.org/10.1038/ngeo2352

Rogers, B. M., Veraverbeke, S., Azzari, G., Czimczik, C. I., Holden, S. R., Mouteva, G. O., … Randerson, J. T. (2014). Quantifying fire-wide carbon emissions in interior Alaska using field measurements and Landsat imagery. *Journal of Geophysical Research: Biogeosciences*, *119*, 1608–1629. https://doi.org/10.1002/2014JG002657

Romps, D. M., Seeley, J. T., Vollaro, D., & Molinari, J. (2014). Projected increase in lightning strikes in the United States due to global warming. *Science*, *346*, 851–854. https://doi.org/10.1126/science.1259100

Roos, C. I., Zedeno, M. N., Hollenback, K. L., & Erlick, M. M. H. (2018). Indigenous impacts on North American Great Plains fire regimes of the past millennium. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 8143–8148. https://doi.org/10.1073/pnas.1805259115

Rothermel, R. C. (1972). *A mathematical model for predicting fire spread in wildland fuels*. USDA Forests Service Research Paper, Intermountain Forest and Range Experiment Station, 40 pp.

Roy, D. P., Boschetti, L., Justice, C. O., & Ju, J. (2008). The collection 5 MODIS burned area product—Global evaluation by comparison with the MODIS active fire product. *Remote Sensing of Environment*, *112*, 3690–3707. https://doi.org/10.1016/j.rse.2008.05.013

Rupp, T. S., Olson, M., Adams, L. G., Dale, B. W., Joly, K., Henkelman, J., … Starfield, A. M. (2006). Simulating the influences of various fire regimes on caribou winter habitat. *Ecological Applications*, *16*, 1730–1743. https://doi.org/10.1890/1051-0761(2006)016[1730:STIOVF]2.0.CO;2

Ryan, K. C., Knapp, E. E., & Varner, J. M. (2013). Prescribed fire in North American forests and woodlands: History, current practice, and challenges. *Frontiers in Ecology and the Environment*, *11*, E15–E24. https://doi.org/10.1890/120329

Scheiter, S., Langan, L., & Higgins, S. I. (2013). Next-generation dynamic global vegetation models: Learning from community ecology. *New Phytologist*, *198*, 957–969. https://doi.org/10.1111/nph.12210

Scheller, R., Kretchun, A., Hawbaker, T. J., & Henne, P. D. (2019). A landscape model of variable social-ecological fire regimes. *Ecological Modelling*, *401*, 85–93. https://doi.org/10.1016/j.ecolmodel.2019.03.022

Scheller, R. M., Kretchun, A. M., Loudermilk, E. L., Hurteau, M. D., Weisberg, P. J., & Skinner, C. (2018). Interactions among fuel management, species composition, bark beetles, and climate change and the potential effects on forests of the Lake Tahoe Basin. *Ecosystems*, *21*, 643–656. https://doi.org/10.1007/s10021-017-0175-3

Scheller, R. M., & Swanson, M. E. (2015). Simulating forest recovery following disturbances: Vegetation dynamics and biogeochemistry. In A. Perera, B. Sturtevant, & L. Buse (Eds.), *Simulation modelling of forest landscape disturbances* (pp. 263–285). Geneva, Switzerland: Springer.

Schoennagel, T., Balch, J. K., Brenkert-Smith, H., Dennison, P. E., Harvey, B. J., Krawchuk, M. A., … Whitlock, C. (2017). Adapt to more wildfire in western North American forests as climate changes. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 4582–4590. https://doi.org/10.1073/pnas.1617464114

Sherriff, R. L., & Veblen, T. T. (2008). Variability in fire-climate relationships in ponderosa pine forests in the Colorado Front Range. *International Journal of Wildland Fire*, *17*, 50–59. https://doi.org/10.1071/WF07029

Short, K. C. (2014). A spatial database of wildfires in the United States, 1992–2011. *Earth System Science Data*, *6*, 1–27. https://doi.org/10.5194/essd-6-1-2014

Simon, M. F., Grether, R., de Queiroz, L. P., Skema, C., Pennington, R. T., & Hughes, C. E. (2009). Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 20359–20364. https://doi.org/10.1073/pnas.0903410106

Singleton, M. P., Thode, A. E., Meador, A. J. S., & Iniguez, J. M. (2019). Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. *Forest Ecology and Management*, *433*, 709–719. https://doi.org/10.1016/j.foreco.2018.11.039

Smucker, K. M., Hutto, R. L., & Steele, B. M. (2005). Changes in bird abundance after wildfire: Importance of fire severity and time since fire. *Ecological Applications*, *15*, 1535–1549. https://doi.org/10.1890/04-1353

Sparks, A. M., Smith, A. M. S., Talhelm, A. F., Kolden, C. A., Yedinak, K. M., & Johnson, D. M. (2017). Impacts of fire radiative flux on mature *Pinus ponderosa* growth and vulnerability to secondary mortality agents. *International Journal of Wildland Fire*, *26*, 95–106. https://doi.org/10.1071/WF16139

Steel, Z. L., Koontz, M. J., & Safford, H. D. (2018). The changing landscape of wildfire: Burn pattern trends and implications for California's yellow pine and mixed conifer forests. *Landscape Ecology*, *33*, 1159–1176. https://doi.org/10.1007/s10980-018-0665-5

Steel, Z. L., Safford, H. D., & Viers, J. H. (2015). The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere*, *6*. https://doi.org/10.1890/ES14-00224.1

Stevens-Rumann, C. S., Kemp, K. B., Higuera, P. E., Harvey, B. J., Rother, M. T., Donato, D. C., … Veblen, T. T. (2018). Evidence for declining forest resilience to wildfires under climate change. *Ecology Letters*, *21*, 243–252. https://doi.org/10.1111/ele.12889

Stevens-Rumann, C. S., & Morgan, P. (2019). Tree regeneration following wildfires in the western US: A review. *Fire Ecology*, *15*. https://doi.org/10.1186/s42408-019-0032-1

Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., … Swanson, F. J. (2011). The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, *9*, 117–125. https://doi.org/10.1890/090157

Swetnam, T. W., & Betancourt, J. L. (1998). Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate*, *11*, 3128–3147. https://doi.org/10.1175/1520-0442(1998)011<3128:MDAERT>2.0.CO;2

Taylor, A. H., & Skinner, C. N. (2003). Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecological Applications*, *13*, 704–719. https://doi.org/10.1890/1051-0761(2003)013[0704:SPACOH]2.0.CO;2

Taylor, A. H., Trouet, V., Skinner, C. N., & Stephens, S. (2016). Socioecological transitions trigger fire regime shifts and modulate fire-climate interactions in the Sierra Nevada, USA, 1600–2015 CE. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 13684–13689. https://doi.org/10.1073/pnas.1609775113

Tepley, A. J., Thomann, E., Veblen, T. T., Perry, G. L. W., Holz, A., Paritsis, J., … Anderson-Teixeira, K. J. (2018). Influences of fire-vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes. *Journal of Ecology*, *106*, 1925–1940. https://doi.org/10.1111/1365-2745.12950

Tepley, A. J., Thompson, J. R., Epstein, H. E., & Anderson-Teixeira, K. J. (2017). Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. *Global Change Biology*, *23*, 4117–4132. https://doi.org/10.1111/gcb.13704

Tepley, A. J., Veblen, T. T., Perry, G. L. W., Stewart, G. H., & Naficy, C. E. (2016). Positive feedbacks to fire-driven deforestation following human colonization of the South Island of New Zealand. *Ecosystems*, *19*, 1325–1344. https://doi.org/10.1007/s10021-016-0008-9

Tierney, J. A., Hedin, L. O., & Wurzburger, N. (2019). Nitrogen fixation does not balance fire-induced nitrogen losses in longleaf pine savannas. *Ecology*, *100*, e02735. https://doi.org/10.1002/ecy.2735

van der Werf, G. R., Randerson, J. T., Giglio, L., Collatz, G. J., Kasibhatla, P. S., & Arellano, A. F. (2006). Interannual variability in global biomass burning emissions from 1997 to 2004. *Atmospheric Chemistry and Physics*, *6*, 3423–3441. https://doi.org/10.5194/acp-6-3423-2006

van der Werf, G. R., Randerson, J. T., Giglio, L., van Leeuwen, T. T., Chen, Y., Rogers, B. M., … Kasibhatla, P. S. (2017). Global fire emissions estimates during 1997–2016. *Earth System Science Data*, *9*, 697–720. https://doi.org/10.5194/essd-9-697-2017

Van Wagner, C. E. (1973). Height of crown scorch in forest fires. *Canadian Journal of Forest Research*, *3*, 373–378. https://doi.org/10.1139/x73-055

van Wagtendonk, J. W. (2018). *Fire in California's ecosystems*. Berkeley, CA: University of California Press.

Varner, J. M., Kane, J. M., Kreye, J. K., & Engber, E. (2015). The flammability of forest and woodland litter: A synthesis. *Current Forestry Reports*, *1*, 91–99. https://doi.org/10.1007/s40725-015-0012-x

Varner, J. M., Putz, F. E., O'Brien, J. J., Hiers, J. K., Mitchell, R. J., & Gordon, D. R. (2009). Post-fire tree stress and growth following smoldering duff fires. *Forest Ecology and Management*, *258*, 2467–2474. https://doi.org/10.1016/j.foreco.2009.08.028

Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, *85*, 183–206. https://doi.org/10.1086/652373

Verdu, M., & Pausas, J. G. (2007). Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *Journal of Ecology*, *95*, 1316–1323. https://doi.org/10.1111/j.1365-2745.2007.01300.x

Walker, X. J., Rogers, B. M., Baltzer, J. L., Cumming, S. G., Day, N. J., Goetz, S. J., … Mack, M. C. (2018). Cross-scale controls on carbon emissions from boreal forest megafires. *Global Change Biology*, *24*, 4251–4265. https://doi.org/10.1111/gcb.14287

Wardle, D. A., Jonsson, M., Mayor, J. R., & Metcalfe, D. B. (2016). Above-ground and below-ground responses to long-term nutrient addition across a retrogressive chronosequence. *Journal of Ecology*, *104*, 545–560. https://doi.org/10.1111/1365-2745.12520

Westerling, A. L. (2016). Increasing western US forest wildfire activity: Sensitivity to changes in the timing of spring. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *371*. https://doi.org/10.1098/rstb.2015.0178

Whitman, T., Whitman, E., Woolet, J., Flannigan, M. D., Thompson, D. K., & Parisien, M.-A. (2019). Soil bacterial and fungal response to wildfires in the Canadian boreal forest across a burn severity gradient. *bioRxiv*, 512798.

Yue, C., Ciais, P., Cadule, P., Thonicke, K., Archibald, S., Poulter, B., … Viovy, N. (2014). Modelling the role of fires in the terrestrial carbon balance by incorporating SPITFIRE into the global vegetation model ORCHIDEE—Part 1: Simulating historical global burned area and fire regimes. *Geoscientific Model Development*, *7*, 2747–2767. https://doi.org/10.5194/gmd-7-2747-2014

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: McLauchlan KK, Higuera PE, Miesel J, et al. Fire as a fundamental ecological process: Research advances and frontiers. *J Ecol*. 2020;00:1–23. https://doi.org/10.1111/1365-2745.13403