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## EDITORIAL

Fire as a Dynamic Ecological and Evolutionary Force

# The eco-evolutionary role of fire in shaping terrestrial ecosystems

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## Abstract

- 1. Fire is an inherently evolutionary process, even though much more emphasis has been given to ecological responses of plants and their associated communities to fire.
- 2. Here, we synthesize contributions to a Special Feature entitled 'Fire as a dynamic ecological and evolutionary force' and place them in a broader context of fire research. Topics covered in this Special Feature include a perspective on the impacts of novel fire regimes on differential forest mortality, discussions on new approaches to investigate vegetation-fire feedbacks and resulting plant syndromes, synthesis of fire impacts on plant-fungal interactions, and a meta-analysis of arthropod community responses to fire.
- 3. We conclude by suggesting pathways forward to better understand the ecological and evolutionary consequences of fire. These include developing ecological and evolutionary databases for fire ecology, integrating hierarchical genetic structure or phylogenetic structure, and developing new experimental frameworks that limit context-dependent outcomes.

### KEYWORDS

arthropod, eco-evolutionary dynamics, evolution, fire regimes, plant-fungal interactions, traits, wildfires

Fire is an ancient, common and a complex phenomenon that affects most biomes and ecosystems worldwide (Bond, 2019; Bowman et al., 2009; Pausas & Keeley, 2009), and is steadily increasing in a warming world (Abatzoglou & Williams, 2016; Jolly et al., 2015). Climate and weather conditions regulate vegetation distribution and fuel amounts, as well as fire activities, patterns and behaviour. For example, a combination of high solar radiation, low relative humidity and drought increases fuel dryness, resulting in highly flammable vegetation biomass. Hotter and drier conditions have increased the risk of large, high-intensity fires (Abram et al., 2021). Fire can change vegetation spatial distribution, composition and fuel amounts through loss of overstory canopy, while also influencing climate through direct emission of aerosols (e.g. soot), greenhouse gases (e.g.  $CH_4$ ,  $CO_2$ ) to the atmosphere and altering albedo (Soja et al., 2007; Zheng et al., 2023). As such, fire feeds back on climate by altering emissions, surface albedo, carbon cycling and hydrology. The interactions between climate, fire and vegetation generate variation in fire regimes (i.e. size, frequency, intensity, season and extent) have shaped the way ecosystems have evolved for millennia (Keeley & Pausas, 2022), and are likely shaping patterns of evolution today.

Fire is an inherently evolutionary process, even though much more emphasis has been given to ecological responses of plants and their associated communities to fire. There is ample evidence of both macro- and microevolutionary trait changes occurring across time scales (Bailey et al., 2009; Forsman et al., 2011; He et al., 2012; Jin et al., 2021; Rice & Emery, 2003). These include the dark coloration (i.e. melanism) of grasshoppers (Forsman et al., 2011), thick bark and serotiny in pines (Pausas, 2015) and germination in heath shrubs (Leonard et al., 2018), but many important questions remain. First, the direct and indirect effects of fire on plant functional traits and the



amount of genetic variation underlying those traits within populations remain obscure. Second, species evolution might not always be exclusively a consequence of adaptation to fire, but of a combination of other co-occurring pressures interacting with fire such as drought (Bradshaw et al., 2011). Third, studies have historically focused more on vegetation than on animals and microorganisms or species interactions, such as mutualisms and how these might change, in response to fire (McLauchlan et al., 2020). Because there is mounting evidence for genetic variation in fire-related plant traits, such as those associated with fire damage, resistance and recovery (Castellanos et al., 2015; Gómez-González et al., 2011; Hernández et al., 2022), species are likely capable of adapting to new fire regimes. As such, examining the microevolutionary processes affected by fire is critical to understand individual species-level responses, shifts in species interactions that may occur due to differential responses to fire, and ultimately community changes that impact ecosystem function as a response to contemporary and future shifts in historical fire regimes.

Two important approaches to examining the evolutionary consequences of fire are fire-driven selection in plant functional traits and fire-driven changes to species interactions, both of which can lead to eco-evolutionary feedbacks. The topics covered by papers included in this Special Feature include a perspective on the impacts of novel fire regimes on differential forest mortality, discussions on new approaches to investigate vegetation-fire feedbacks and resulting plant syndromes, synthesis of fire impacts on plant-fungal interactions, and a meta-analysis of arthropod community response to fire. Here, we synthesize these contributions to the Special Feature on fire as a dynamic ecological and evolutionary force and place them in a broader context of fire research.

## 1 | PLANT RESPONSE TO FIRE

Understanding how species evolve to persist in novel fire regimes reguires fundamental knowledge of the feedbacks involving climate, fire and vegetation. Liang and Hurteau (2023) provide an overview and synthesis of these historical feedbacks and associated species traits in western US forests. Their work suggests that novel fire regimes, amplified by human interventions, are changing plant species distributions by creating large-scale homogeneous patches of high tree mortality after fire and acting as an important selective filter. Based on compiled data, the authors show that human activity in the form of fire suppression has led to 149% increase in live tree biomass in mixed-conifer forest, 26% increase in old-growth mixed-conifer forests and 124% increase in ponderosa pine forests in California alone. Upon mortality, increased forest biomass is converted to dead biomass (or fuel) over time, thereby contributing to unprecedented fire behaviour in western US. The synthesis paper by Liang and Hurteau (2023) aligns with the idea that a decrease in the spatial heterogeneity of coexisting trees that vary in climatic-driven and postfire regeneration mechanisms (i.e. seed source) and fuel production is associated with forests that are less resistant and resilient to fire (Hessburg et al., 2019). Anticipated shifts in fire regimes to high-severity fires under a warmer climate will

require not only management and conservation strategies, but also incorporation of evolutionary concepts by managers as an effort to restore postfire tree regeneration and increase the compositional, genetic, structural and spatial heterogeneity of forests to prevent catastrophic forest loss in the western US.

New insights into plant species persistence under a changing climate also requires embracing new perspectives that build upon previous work on contemporary plant evolution and be applicable across different ecosystems. It is now well-accepted that fire selects for traits that influence plant fitness in response to fire and enable plants to persist in a particular fire regime (Keeley et al., 2011), including thick basal bark, serotiny, fire flowering and fire-stimulated germination (He et al., 2012; Lamont et al., 2019; Pausas, 2015). While plant response traits (as 'fire response syndromes') such as fire-stimulated resprouting and seeding have been framed in the context of a fire syndrome, the incorporation of effect function traits, such as the propensity of plant biomass to ignite and propagate a fire (or 'flammability'), into fire syndrome models had not been considered until now. In this Special Feature, Jaureguiberry and Díaz (2023) suggest a three-dimensional approach to integrate and explore the relationships between both resprouting and germination (i.e. as trait responses to burning) and plant flammability (i.e. as plant trait effects) to better understand and predict vegetation responses to, and impacts on, fire regimes. They compiled data, compared categories and found that some regions have evolved extreme fire syndromes, that is, plant species with extreme values of resprouting, seeding and/or flammability. The authors demonstrate that this proposed approach can allow for better understanding of the evolutionary effects of fire and can aid predictability in ecosystem models simulating fire effects on plants.

What both of these studies suggest is that understanding not only patterns of differential mortality but also variation in plant traits in response to fire regime is critical to understanding, predicting and managing eco-evolutionary dynamics in response to fire. An important but missing piece to enable this research is curated databases that compile and allow for broad syntheses to be undertaken and modelled. Table 1 compiles some of the major known databases on plant and other organismal responses to fire. This table and recent reviews show that long-term studies of plant traits and fire are rare, those that exist are likely maintained by individuals, institutes or local organizations and are not always freely available. Moreover, there is a pressing need to standardize data methods, align these data with accurate fire regime/history/details and make these data discoverable and available for analysis. Once these data are available, important analyses and synthesis can be undertaken to ask important eco-evolutionary questions across scales to understand patterns of trait change and model the community and ecosystem consequences of evolutionary change.

# 2 | SPECIES INTERACTIONS AND FIRE

Another important, yet less explored topic, relates to how shifts in fire regimes impact the way evolution shapes the interactions and TABLE 1 Examples of major publicly available databases containing several datasets associated with fires.

Database	Datasets	Link
USDA Fire Effects Information System (FEIS)	Effects/regime information by species name	https://www.feis-crs.org/feis/
Landfire program	Vegetation, fuels, historical fire regime	https://landfire.gov/
Fire and Tree Mortality Database	Fire injury, tree diameter and mortality $^{\left[ 1\right] }$	https://www.fs.usda.gov/research/trees earch/60342
ORNL Distributed Active Archive Center (DAAC)	Biogeochemical data associated with fire	https://daac.ornl.gov/cgi-bin/theme_datas et_lister.pl?theme_id=8
Plant trait database for Mediterranean Basin species (BROT)	Plant functional traits <sup>[2]</sup>	https://www.uv.es/jgpausas/brot.htm
TRY Plant trait database	Plant traits, including those fire related $^{\left[ 3 ight] }$	https://www.try-db.org
Fine-root ecology database (FRED)	Root traits, including those fire related $^{\left[ 4  ight]}$	https://roots.ornl.gov/
Global P50 & resprouting database	Postfire resprouting <sup>[5]</sup>	https://www.uv.es/jgpausas/databases.htm
Global Belowground Bud Bank (BBB) database	Belowground bud bank in fire-prone ecosystems <sup>[6]</sup>	https://www.uv.es/jgpausas/bbb.htm
Joint Fire Science Program	Papers, summaries and reports	https://www.firescience.gov/JFSP_resea rch.cfm
European Forest Fire Information System	Fire regime/weather	https://effis.jrc.ec.europa.eu/
European Space Agency Fire Disturbance project	Fire regime/weather	https://climate.esa.int/en/projects/fire/
National Institute for Space Research-INPE, Brazil	Fire regime/weather	http://www.inpe.br/queimadas
Global Fire Emissions Database	Fire regime/weather <sup>[7]</sup>	https://www.globalfiredata.org/
Monitoring of the Andean Amazon Project	Fire regime/weather	https://maaproject.org/fire/
Forest Services National Datasets, USA	Fire regime/weather	https://data.fs.usda.gov/geodata/edw/datas ets.php?xmlKeyword=fire
USGS Burn Severity Portal	Fire regime/weather	https://burnseverity.cr.usgs.gov/
Monitoring Trends in Burn Severity (MTBS)	Fire regime/weather	https://www.mtbs.gov/
Earth Data Wildfires, NASA, USA	Fire regime/weather	https://www.earthdata.nasa.gov/learn/ toolkits/disasters-toolkit/wildf ires-toolkit
Global fire weather database, NASA	Fire regime/weather	https://data.giss.nasa.gov/impacts/gfwed/
Alaska Large Fire Database, USA	Fire regime/weather	https://www.frames.gov/catalog/10465
Canadian National Fire Database (CNFDB)	Fire regime/weather	https://cwfis.cfs.nrcan.gc.ca/ha/nfdb

*Note*: [1] Cansler, C. A., Hood, S. M., Varner, J. M. et al. (2020). The fire and tree mortality database, for empirical modelling of individual tree mortality after fire. *Sci Data*, 7, 194; [2] Paula S, Arianoutsou M, Kazanis D, Tavsanoglu Ç, Lloret F, Buhk C, Ojeda F, Luna B, Moreno JM, Rodrigo A, Espelta JM, Palacio S, Fernández-Santos B, Fernandes PM, & Pausas JG. (2009). Fire-related traits for plant species of the Mediterranean Basin. *Ecology*, *90*, 1420; [3] Kattge, J., Ogle, K., Bönisch, G., Díaz, S., Lavorel, S., Madin, J., ... Wirth, C. (2011). A generic structure for plant trait databases. *Methods in Ecology and Evolution*, *2*(2), 202–213; [4] Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., ... Violle, C. (2017). A global fine-root ecology database to address belowground challenges in plant ecology. *New Phytologist*, *215*(1), 15–26; [5] Pausas, J. G., Pratt, R. B., Keeley, J. E., Jacobsen, A. L., Ramirez, A. R., Vilagrosa, A., Paula, S., Kaneakua-Pia, I. N. & Davis, S. D. (2016). Towards understanding resprouting at the global scale. *New Phytologist*, 209, 945–95; [6] Pausas, J. G., Lamont, B. B., Paula, S., Appezzato-da-Glória, B., & Fidelis, A. (2018). Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist*, *217*(4), 1435–1448; [7] Giglio, L., Randerson, J. T., & Van Der Werf, G. R. (2013). Analysis of daily, monthly, and annual burned area using the fourth-generation global fire emissions database (GFED4). *Journal of Geophysical Research: Biogeosciences*, *118*(1), 317–328.

feedbacks between plants and organisms such as microbes, endophytes, herbivores and pollinators. From an eco-evolutionary dynamics perspective, plant functional traits can change soil and soil can drive the evolution of plant functional traits and how these traits will feed back to soil. While the evolutionary implications of plantsoil interactions (Cortois et al., 2016; Govaert et al., 2019; Pregitzer et al., 2013; Schweitzer et al., 2014; terHorst & Zee, 2016; Van Nuland et al., 2016; Ware et al., 2019) have been extensively discussed, the specific role of fire in changing functional traits and ecological functions associated with plant-microbial feedbacks remains unknown. In this Special Feature, Hewitt et al. (2022) addresses this uncertainty by synthesizing previous knowledge on postfire plant-fungal interactions in the boreal forest and posed that the direction of fire impacts on plant-soil feedbacks is context and mycorrhizal-partner dependent. The authors provided several recommendations to link postfire fungal traits and ecosystem function that can benefit the scientific community going forward and advance our understanding of eco-evolutionary impacts of fire.

Much less is known about how shifts in fire regimes affect the way evolution drives animals' behaviour and fitness (Koltz et al., 2018; McLauchlan et al., 2020; Pausas & Parr, 2018). For example, it is thought that animals have the capacity to detect and avoid fires through sensory 'cues' (scent, sound and sight) emitted by fires (Nimmo et al., 2021). If fire influences the evolution of animal capacity to perceive these sensory clues, changing in historical fire regimes will likely affect the persistence of these animals. We are just beginning to collect more evidence for adaptive behavioural traits that will enable us to understand the implication of fire for biodiversity under a changing climate (Doherty et al., 2022). Fire is also known to select for traits in insects, thereby enabling insects to better adapt to frequent fire (Forsman et al., 2011; Koltz et al., 2018). However, the evolutionary role of fire on arthropods and the impact of fire on arthropod functional traits are relatively understudied. In this special issue, Bieber et al. (2022) separated arthropod communities into different functional groups, based on information gathered by previous literature, which included herbivores and pollinators. They found that, unlike other functional groups, herbivores increased in abundance, richness and diversity after fire, which can have important indirect effects on plant functional traits that may alter the evolution of secondary chemistry and resilience traits, as well as have ecosystem-level consequences.

Both of these studies show that complex species interactions occur above- and below-ground in response to fire that will have both ecological and evolutionary consequences that likely vary across the landscape. Fire is a nonrandom process, differentially affecting hotter and drier geographic locations as well as different populations within a species. One particularly interesting question is whether fire may indirectly select against those populations of organisms that are adapted to hot and dry climatic conditions, but not necessarily fire. The reduction of variation in traits associated with water use, productivity or even phenology may have significant extended consequences for associated species interactions, biodiversity and ecosystem function, as well as plant-atmosphere and plant-soil feedbacks (sensu Bayliss et al., 2020; Van Nuland et al., 2021; Ware et al., 2021) that are currently rarely quantified and largely overlooked.

## 3 | MOVING FORWARD

Ecological and evolutionary databases have become powerful tools for large-scale analyses and broad syntheses. With the increased frequency and severity of fires on the landscape, developing similar databases for fire ecology is an imperative challenge that needs to be met if we are to identify the ecological and evolutionary consequences of fire across levels of organization. Secondarily, it is also important to identify many of the barriers to broad inference in ecology and evolution. It is increasingly clear that integrating hierarchical genetic structure or phylogenetic structure is critical to the accuracy of results and scope of conclusions one can draw in most systems (Bayliss, Papeş, et al., 2022; Bayliss, Mueller, et al., 2022; Love et al., 2023; Read et al., 2016). Finally, it is important to develop new experimental frameworks that limit context-dependent outcomes (Catford et al., 2021) and can be used to understand geographic variation in species interactions and feedbacks that drive ecosystem function (Van Nuland et al., 2016; Ware et al., 2019), as they related to fire disturbances. Any of these frameworks—either independently or in combination represent positive steps forward in a broader synthesis of ecological and evolutionary fire dynamics. Incorporating evolutionary concepts and perspectives into future frameworks is essential to understand how species will persist given that the pressures of fire are anticipated to be amplified under a warmer climate.

Interest in better representing fire as a microevolutionary pressure on ecosystems has emerged in recent years (Archibald et al., 2018). In their review on biological and geophysical feedbacks with fire, Archibald et al. (2018) incorporate evolution to their conceptual framework. Ongoing efforts to better represent eco-evolutionary responses from plants and microbes into predictive models are promising (Abs et al., 2022) and could be incorporated into a broader framework for how ecosystem resilience and functioning will respond to selective pressures by fire. However, we acknowledge this is not an easy task, as ecologists and evolutionary biologists face other challenges in the context of fire, some of which are discussed in more detail in this Special Feature (see, e.g. Bieber et al., 2022; Hewitt et al., 2022). These challenges include limited sample size and available datasets, limited functional trait knowledge, underrepresentation of ecological communities in the literature and context dependency. Establishing networks, forming interdisciplinary partnerships, unifying metrics and incorporating knowledge from diverse communities should be considered in future studies (Archibald et al., 2018; Buma, 2021; Shuman et al., 2022, Fire Community Database Network; https://firedata.ornl.gov/). Addressing these challenges and limitations will enable researchers to answer critical questions on the evolutionary responses to fire (Abs et al., 2022; McLauchlan et al., 2020). Increased appreciation of fire effects on evolutionary changes can also help elucidate whether fires can lead to novel impacts on ecosystem biodiversity, resilience and function.

## AUTHOR CONTRIBUTIONS

Fernanda Santos, Joseph K. Bailey and Jennifer A. Schweitzer conceived the ideas for the editorial; and Fernanda Santos led the writing of the editorial. All authors contributed critically to the drafts and gave final approval for publication.

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#### CONFLICT OF INTEREST STATEMENT

Fernanda Santos, Joseph K. Bailey and Jennifer A. Schweitzer declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

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