

Terrestrial carbon dynamics in an era of increasing wildfire

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Tara Hudiburg¹✉, Justin Mathias¹, Kristina Bartowitz²,
Danielle M. Berardi¹, Kelsey Bryant¹, Emily Graham^{1,3,4}, Crystal A. Kolden⁵,
Richard A. Betts^{6,7} & Laurel Lynch⁸

In an increasingly flammable world, wildfire is altering the terrestrial carbon balance. However, the degree to which novel wildfire regimes disrupt biological function remains unclear. Here, we synthesize the current understanding of above- and belowground processes that govern carbon loss and recovery across diverse ecosystems. We find that intensifying wildfire regimes are increasingly exceeding biological thresholds of resilience, causing ecosystems to convert to a lower carbon-carrying capacity. Growing evidence suggests that plants compensate for fire damage by allocating carbon belowground to access nutrients released by fire, while wildfire selects for microbial communities with rapid growth rates and the ability to metabolize pyrolysed carbon. Determining controls on carbon dynamics following wildfire requires integration of experimental and modelling frameworks across scales and ecosystems.

Wildfires are endemic in many terrestrial biomes, but their severity and magnitude have increased in recent decades^{1–3} and threaten critical carbon stocks that have accumulated over hundreds to thousands of years^{4–6}. On an annual basis, fires burn nearly 500 million hectares of vegetated land⁷ and release the carbon equivalent to a -1 ppm increase in atmospheric carbon dioxide. The amount and moisture content of aboveground biomass, the depth of carbon-rich organic soil horizons and the extent and severity of wildfire all overwhelmingly influence both the quantity of carbon released and the timescale over which carbon recovery occurs. Indeed, frequent and/or severe wildfires may permanently convert carbon-dense ecosystems (for example, forests) to those with a lower carbon-carrying capacity (for example, grasslands)⁸, particularly in regions where changing climate regimes are already altering plant and microbial species compositions⁹. Because increasingly hotter and drier growing seasons largely driven by anthropogenic climate change have the potential to increase wildfire activity¹⁰, it is critical to resolve the underlying biological and physical mechanisms that govern ecosystem carbon dynamics to improve predictions of wildfire impacts on the global terrestrial carbon sink.

Improved representation of interactions among wildfire, vegetation and climate is essential to capture feedbacks and forecast coupled climate–fire–carbon dynamics. Although coupled climate–fire–carbon modelling has advanced substantially in recent years^{11–16}, major gaps remain. A particular focus on developing and evaluating modelling frameworks that explicitly quantify the recovery, or loss, of post-fire carbon will therefore be invaluable as climate variability progresses and wildfires become more extreme¹⁷. For example, while model-data frameworks^{18,19} enable quantification and validation of carbon emissions across a variety of scales, they do not capture coupled above- and belowground responses to wildfire or represent the fine-scale biological processes that control carbon dynamics and recovery across scales.

To date, syntheses and reviews have focused primarily on quantifying burned area and carbon emissions that result from wildfire and/or anthropogenic burning. However, intensifying wildfire regimes are clearly disrupting biological communities and altering underlying plant and microbial traits that govern ecosystem carbon dynamics (for example, regrowth, acclimation strategies, community assembly, metabolic efficiency)^{20–27}. Despite recent recognition of the importance of identifying and characterizing the traits and biogeochemical

¹Department of Forest, Rangeland, and Fire Science, University of Idaho, Moscow, ID, USA. ²American Forests, Washington, DC, USA. ³Earth and Biological Sciences Directorate, Pacific Northwest National Laboratory, Richland, WA, USA. ⁴School of Biological Sciences, Washington State University, Pullman, WA, USA. ⁵Management of Complex Systems, University of California Merced, Merced, CA, USA. ⁶Met Office Hadley Centre, Exeter, UK. ⁷Global Systems Institute, University of Exeter, Exeter, UK. ⁸Department of Soil and Water Systems, University of Idaho, Moscow, ID, USA. ✉e-mail: thudiburg@uidaho.edu

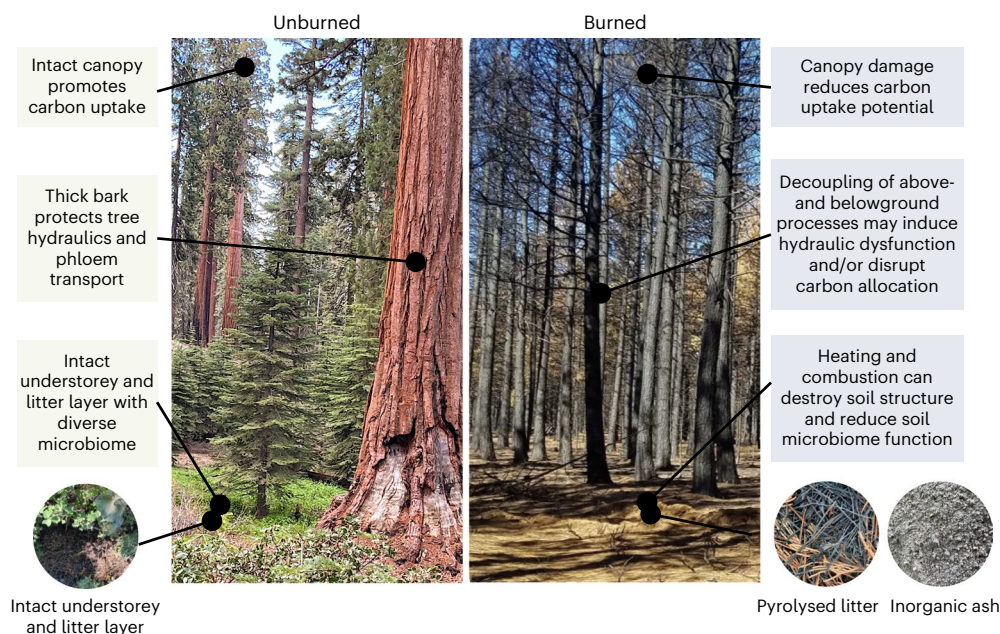


Fig. 1 | Wildfire impacts above- and belowground carbon stocks by combusting biomass and surface soil horizons. There are cascading effects on carbon fluxes such as carbon uptake through photosynthesis and release through microbial respiration. In addition, fire releases a complex mixture of char (rich in aromatics and adsorbed volatiles) and ash (rich in metals and nutrients) that can directly inhibit or stimulate plant and microbial growth, with

implications for rates of ecosystem carbon recovery. Plants and microbes have evolved traits to survive fire, but it is unclear how these adaptations will help organisms cope with climate-driven changes in fire regimes. Photos show an unburned mixed temperate forest in Yosemite National Park, California, USA (left), and a burned ponderosa pine forest at the AmeriFlux Metolius site, Oregon, USA (right). Credit: left image, Crystal Kolden; right image, Tara Hudiburg.

processes that influence carbon dynamics in the context of wildfire, there remains scant literature synthesizing these topics.

To address this critical knowledge gap, we review relevant literature on carbon dynamics in fire-affected ecosystems to evaluate how wildfire impacts above- and belowground processes (for example, photosynthesis and microbial respiration) that drive carbon uptake and release. Where possible we distinguish between wildfire and anthropogenic burning (for example, slash and burn and prescribed fire). We first combine existing datasets of global carbon stocks and all fire activity to highlight where global live biomass carbon stocks have been vulnerable to fire in recent decades. We then synthesize the current state of the knowledge on fundamental principles regulating carbon recovery following wildfire across ecosystems (for example, plant, soil biogeochemical, microbial and total ecosystem carbon fluxes) and highlight modelling studies that incorporate carbon dynamics. Finally, we discuss the relevance of this Review in the context of climate mitigation and global carbon wildfire emissions, concluding with recommendations for reducing uncertainty in projections of the global carbon budget.

Live biomass carbon vulnerability to wildfire

Wildfire immediately impacts ecosystem carbon content by combusting aboveground biomass and surface soil horizons, where soil organic carbon stocks, fine roots and microbial biomass are concentrated (Fig. 1). The persistence of these effects depends on the severity and duration of the fire, which is a function of the quantity of biomass (determined by climatology, land-use history, human development/land management, resource use) and its flammability (determined by seasonal aridity)^{1,28}. The severity of a given fire is typically defined by the magnitude of ecological change it induces (for example, degree of canopy scorch or biomass and/or soil organic matter consumption), with fires in xeric environments typically being biomass limited and those in mesic environments being fuel dryness limited²⁹. Consequently, rates of carbon recovery depend on localized environmental conditions, degree of biological damage, regrowth dynamics and plant and microbial traits

specific to each system. For example, after wildfire disturbance, grasses primarily allocate biomass belowground, enabling rapid recovery (for example, <3 yr), while trees may take decades to centuries to recoup aboveground biomass, if they recover at all³⁰. Ultimately, from a carbon and climate perspective, the expectation is that the most consequential wildfires (for example, those with the greatest net emissions and/or impact on the total terrestrial carbon balance) will occur at high severity, in areas of high carbon density and for species compositions with lower biological recovery rates¹⁹.

To identify regions of high carbon vulnerability across the globe, we combined estimates of live biomass carbon density³¹ with those for mean annual burned area³² averaged over a recent 20 yr period (1997–2016). This approach provides a conservative estimate of belowground carbon vulnerability (for example, combustible pools such as woody debris and soil organic matter are not represented) and a liberal estimate of aboveground carbon vulnerability (that is, all aboveground biomass could potentially combust, equivalent to gross carbon emissions). Nevertheless, these remotely sensed data products represent the only harmonized dataset of globally gridded carbon density for above- and belowground pools and are useful for identifying regions where live biomass carbon has been the most vulnerable to burning over the past two decades (Fig. 2 and Supplementary Figs. 1 and 2; see Supplementary Methods for details). Future efforts should work towards harmonizing more comprehensive carbon datasets (for example, including soil organic carbon, accounting for regrowth dynamics to calculate net emissions and so on) to better predict the impact of wildfire on the global carbon balance.

Given projected increases in wildfire occurrence, historically vulnerable regions will probably remain at risk. However, it is important to recognize that the utility of applying past wildfire occurrence to predict future trends may decline. For instance, human-caused climate change is driving greater fire activity in boreal and Arctic regions, which are warming at four times the global average³³, and lower-latitude ecosystems are experiencing greater overlap of fire and drought conditions that can induce megafire events^{3,10}. Nevertheless, we highlight some of the most recent global hotspots for carbon vulnerability to fire.

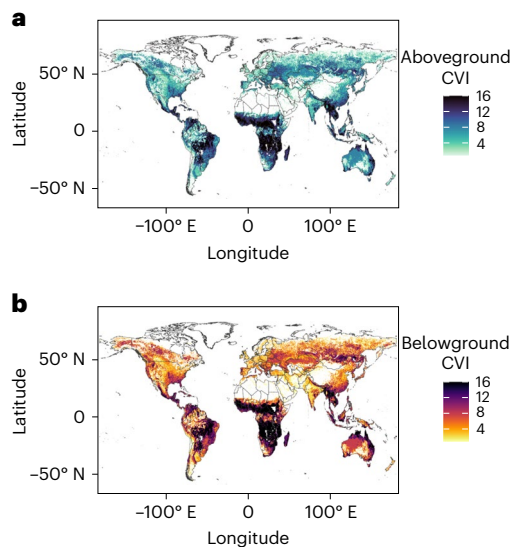


Fig. 2 | Aboveground and belowground carbon stocks vary in their vulnerability to fire. **a, b**, The carbon vulnerability index (CVI) represents the mean annual burned area quartile (from the Global Fire Emissions Database), multiplied by the carbon density quartile (harmonized aboveground (**a**) and belowground (**b**) live biomass carbon, in megagrams of carbon per hectare, from ref. 31). The CVI ranges from 1 (light shading, for example, deserts that burn infrequently and contain little carbon) to 16 (dark shading, for example, African savannas and grasslands that burn regularly and have high live biomass carbon densities), and highlights regions that should be prioritized for management and climate mitigation policy (see Supplementary Figs. 2 and 3 for CVI estimates within eight fire-vulnerable biomes).

Consistent with previous analyses^{5,34}, aboveground (Fig. 2a) and belowground (Fig. 2b) live biomass carbon is most vulnerable in the tropical forests of South America and Southeast Asia (Supplementary Figs. 2 and 3) and the subtropical savannas and grasslands of Africa and Australia (Supplementary Figs. 2 and 3). Although savannas and grasslands occupy <40% of the global land surface area, they account for ~80% of burning³⁰. Their elevated carbon vulnerability is driven by frequent, low-severity fire (primarily caused by sociocultural practices)²³. Decreases in fire frequency can increase woody biomass in Australian savannas³⁵, increasing their carbon density and shifting carbon allocation from relatively protected belowground pools to more vulnerable aboveground pools³⁶.

Carbon in boreal and temperate forests is most vulnerable in the mountain ranges of western Northern America, the Himalayan regions of Southern Asia and the eastern coast of Australia (Supplementary Figs. 2 and 3). For example, fire-adapted giant sequoia forests of California are experiencing above-average mortality as a result of high-severity crown fire (versus low-severity but more frequent fire at 15–30 yr intervals), which is relatively new in the modern era³⁷.

Across mid- and northern latitudes, boreal and temperate forest carbon stocks are moderately vulnerable to wildfire (Supplementary Figs. 2 and 3). We note that novel fire regimes, driven by rising temperatures and reductions in soil moisture, are likely to increase the vulnerability of carbon in regions with historically lower risk (for example, Arctic tundra³⁸ and boreal peatlands³⁹). Low-frequency but high-severity wildfire events require decades to centuries to reestablish carbon parity, but climate-driven increases in fire frequency increasingly threaten the regeneration of boreal conifer forests and their carbon sequestration potential^{6,40}. The physiological and life-history traits of biological communities may increasingly control regional carbon recovery rates (including live biomass and belowground carbon stocks) and determine ecosystem resilience to future fire.

Plant traits affect ecosystem carbon recovery

Determining how plants alter resource allocation to compensate for fire damage is critical for accurately predicting carbon cycling during recovery. For example, carbon recovery, from the organism to ecosystem scale, is influenced by plant regrowth strategies (Fig. 3), local climate conditions and water availability^{41,42}. For example, many woody species have evolved traits that allow them to survive stressors such as fire and drought⁴³—these include relatively static morphological features (tracheid diameter, sunken stomata, waxy cuticles, thick bark, rooting depth), dynamic physiological adaptations (stomatal control, resource allocation strategies) and phenological traits (deciduousness⁴¹). Grassland and savanna species have also evolved traits that enable high tolerance to fire⁴⁴, including belowground storage reserves (for example, non-structural carbohydrates and nitrogen can be translocated to rhizomes during plant senescence) and well protected buds that facilitate rapid resprouting. For instance, in temperate grasslands, high-frequency fire can increase carbon allocation belowground by increasing root growth (+25%) and root biomass C:N ratios (from 40 to 60) relative to low-frequency fire⁴⁵. The evolution of life-history strategies therefore influences proximate plant recovery, while ultimately driving carbon trajectories (that is, changes in carbon stocks and fluxes over time) at the landscape scale.

Trade-offs between plant functional types, growth and carbon sequestration rates, and fire frequency and severity interact to shape ecosystem carbon dynamics. Landscapes dominated by resprouters (for example, grasslands/savannas) will recover aboveground biomass more rapidly than those dominated by seeders (for example, shrublands/forests), which require longer recovery time between fire events. As a result, low fire frequency is strongly correlated with woody abundance³⁵. Fire severity also influences organism acclimation and rates of ecosystem carbon recovery⁴⁶. While wildfires in grassland and savanna ecosystems tend to burn widely and quickly, as the amount of fuel available to combust is generally less than in forests⁴⁴, this depends on fuel loads (for example, some grasslands can have relatively high fuel loads following above-average rainfall and some forests can store a lot of carbon in aboveground biomass that is too wet to combust). Furthermore, low-severity fires in savannas often consume aboveground grass biomass without impairing tree function or removing established resprouting woody plants⁴⁷. While regrowth strategies help determine ecosystem carbon recovery rates, the persistence of vegetative communities also depends on the ability of surviving plants to protect and rebuild their photosynthetic machinery and access water and nutrients. Interestingly, variability in species tolerances to shifting fire regimes (for example, severity, frequency) is seldom investigated, despite potential impacts on vegetation resprouting and/or topkill rates⁴⁸, probability of underground bud survival, and compensatory allocation of carbon and nitrogen to roots versus shoots.

Plant responses to fire are highly variable (Fig. 3) and mortality thresholds are complex and largely unresolved^{49,50}. While it has been hypothesized that fire-induced hydraulic damage can lead to tree mortality^{51,52}, recent empirical evidence questions the degree of damage directly inflicted to water-transporting structures (xylem) and further suggests that phloem damage drives tree death by reducing mobilization of non-structural carbohydrates⁵³. Regardless of the direct physical impacts of fire on plant mortality (for example, hydraulic versus phloem damage), responses are clearly species specific⁵². In addition, negative correlations between tree water flow (sap flux) and forest floor damage⁵⁴ suggest that indirect effects, such as the loss of fine roots⁵⁵, changes to soil water holding capacity/physical structure and reductions in soil microbial function, may be more consequential to hydraulic failure than direct xylem damage. Our evolving understanding of drivers of woody plant mortality suggests that responses are complex and require further investigation, particularly in mature trees and following in situ (not laboratory-simulated) wildfire.

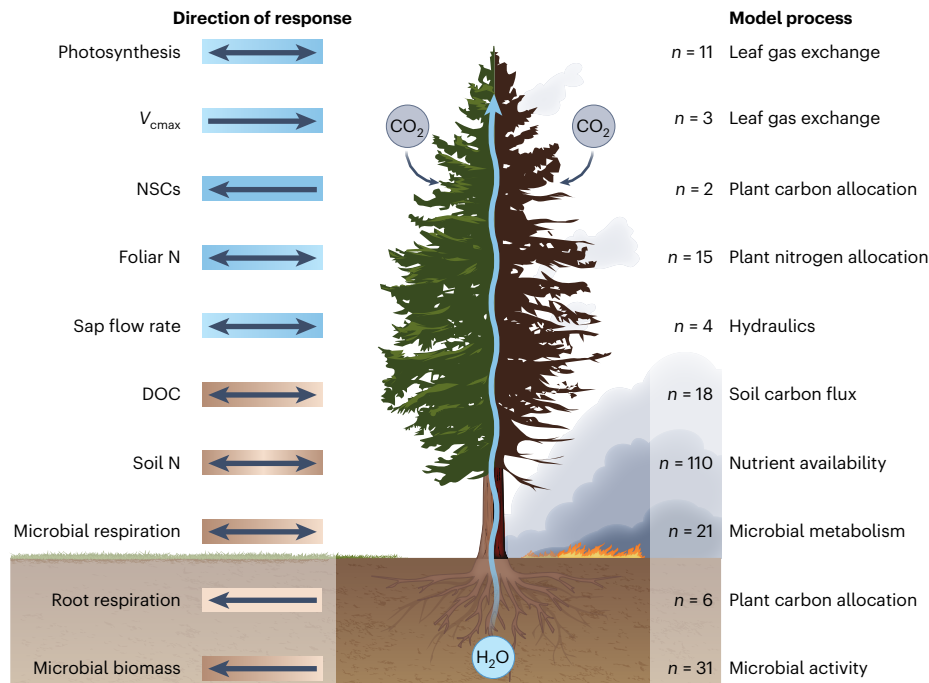


Fig. 3 | Studies including carbon and model-relevant traits exhibit strong variability in both the magnitude and direction of response following wildfire. The arrow direction indicates whether a response is positive or negative (relative to the study control); colour intensity indicates the strength of the response (white, no change; light, moderate change; dark, doubled change), with the number of studies reporting that response shown on the right. For example, wildfire increased, decreased or did not change soil nitrogen concentrations

relative to control plots/sites ($n = 110$ observations). By contrast, dissolved organic carbon (DOC) strongly decreased in most studies but did not change or increase in several ($n = 18$ observations). Lack of observations, particularly those replicated within the same biome, time frame and/or fire severity, highlights data gaps that should be prioritized to improve model representation of plant physiological, soil and microbial processes following wildfire. V_{max} , maximum photosynthetic capacity; NSCs, non-structural carbohydrates.

The ability of plants to translocate available nitrogen from roots to leaves probably facilitates the recovery of carbon uptake in many ecosystems. Nitrogen concentrations are often elevated in post-fire soils^{56,57}, with direct implications for the recovery of forest²⁰ and grassland⁵⁸ plant species. For example, leaf nitrogen content drives photosynthetic capacity and is consequently one of the most sensitive parameters for predicting rates of photosynthesis in Earth system models⁵⁹. Supporting this, the leaf nitrogen content of temperate and boreal tree species often increases following fire^{20,60}, which may facilitate increases in the maximum photosynthetic capacity of canopy-dominant trees²⁰ and understorey shrubs⁶¹. These results suggest that compensatory mechanisms can offset reductions in leaf area and fine roots that have been combusted during fire.

Resolving the physiological mechanisms employed by plants recovering from fire (Fig. 3) is hampered by methodological limitations and sparse data collection efforts⁴⁹. Advancing understanding of plant functional responses would benefit from emerging techniques that can characterize mechanisms underpinning biological function (for example, genotypic variation, physiological traits, hydraulic processes and carbon allocation). For example, high-throughput phenotyping⁶² can track photosynthetic recovery at the spatial and temporal scales necessary to infer fire effects on plant survival and recovery, particularly in forests where tall trees limit the feasibility of data collection. There is also an urgent need to identify factors influencing fire-induced early signalling cascades, stomatal responses, biochemical reactions and critical defence mechanisms. Progress in these areas will require the innovative use and integration of foundational (for example, in situ physiological measurements) and emergent (for example, ECOSTRESS⁶³) data streams.

Soil and microbiome feedbacks after wildfire

Wildfires tend to decrease soil organic carbon concentrations by combusting surface soils, where biological pools (for example, fine roots

and microbial biomass) and soil organic matter are concentrated⁶⁴. While deeper, mineral soil carbon stocks can also be affected (particularly when protected horizons are exposed to wind and photooxidation disturbance^{44,65–67}), they tend to be buffered from direct heating in all but the most severe fires. For instance, the deep rooting profiles of grasses may protect carbon at less vulnerable depths and catalyse aboveground recovery⁴⁴, while low-severity (smouldering) fires in peatlands may increase soil carbon concentrations by depositing pyrolysed char that resists microbial decomposition²⁶. While the loss of belowground function may catalyse compensatory physiological responses above ground, more observations are needed to effectively couple relevant metrics (for example, linking soil biogeochemistry with foliar nutrient and photosynthetic dynamics).

Tracking temporal trends in post-fire soils may reveal ecosystem variables that recover quickly versus those that persist for decades. For example, instantaneous fire effects, such as rapid temperature increases and organic matter combustion, may induce longer-term changes in soil structure and chemistry (Fig. 1). Across all ecosystems, wildfire can transform fast-cycling carbon into slow-cycling (pyrolysed) carbon pools, elevate soil pH, destroy soil aggregation, promote erosion and create a hydrophobic barrier that limits water infiltration and carbon dioxide efflux^{44,68,69}. While shifts in soil chemistry may have profound effects on microorganisms, few studies track changes in soil microbiome function over time, making it difficult to predict how shifts in microbial community composition and activity will drive rates of carbon recovery.

The delivery of nutrients from soils to plants is mediated by the soil microbiome. The effect of fire on microbial community composition and function will therefore impact the strength of aboveground–belowground coupling and rates of ecosystem recovery. Furthermore, fire is a selective filter on soil microorganisms because it directly impacts microbial survival (or mortality), generates resources and toxins that

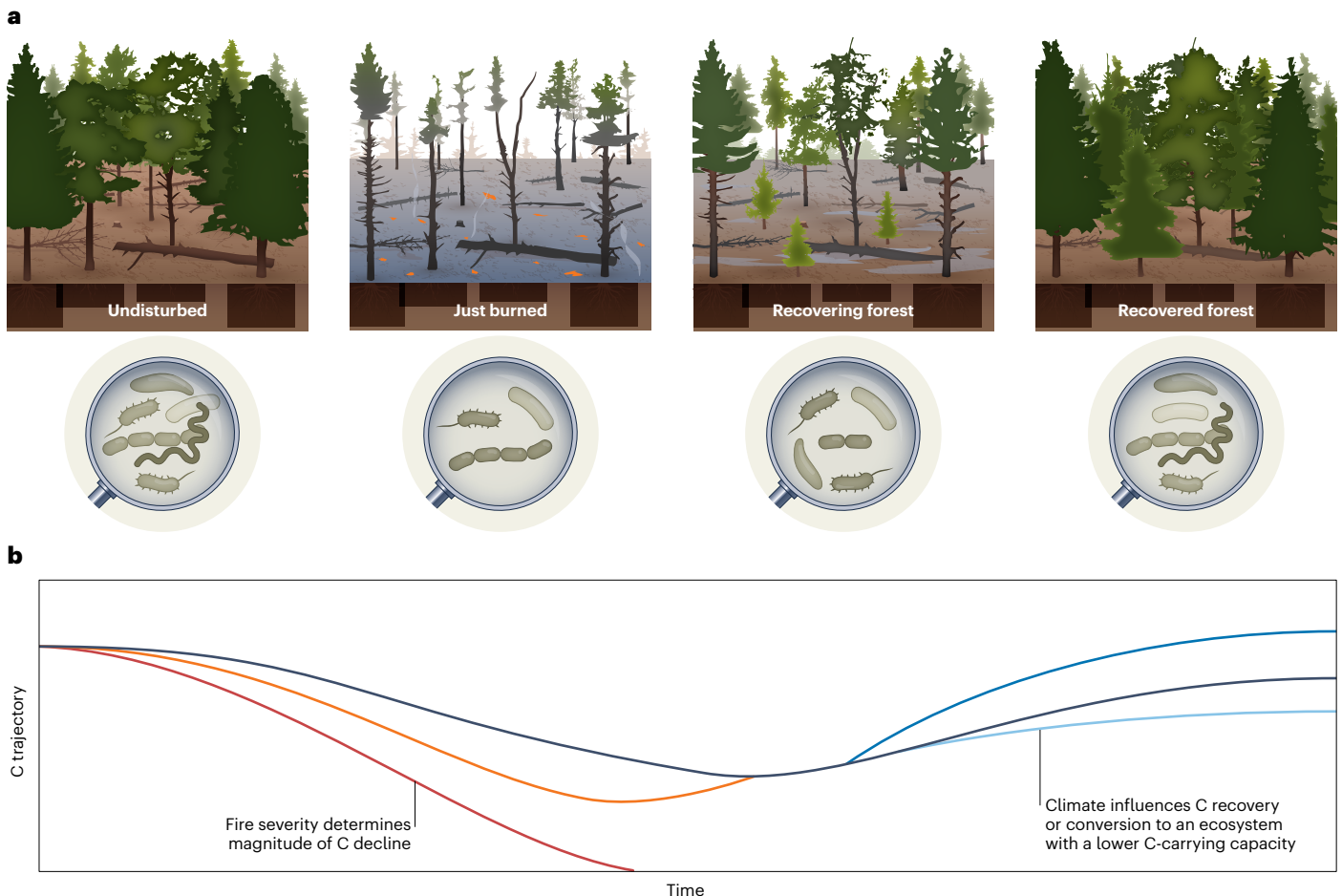


Fig. 4 | Conceptual figure of wildfire-affected carbon trajectories.

a, b, Recently burned ecosystems are dominated by dead biomass pools, which are slowly replaced by live biomass as plant and microbial communities recover over discrete (**a**) and continuous (**b**) timesteps. Ecosystems recover from wildfire (blue and black lines) and may reach previous carbon-carrying capacities in the

absence of other novel conditions or stressors (black line). However, increases in fire severity and frequency may convert ecosystems from higher to lower carbon-carrying capacities (red and orange to light-blue lines). Recovery of above- and belowground carbon stocks depends on a host of factors, including future climate conditions, reburns, management and land-use change.

induce strong environmental pressures, and shifts available niche space and community assembly dynamics⁵⁷. Depending on their location in the soil profile, microorganisms may be partially buffered from direct heating effects by the litter, organic and/or mineral soil horizons^{70–72}. However, high-severity fires probably reset soil microbiomes by combusting biomass, destroying habitat and cutting off the supply of plant-derived carbon inputs⁷³. Compounding stressors, such as fire followed by persistent drought, may therefore elicit the strongest negative biological responses, which can delay belowground ecosystem recovery for decades (Fig. 4).

In general, fungi appear more vulnerable to fire than bacteria^{69,74–76}. Declines in fungal biomass and diversity are often driven by increases in soil pH and the combustion of plant symbionts and root exudates^{77,78}. In one boreal forest ecosystem, ectomycorrhizal taxa (that is, root symbionts) declined by 90% (ref. 22) and took 15 years to recover to pre-burn levels⁷⁸. These marked declines in fungal biomass can reduce extracellular enzyme activities (particularly of phenol oxidases, which catalyse lignin turnover⁷⁷, thereby suppressing litter decomposition and soil respiration^{64,78}). Fungi in the arid and mountainous shrublands of Spain appear to withstand fire better than bacteria because they can degrade post-fire inputs of toxic and/or recalcitrant compounds (that is, polycyclic aromatic hydrocarbons)⁷⁹. Together, these findings suggest that the net effect of fire on fungal versus bacterial growth hinges on initial community diversity, relative reductions in resource availability, and traits expressed by surviving taxa, all of which vary across biomes.

The timing and origin of post-fire species immigration (that is, from unburned refugia, aboveground deposition or deep soils⁸⁰) can determine microbiome diversity, composition and functional attributes⁸¹ that ultimately regulate belowground carbon cycling. Temporal turnover of microbial communities appears to occur quickly in burned soils (for example, months to years in low-severity fires; years to decades in high-severity fires)⁸² and may follow a predictable trajectory from ephemeral, pyrophilic taxa (for example, Proteobacteria, Ascomycetes and Actinobacteria) to more stable, oligotrophic communities (for example, Planctomycetes, Acidobacteria, Verrucomicrobia and mycorrhizal fungi; Fig. 4a)^{72,83}. Regardless of the nature of post-fire microbial trajectories, we emphasize the importance of reconciling temporal trends in soil microbial, chemical and physical properties with net changes in soil carbon storage.

Developing a predictive framework that merges microbial taxonomy, ecological function and stress response is critical for modelling soil carbon response to fire. Investigators often posit that pyrophilic taxa possess traits that help them launch ecological succession after fire. These include stress tolerance to ultraviolet exposure, heavy metals, elevated pH and/or high heat, the ability to degrade pyrolysed carbon and rapid growth rates (that is, high rRNA copy numbers)^{22,80,84}. Metagenomic studies can shed light onto the impacts of fire on microbial function but are rare. In general, metagenomes from burned soils appear to be more heterogeneous than those from unburned soils and are characterized by shifts in carbohydrate metabolism and nitrogen

assimilation versus mineralization pathways^{22,68,85}. Identifying common strategies employed by surviving taxa (including aboveground phyllosphere communities) and their biogeochemical consequences will improve our ability to predict post-fire carbon trajectories but will probably require investigation at molecular and cellular scales.

Ecosystem carbon uptake declines after fire

Net ecosystem carbon uptake represents the balance of photosynthesis to respiration and determines whether an ecosystem is a carbon sink or source. Carbon sinks develop when more carbon is taken up through photosynthesis and stored in biomass than is released through plant and microbial respiration. Given that wildfire disturbance can reduce photosynthesis on timescales from years to decades⁸⁶ and has variable effects on ecosystem respiration^{87,88} it is therefore critical to track carbon pools and fluxes over time and with variability in local climate conditions and fire severity^{87,89}. Recouping lost carbon and regaining carbon parity at the ecosystem scale requires carbon storage to persist, as combusted carbon may have been fixed hundreds (for example, forests) to thousands (for example, peatlands) of years previously. In other words, simply recovering carbon uptake potential (that is, switching from a carbon source to sink) does not mean carbon stocks have been recouped.

Studies examining net ecosystem carbon trajectories consistently report that the recovery of ecosystem carbon (Fig. 4b) varies with fire severity, species compositions and other site-specific stressors (for example, drought). At low-to-mid latitudes, fire-adapted savannas and woodlands tend to recover carbon losses within months to years because low-severity fires primarily combust rapidly regrowing grasses and minimally disturb belowground carbon stocks^{90–92}. In grasslands of the Tibetan Plateau, fire enhances plant growth (and inorganic nitrogen availability) more than ecosystem respiration, leading to increases in net ecosystem carbon uptake within three years⁹³. In mid-latitude, fire-adapted forests, stand-replacing crown fires yield large soil and aboveground carbon losses; transitioning from a carbon source to sink takes multiple decades as woody biomass and soil organic carbon stocks slowly rebuild^{19,86}. High-latitude boreal forest and peatland carbon sinks lose disproportionately more soil carbon during severe fires and take the longest to recover (decades to centuries) due to low plant productivity and changes in the soil thermal profile that accelerate soil decomposition rates^{94,95}. For example, net ecosystem carbon uptake remained negative (that is, the forest was a carbon source) for 200 years following a severe wildfire event in a Siberian pine stand⁹⁶. While this is an extreme example (most boreal systems require ~50 yr to recover pre-burn function), it may be a harbinger of wildfires to come, particularly as these ecosystems experience rapid climate change. These results underscore how simultaneously measuring the component fluxes of net ecosystem carbon uptake (for example, photosynthesis, plant respiration, microbial respiration) is pivotal to advance a mechanistic understanding of carbon dynamics in fire-affected systems.

Recent decades have witnessed the permanent loss of ancient carbon sinks to anomalously high-severity fires, a trend that is increasing across multiple continents and particularly in high-altitude and latitude ecosystems^{6,97,98}. For forests, this type of ecosystem conversion reduces carbon-carrying capacities at the stand scale (Fig. 4a) that cannot be easily reversed through tree-planting strategies⁹⁹, which remain highly vulnerable to extreme wildfire¹⁰⁰. Even where forests currently persist despite changing fire regimes, overall carbon storage may be permanently reduced by shifting to different species compositions (for example, from evergreen conifer to broadleaf deciduous species¹⁰¹) or to younger age classes⁸⁶. More alarmingly, climate change is drying out peatlands and increasing their vulnerability to fire; the combustion of deep peat layers affects ancient carbon stocks that have not been part of the active carbon cycle for centuries to millennia and may never be recovered⁹⁸.

Predicting climate–fire–carbon feedbacks through time

Empirical approaches are essential for determining influential environmental and climate drivers of total ecosystem carbon dynamics, but process-based models provide the only means to predict the impact of novel conditions (for example, changes in climate, atmospheric carbon dioxide concentrations, vegetation and wildfire regimes) on carbon vulnerability to fire¹⁰². Fortunately, a diverse set of models that vary in complexity and scale^{11,13,103,104} and bring complementary strengths and algorithms to effectively represent biological mechanisms has been developed. Although results are not directly comparable due to variability in modelled fire processes (Supplementary Table 1), we highlight several examples from site to global scales that address uncertainty or knowledge gaps associated with the impacts of wildfire on ecosystem processes. For instance, these models vary in their ability to represent rates of leaf gas exchange (for example, carboxylation rate, stomatal conductance, transpiration), plant physical properties (for example, specific leaf area and conductance, hydraulic risk), carbon allocation (for example, to net primary productivity versus belowground storage), soil properties (for example, concentrations of pyrogenic carbon and nitrogen) and microbial traits (for example, carbon use efficiency, biomass). However, we are aware of no model that represents all these mechanisms simultaneously, let alone the sensitivity of these processes to fire.

Historically, fire modelling studies at all scales tended to focus on fire prediction, burn area and carbon emissions (see also the collaborative Fire Modeling Intercomparison Project for a comprehensive review on the status and challenges of global fire modelling¹⁰⁵). While not explicitly focused on simulating carbon dynamics, advances in vegetation–fire feedbacks¹⁰² have significantly improved the ability to determine carbon trajectories. For example, net ecosystem carbon uptake increased when vegetation feedbacks were excluded from global circulation model simulations, while including them reduced net ecosystem carbon uptake—particularly when progressive soil moisture limitation caused forests to convert to grasslands¹⁰⁶. Such advances allow modellers to explicitly examine carbon dynamics over time and space, but process-based models continue to be restricted by a lack of studies in non-boreal and temperate regions, and an incomplete representation of biological processes.

Most modelling studies, regardless of model skill or scale, report greater carbon losses and emissions with more frequent and intense fire^{107,108}. For example, a global simulation accounting for increases in fire frequency since the 1980s reported a reduction in the global terrestrial carbon sink by -0.6 Pg carbon yr⁻¹ (ref. 109). Carbon losses are predicted to be greatest in ecosystems with high carbon storage (for example, peatlands and tropical forests¹⁰⁹). At site-to-regional scales, models predict conversion of ecosystems from carbon sinks to sources following wildfire activity (for example, see modelling efforts in savanna¹¹⁰, tropical forest¹¹¹ and temperate forest¹¹² ecosystems), and when shifts in plant species composition reduce landscape-level carbon sequestration potential^{14,113}. Similarly, shorter fire return intervals in some ecosystems may remove carbon from the landscape faster than it can be recovered in soils and aboveground biomass (for example, return intervals of <150 yr in boreal biomes^{114–117}), while in others longer return intervals may promote landscape conversion to woody dominance (for example, return intervals of >3 yr in grassland biomes⁴⁷). Together, these complex climate–fire–vegetation feedbacks that impact carbon storage potential can be used to identify regions that should be prioritized for management and climate mitigation policy.

Informing management and climate mitigation policy

Under rising greenhouse gas emissions scenarios (for example, IPCC RCP8.5), forests on every continent are predicted to face 30 additional days above critical vapour pressure deficit thresholds for fire activity by 2100^{34,118}. Exceeding these vapour pressure deficit thresholds will

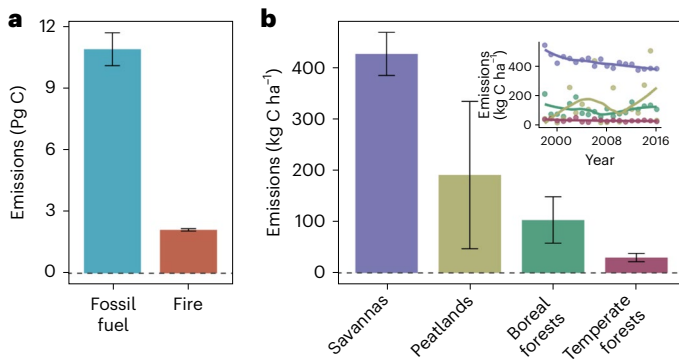


Fig. 5 | Global wildfire carbon emissions. **a**, Excluding agricultural and deforestation-related fires, average annual fire-related emissions are approximately 1.7 Pg annually, equivalent to 16% of fossil fuel and land-use change emissions. **b**, On an area basis, fires in savannas, grasslands and shrublands, peatlands, boreal forests and temperate forests contribute 427, 191, 103 and 30 kg C ha⁻¹, respectively. Error bars represent the s.d. over the period for which data were averaged (1997–2016). Inset: temporal evolution of wildfire emissions for each biome. Estimates of wildfire emissions are not reported in annual global carbon budgets as they are too difficult to disentangle from other carbon sources. Until we can accurately model fire–carbon feedbacks, we will not know the extent to which wildfire is affecting the global carbon budget.

increasingly drive ecosystems to drier and more fire-prone states with greater potential for catastrophic carbon loss^{3,34,119}. Earth system models of wildfire impacts on global carbon budgets^{13,18} can improve our ability to assess proposed climate mitigation strategies such as massive tree-planting projects⁹⁹, natural climate solutions¹²⁰ and carbon-offset markets¹²¹.

Accurate models of fire and carbon dynamics are critical for developing science-informed global emissions treaties. Fortunately, numerous studies deposit site-to-regional wildfire emissions in the Global Fire Emissions Database³². Using the Global Fire Emissions Database, we find that savannas, grasslands and shrublands account for 65% of annual wildfire carbon emissions (Fig. 5b). Even though forests generally release more emissions per unit burned area¹⁹, savannas and grasslands burn more frequently over time and space (for example, every 1–5 yr versus 30–50+ yr in temperate and boreal forests²⁹), accounting for their higher long-term average. However, these systems also recover carbon losses within several years by rapidly regrowing aboveground biomass^{23,67}. By contrast, peatlands, boreal forests and temperate forests contribute less to total wildfire emissions (4%, 7% and 2%, respectively), but are of far greater concern because they have higher carbon densities and are comprised of slower-growing species (Fig. 2). Although warming may stimulate plant growth and carbon uptake, deeper soil burn depths coupled with slower plant growth rates make it unlikely that peat and forest regeneration will fully offset fire-induced carbon loss if current wildfire trends continue.

The IPCC framework uses the United Nation’s Reducing Emissions from Deforestation and Forest Degradation, the Global Fire Emissions Database and other global carbon accounting and forest management initiatives to quantify country-level emissions. Modelling efforts must therefore accurately account for post-fire recovery to set equitable and realistic emissions reduction targets and associated pathways for meeting them. In this effort, it is critical to recognize that total wildfire-related emissions are dwarfed by fossil fuel emissions, which accounted for 89% of global carbon emissions in 2022^{7,122} (Fig. 5a). Two countries (China and the United States) are responsible for nearly half of global fossil fuel emissions^{7,122}, with <2% of their annual emissions budget contributed from wildfire⁷, while Australia represents a country with very high per capita fossil fuel emissions and relatively high fire emissions^{123,124}. By contrast, countries in central and eastern Africa

have extremely low per capita fossil fuel emissions and high annual fire activity (Fig. 2); however, much of the area burned is grasslands and savannas that will recoup lost carbon quickly²³. Models that accurately represent fire across scales will be critical for ascertaining the potential success and long-term trade-offs of proposed climate mitigation activities involving slowly accumulating carbon stocks (such as forests and peatlands) impacted by rapidly changing fire regimes.

The lack of consensus on how to minimize carbon emissions from wildfire further complicates ecosystem management. For example, the range of published short-term forest wildfire risk-reduction strategies (which are also intended to reduce carbon emissions) includes reducing tree density, post-fire salvage logging and replanting disturbed landscapes to restore native species. However, many of these strategies do not account for carbon parity—the time it takes to recover carbon removed through disturbance, including the carbon that would have accumulated in the absence of that disturbance¹²⁵—and/or regional variability, which must be accounted for in carbon management recommendations¹²⁶. To increase carbon stores long term, mechanical density reduction (for example, thinning treatments that do not remove large, fire-resistant overstorey trees¹²⁷, shrub removal) should be combined with or even replaced by prescribed fire¹²⁸, dead trees should be left standing rather than salvage logged¹²⁹ and the planting of new forests should account for novel climate conditions that may no longer support historic ecological communities⁹. Future work must address the tension between wildfire risk reduction, which varies by proximity to the built environment^{17,130}, and carbon storage, with a focus on balancing short-term (for example, fuel reduction) with long-term (carbon storage and forest restoration) objectives.

Summary and recommendations

Fire is a critical component of global ecosystem function, but the Anthropocene has increased the frequency, magnitude and threat of fire to human health, infrastructure and ecosystem services¹⁷. Although fire suppression has led to an increase of available biomass to burn and humans have shifted vegetation to less fire-adapted species compositions³¹, anthropogenic climate change is overwhelmingly responsible for increasing aridity and biomass flammability¹⁰. Adapting to an increasingly flammable world therefore requires a deeper understanding of how fire will further alter the terrestrial carbon balance. In reviewing the current state of knowledge, we find that most studies focus on carbon emissions from wildfire, few investigate plant and/or microbial physiological responses that govern carbon recovery and even fewer report flux-based measurements (for example, photosynthesis, respiration) or soil microbiome functional responses, highlighting crucial avenues for future research. We also find that wildfire studies in peatlands and tropical forests are notably underrepresented in the literature, despite these ecosystems being disproportionately vulnerable to net carbon losses following fire.

Determining fire-induced mechanisms of plant and microbial survival and ecosystem recovery is critical to accurately predict carbon trajectories in process-based models. While it is clear that interdependent relationships between plants and microbes drive ecosystem carbon and nitrogen fluxes, studies designed to represent these relationships experimentally and in models are rare. Recoupling mechanistic knowledge about above- and belowground processes and recovery rates is therefore key to tracking, and predicting, carbon trajectories through time⁴⁹. These efforts could be streamlined by adopting a fire regime perspective, and by designing long-term, multiscale studies, where standardized data are collected before, during and immediately following a fire, and then monitored throughout post-fire recovery.

Because most modelling studies have focused on quantifying or predicting emissions for national reporting requirements, biological responses have rarely been incorporated. Currently, most embedded fire models ignite and spread fire and predict combustion and mortality, which generate an immediate change in live and dead

carbon stocks. Fire spread, combustion and mortality can be a function of morphological traits (bark thickness, crown height), but do not account for physiological responses. We are also unaware of any climate–fire–carbon model that modifies soil properties (pH, bulk density, texture) or microbial function after fire despite belowground systems being highly sensitive to fire and vital to ecosystem recovery. Similarly, current models do not explicitly change plant allocation patterns of carbon or nitrogen in response to fire (for example, the ability to increase maximum photosynthesis or to mobilize non-structural carbohydrates as root exudates for microbes). To accelerate progress, we recommend that modellers are fully integrated into experimental activities to ensure that key model parameters and benchmarking data are collected¹³². These actions will also help inspire the design of coupled above- and belowground experiments that improve our understanding of the organismal processes driving observable change in ecosystem carbon cycling.

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T.H. and L.L. planned the project. All authors contributed to synthesis, figure creation and writing the manuscript.

Competing interests

The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to Tara Hudiburg.

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