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Journal
Environmental Science and Technology, 59(10)

ISSN
0013-936X

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Publication Date
2025-03-18

DOI
10.1021/acs.est.4c11833

Peer reviewed

Environmental Science & Technology

pubs.acs.org/est

Article

Thermal Compensatory Response of Soil Heterotrophic Respiration Following Wildfire

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Cite This: https://doi.org/10.1021/acs.est.4c11833

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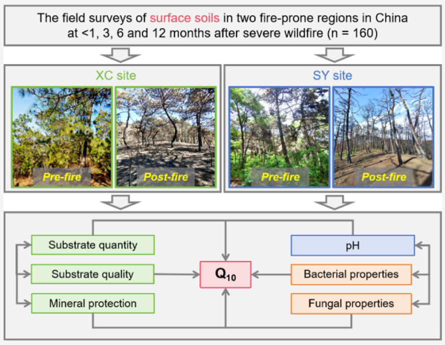
ABSTRACT: Frequent wildfires pose a serious threat to carbon (C) dynamics of forest ecosystems under a warming climate. Yet, how wildfires alter the temperature sensitivity (Q_{10}) of soil heterotrophic respiration (R_h) as a critical parameter determining the C efflux from burned landscapes remains unknown. We conducted a field survey and two confirmatory experiments in two fire-prone regions of China at <1, 3, 6, and 12 months after wildfires (n = 160 soil samples). We found that wildfire generally reduced the Q_{10} for soil organic and mineral horizons within the first year after wildfire mainly due to substrate depletion, which was confirmed by a uniform inoculation experiment. Mineral protection of organic matter in the mineral horizon rich in iron/aluminum (hydr)oxides and a near-neutral pH in organic horizons of postfire soils further suppressed the Q_{10}. Decreased Q_{10} persisted in organic horizons even after removing substrate limitation, reflecting the dominance of a thermally adapted, r-strategist microbial community in postfire soils. Moreover, fire-induced low C quality increased Q_{10}, which supported the C quality-temperature hypothesis, but a C-limited condition restricted this stimulatory effect. This study illustrates that a thermal compensatory response of R_h will help maintain C stocks in forest ecosystems after wildfires in a warming world.



KEYWORDS: *forest fire, temperature sensitivity, substrate depletion, microbial thermal adaptation, soil carbon sequestration, climate warming*

■ INTRODUCTION

Wildfires threaten to significantly alter the carbon (C) stock (460 Pg C) of terrestrial surface soils (<30 cm depth), with fire combustion releasing ~19.2 Pg C to the atmosphere annually,[1] thereby enhancing the atmospheric CO_2 concentration as a greater societal concern. As the climate warms,[2] the global area experiencing frequent fires is expected to increase by ~29% by the end of the century (RCP8.5),[3] imposing serious ramifications for soil C stocks. Fire-driven changes in the chemical composition of soil organic matter (SOM) and a subsequent decrease in soil heterotrophic respiration rate (R_h) are important feedbacks affecting forest C dynamics following wildfires.[1,4−6] The exponential increase of R_h within common soil temperature regimes infers that the temperature sensitivity (Q_{10}) of R_h is a critical factor affecting forest C storage in a warming world.[7] However, the Q_{10} response of R_h to wildfire disturbance in forest soils remains highly uncertain. Addressing this knowledge gap will appreciably improve global climate-C cycle feedback (CCF) models given the projections for increased wildfires in a warming world.[7−9]

Currently, only a few studies have assessed the temperature dependence of soil R_h to wildfires. They found contradictory results, such as an enhanced response,[10−12] no response[13] or compensatory response,[14−17] with the overall response attributed to changes in substrate and microbial properties.[18−21] According to the C quality-temperature (CQT) hypothesis, the recalcitrant C fraction (low quality) has a higher Q_{10} owing to its higher activation energy as compared to the labile C fraction (high quality).[20,22−24] Moreover, enzyme kinetic theory posits that Q_{10} is controlled by substrate availability (e.g., substrate quantity, mineral protection of SOM) according to the Michaelis−Menten equation.[25−29] For example, Liu et al. (2021) found that glucose addition significantly increased Q_{10} across eight soils from tropical to cold-temperate forests.[30] Moinet et al. (2018) found that low substrate accessibility reduced Q_{10} when adding allophane, a clay mineral with strong-binding properties for SOM.[31] In wildfire-prone areas, C pools in surface soils usually exhibit low quality along with low quantity and high mineral protection (low substrate availability) due to production of highly aromatic pyrogenic charcoal, loss of organic materials to

Received: November 5, 2024
Revised: February 27, 2025
Accepted: February 28, 2025

combustion and metal release and accumulation in the residual ash.[1,32,33] However, a trade-off between low C quality and availability may exist in the Q_{10} response after wildfires, implying that these two factors should be simultaneously considered to ensure robust predictions by global CCF models.[23,26,34]

The soil microbiome, as decomposers of SOM, has a disproportionate influence on variations in Q_{10} compared to substrate properties and climatic conditions at the global scale.[7] Microbial r-/K-strategies may provide insights for elucidating microbial regulation of Q_{10} from a phylogenetic perspective.[35−38] The r-strategists (copiotrophic taxa) have rapid growth and C mineralization rates and prefer labile C-rich environments.[35,38] In contrast, K-strategists (oligotrophic taxa) are slow-growing organisms that dominate C-limited niches where they decompose recalcitrant C compounds with high C-use efficiency.[35,38] In the initial postwildfire phase, soil microbes with r-strategies typically dominate due to the ecological niches created by considerable biotic mortality, as well as a distinct pulse in nutrient availability.[39−41] Considering that microbial strategies are shaped by a combination of substrate availability and quality, the link between specific microbial strategies and soil Q_{10} values after wildfires cannot be directly predicted.[23,36,42] Hence, there is a critical need for basic information on these uncertain relationships created by wildfire disturbance.

The initial recovery stages following wildfires are a critical period for mitigating indirect C efflux due to microbial death, but there are also many triggers for soil R_h at this stage, such as elevated surface temperatures, high respiratory quotients, and large priming effects.[43−45] Given a large global C flux from soil R_h (49 Pg C yr^{-1}),[46] the Q_{10} is a critical but neglected parameter for wildfire-perturbed soils. Consequently, this study aimed to investigate the Q_{10} response to wildfire disturbance and its various drivers (e.g., substrate quantity, substrate quality, mineral protection of SOM, microbial properties and soil pH) during the initial stages of postfire ecosystem recovery (Figure S1). We tracked two fire-prone forest regions in northeastern and southwestern China and collected soil organic and mineral (0−10 cm) horizons at <1, 3, 6, and 12 months after stand-replacing wildfires (n = 160 soil samples). We determined soil R_h at five incubation temperatures (5−35 °C) and applied an exponential model to fit Q_{10} per unit of microbial biomass. Further, we determined changes in five categories of soil properties and their relationships with Q_{10} after wildfires to assess potential causal relationships. To verify the relationships of Q_{10} with these substrate and microbial properties, we conducted two microcosm experiments utilizing uniform inoculation and glucose addition incubation. We hypothesized that wildfire would decrease Q_{10} through alteration of soil properties, similar to that found for long-term soil warming experiments,[21,24,29,47] thereby helping forest ecosystems adapt to climate warming. This is the first study to comprehensively explore the multifactorial regulation of wildfire disturbance on the Q_{10} of soil R_h, which contributes new insights into postfire soil biogeochemical dynamics and improves the cognition of global C fluxes.[10−17]

■ MATERIALS AND METHODS

Study Area and Soil Sampling. Two coniferous forests were selected in Xichang (XC), Sichuan Province (28.24°N, 102.19°E) and Shenyang (SY), Liaoning Province (42.00°N, 123.78°E) having dominant vegetation of *Pinus yunnanensis* and *Pinus thunbergii Parl.*, respectively. The XC and SY sites had subtropical monsoon and temperate continental climates, with a mean annual temperature of 18.3 and 9.7 °C, and a mean annual precipitation of 896 and 965 mm, respectively (Figure S2). Soil types were Oxisols at XC and Ultisols at SY (USDA Taxonomy). Geologic parent materials were weathered basalt and quaternary loess deposits at XC and SY, respectively.

Stand-replacing wildfires occurred in February and April 2022 at XC and SY, respectively. The fires killed most of the trees and understory, consumed all the litter layer, and produced a surface layer of gray-white ash. Postfire, both forests experienced natural recovery without human disturbance (e.g., cutting, replanting, tillage, etc.). We conducted paired surveys of burnt and unburnt treatments and collected soil samples of the entire organic horizon and 0−10 cm mineral horizon at <1, 3, 6, and 12 months after the wildfires. The organic horizon of the burnt treatment was mainly ash and fine pyrogenic charcoal.[48] Five burnt plots representative of the physiographic features of the burned sites were selected and location-marked, which ensured that samples were collected from the same plots at different time points. According to historical records from the local Forest Service, we confirmed that the unburnt treatment had not experienced wildfire for at least 50 years at both sites. Additional information on these two sites is provided in Table S1.

The distance between the unburnt and burnt treatments ranging from 0.1 to 1.0 km limited autocorrelation of plant and soil traits while also ensuring that the forest structure was representative of prefire conditions, which was also confirmed by historical remote sensing images. Each burnt plot had a similar microhabitat to its paired unburnt plot (e.g., aspect, slope, elevation, prefire vegetation, and soil type). Each plot consisted of five replicates (50 m × 50 m) based on a five-point sampling method, spaced more than 50 m apart. A total of 15−20 cores were randomly collected using a stainless steel shovel to create a composite soil sample as one replicate (∼1 kg). We carefully removed all macro-debris, including twigs, roots, fungal hyphae, stones, and large pieces of charcoal before collecting the organic horizon. Soil samples were collected in sterile plastic bags, refrigerated and transported to the laboratory. We obtained a total of 160 soil samples: 2 sites × 2 horizons × 5 replicates × 4 points-in-time × 2 fire treatments (burnt versus unburnt). A subsample of soil was frozen at −80 °C for DNA extraction. The remaining soil was passed through a 2 mm screen and stored at 4 °C for further analyses. All biogeochemical analyses were performed on the 160 soil samples.

Measurement of Q_{10} Related to Ambient Soil Properties. Soil R_h typically increases with increasing temperature, and the intensity of temperature response expressed as the temperature sensitivity of R_h (Q_{10}), i.e., the fold change in R_h for every 10 °C increase in temperature. To assess the Q_{10} of R_h as related to ambient soil characteristics, substrate properties and microbial attributes, we conducted microcosm experiments utilizing in situ soil (see below), and uniform inoculation and glucose addition (see Supplementary Methods) at five temperatures (5, 15, 20, 25, and 35 °C).[36]

Briefly, preincubated soils were held at five temperatures (5, 15, 20, 25, and 35 °C) for 6 h to ensure a uniform soil temperature throughout the bottle. Then, the CO_2 concentration was determined as described in Supplementary Methods (160 soils × 5 temperatures = 800 samples). A

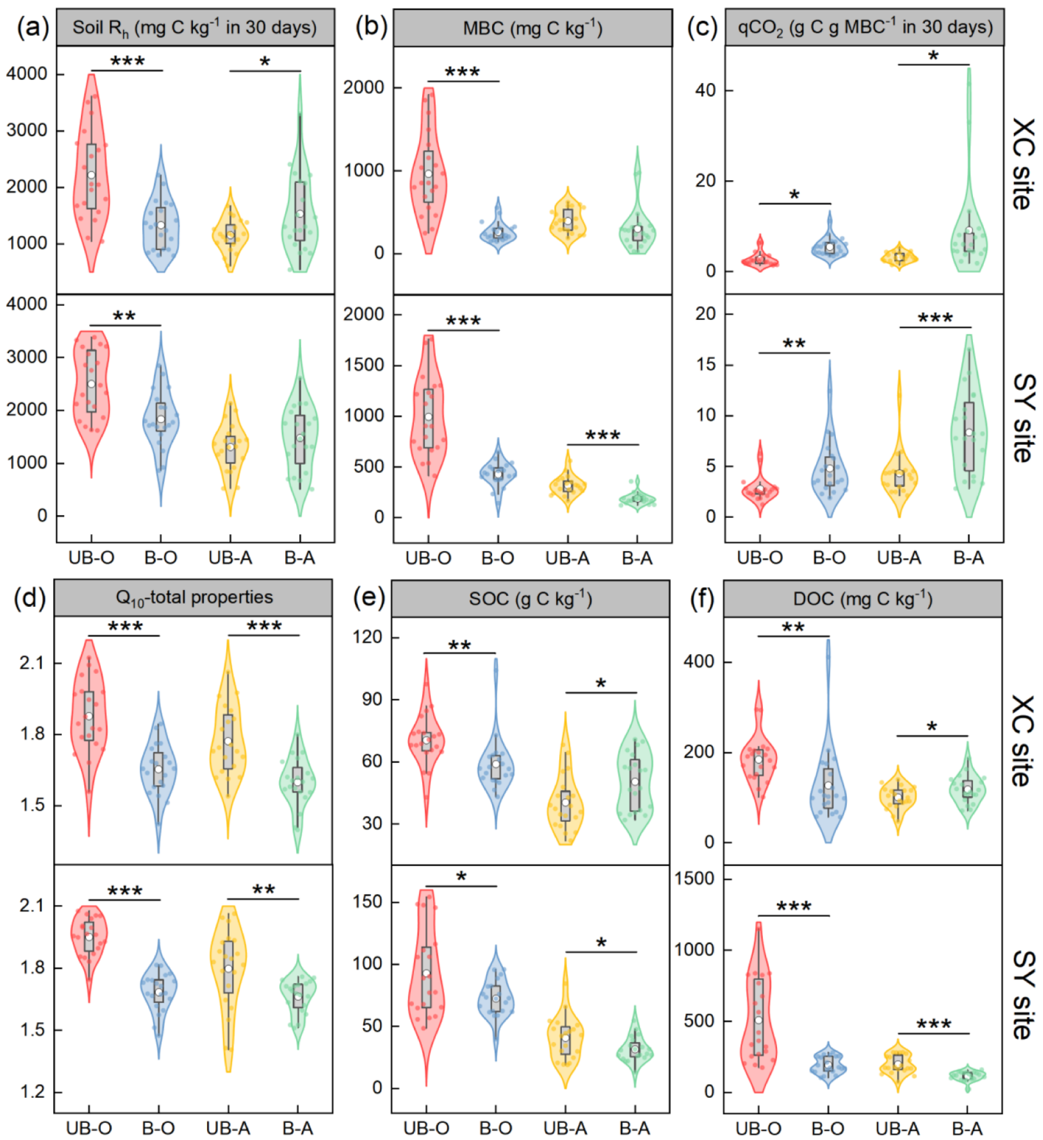


Figure 1. Comparison of C efflux between the unburnt (UB) and burnt (B) soils in organic (O) and mineral (A) horizons. Subpanels correspond to cumulative heterotrophic respiration (R_h) (a), microbial biomass C (MBC) (b), respiration quotient (qCO_2) (c), temperature sensitivity (Q_{10}) of R_h related to overall soil properties (d), and substrate quantity (e,f) at two forest sites within one year after undergoing a stand-replacing wildfire as an overall presentation including four points in time with five replicates ($n = 20$). SOC, soil organic C content; DOC, dissolved organic C content. The whiskers illustrate the 5th and 95th percentiles, box ends represent the 25th and 75th quartiles (interquartile range), and the white points represent the mean values. *, **, and *** represent $p < 0.05$, <0.01, and <0.001, respectively.

short 12-h experiment was utilized to limit the changes in thermodynamic properties at different incubation temperatures. The Q_{10} of R_h was calculated as follows:[7]

$$Q_{10} = e^{10b}$$

where b is the fitting parameter of the relationship between R_h and temperature. This parameter was obtained from

$$R_h = a\,e^{bT}$$

where a is the exponential parameter, R_h is heterotrophic respiration (mg CO_2−C kg^{-1} h^{-1}, per unit of microbial biomass), and T is the incubation temperature (°C). Here, we define the "thermal compensatory response" as a decrease in Q_{10} for R_h.[24] The fitted coefficients for all samples were R^2 > 0.91.

Measurement of Abiotic and Biotic Factors. Soil pH was determined in 1 M $CaCl_2$ (soil: solution = 1:2.5) using a pH meter (FE28, Mettler Toledo, Switzerland). Soil organic C was determined using an elemental analyzer (Vario EL III, Elementar, Germany). Soil dissolved organic C was extracted with 0.5 M K_2SO_4, filtered through a 0.45-μm membrane and determined on an Elementar TOC analyzer (Multi N/C 3100, Analytikjena, Germany).

As for substrate quality, we adopt the acid hydrolysis approach (6 M hydrochloric acid) to determine the recalcitrant C fraction[49] and assessed the humification coefficient by the ΔlogK value and E4/E6 ratio (see Supplementary Methods). The Δlog K value and E4/E6 ratio are high at low optical density and degree of aromatic condensation, indicating a simpler molecular structure.[50]

As for mineral protection of SOM, we measured the contents of mineral-associated C, Ca-associated C, Fe/Al-

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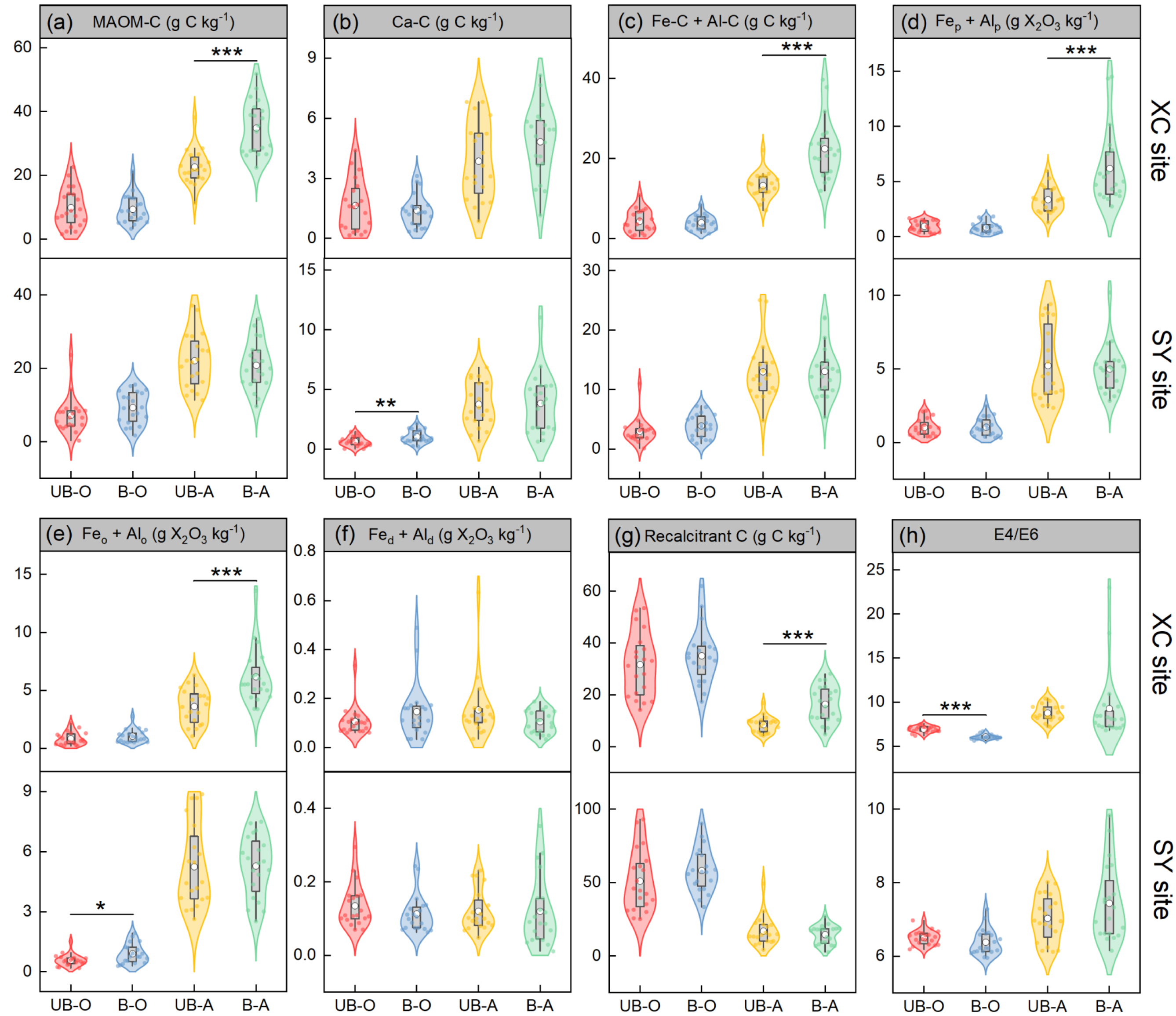

Figure 2. Comparison of C pools between the unburnt (UB) and burnt (B) soils in organic (O) and mineral (A) horizons. Subpanels correspond to mineral protection (a–f) and substrate quality (g–h) of SOM at two forest sites within one year after undergoing a stand-replacing wildfire as an overall presentation including four points in time with five replicates (n = 20). Whiskers illustrate 5th and 95th percentiles, box ends represent the 25th and 75th quartiles (interquartile range), and white points represent the mean value. E4/E6, the optical density determined at 465 and 665 nm (lower values indicate more recalcitrant C fractions and more complex molecular structures); MAOM-C, mineral-associated organic C content; Ca–C, Ca-associated organic C content; Fe–C + Al–C, Fe + Al-associated organic C content; $Fe_p + Al_p$, organically complexed Fe and Al oxides; and $Fe_o + Al_o$, poorly crystalline Fe and Al oxides; $Fe_d + Al_d$, pedogenic Fe and Al (hydr)oxides. *, **, and *** represent p < 0.05, <0.01, and <0.001, respectively.

associated C, pedogenic Fe and Al (hydr)oxides ($Fe_d + Al_d$), organically complexed Fe and Al ($Fe_p + Al_p$), and poorly crystalline Fe and Al ($Fe_o + Al_o$). Briefly, soil samples were divided into particulate organic C (POM-C) and mineral-associated organic C (MAOM-C) using sodium iodide solution with a density of 1.8 g cm^{-3}.[28,51] A sequential extraction of Ca-associated C and Fe/Al-associated C were carried out with 0.5 M sodium sulfate solution[51] and 0.27 M trisodium citrate-0.11 M sodium bicarbonate-0.1 M sodium dithionite (CBD).[52] Fe_d and Al_d, Fe_p and Al_p, and Fe_o and Al_o were extracted with CBD solution, sodium pyrophosphate, and ammonium oxalate, respectively[52] (see Supplementary Methods).

As for bacterial properties, the rRNA operons (rrn) copy number was employed to ascertain the bacterial preference for the K- or r-strategy at the community level[53] using the rrnDB database (https://rrndb.umms.med.umich.edu/). The higher rrn copy number indicates more r-strategists. As for fungal properties, ectomycorrhizal (ECM) fungi and saprotrophic fungi were distinguished by functional assessment using the FUNGuild database as the fungal K- and r-strategists, respectively.[54] More details are given in the Supplementary Methods.

Statistical Analyses. Since the data were not completely independent, we employed linear mixed-effect models to assess differences in soil Q_{10} with substrate and microbial properties between burnt and unburnt soils as an overall presentation at the four time points using "lme4" R package.[55] We further confirmed the normality of residuals and homogeneity of variances. Residuals were checked for normality and log-

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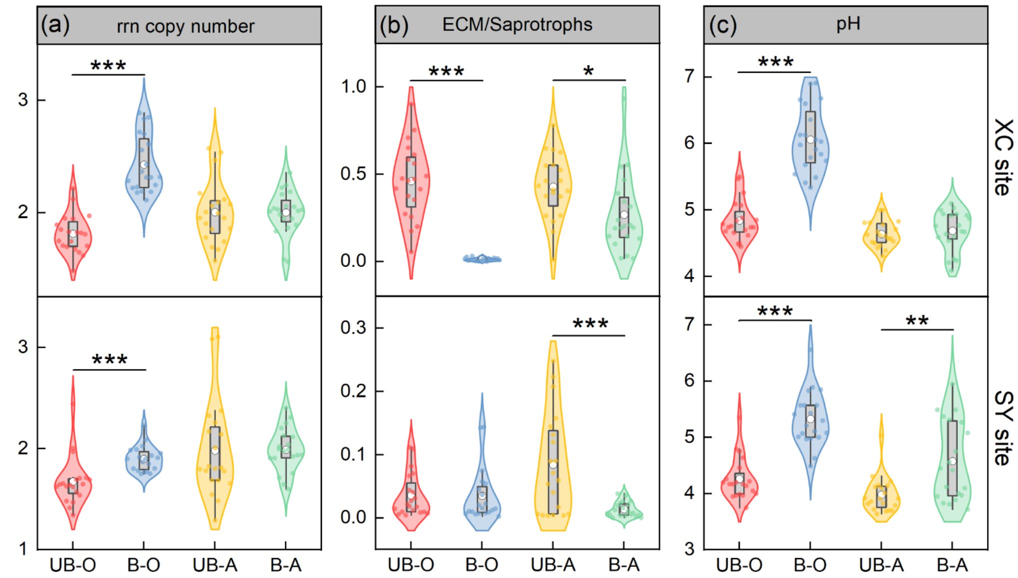

Figure 3. Comparison of microbial properties between the unburnt (UB) and burnt (B) soils in organic (O) and mineral (A) horizons. Subpanels correspond to, rrn copy number (a), ectomycorrhizal and saprotrophic fungi ratios (b), and soil pH in $CaCl_2$ matrix (c) for two forest sites within one year after undergoing a stand-replacing wildfire as an overall presentation including four points in time with five replicates (n = 20). Whiskers illustrate the 5th and 95th percentiles, box ends represent the 25th and 75th quartiles (interquartile range), and the white points represent the mean value. *, **, and *** represent p < 0.05, < 0.01, and <0.001, respectively.

transformed when necessary. In the linear mixed-effect model, wildfire disturbance was considered a fixed effect, while sampling time was considered a random effect (y ∼ wildfire + (1|site)).

Linear regression, heat maps, random forest models, variance partitioning analysis, and structural equation models were used to assess and visualize the five groups of environmental factors (i.e., substrate quality, substrate quantity, mineral protection, microbial properties, pH) on Q_{10}. The relative importance (%, mean square error, MSE) of all the environmental factors to Q_{10} was quantified using the randomForest package.[56] Environmental factors were ranked using rfPermute package to assess the significance of each metric in the random forest model. We conducted variation partitioning analysis using R package vegan to partition the effects of substrate properties and microbial properties on Q_{10}.[57] Considering the presence of covariance among environmental factors, we chose the most important factor for Q_{10} in each group according to the results of linear regression and random forest models to create a structural equation model. The goodness-of-fit of the structural equation model was evaluated using Chi-square, Akaike information criterion, and the whole-model p value. The structural equation model was conducted using R package piecewise SEM.[58] All statistical analyses were conducted with R Statistical Software (v4.2.2; R Core Team 2021).

RESULTS

Soil R_h and Its Q_{10}. Within the first year postfire, soil R_h significantly decreased in organic horizons at both XC and SY (mean decrease of 40% at XC and 27% at SY; p < 0.05; Figure 1a). However, R_h exhibited significant increases in specific months for mineral horizons: the first and sixth months postfire at XC, and the sixth month postfire at SY (p < 0.05; Figure S3). Wildfire notably reduced MBC content at both sites for organic (−73% at XC and −57% at SY) and mineral horizons (−24% at XC and −41% at SY) (p < 0.05; Figure 1b), but there was no significant change of MBC in the first and sixth months postfire in XC mineral horizons (Figure S3).

To evaluate the impact of wildfire on C release per unit of active biomass, we standardized soil R_h using MBC, referred to as the microbial metabolic quotient (qCO_2). Wildfire substantially increased the qCO_2 of both organic (+99% at XC and +72% at SY) and mineral (+187% at XC and +93% at SY) horizons within the first year postfire (p < 0.05; Figure 1c). Additionally, wildfires significantly reduced the Q_{10} value in organic horizons from 1.88 to 1.65 at XC and from 1.95 to 1.68 at SY, and in mineral horizons from 1.77 to 1.60 at XC and from 1.80 to 1.66 at SY (p < 0.05; Figure 1d).

Substrate Properties. Within one year postfire, SOC (−16% at XC and −22% at SY) and DOC (−31% at XC and −62% at SY) contents significantly decreased in most samples, but increased in XC mineral horizons (SOC = +25%; DOC = +17%; p < 0.05; Figure 1e, f). Meanwhile, mineral-associated C content was enhanced in XC mineral horizons (+54%), together with an increase in Fe/Al-associated C (+69%) (p < 0.05; Figure 2a,c). According to the different forms of soil Fe/Al, wildfire significantly increased the contents of $Fe_p + Al_p$ (+84%) and $Fe_o + Al_o$ (+71%) in XC mineral horizons, but had no significant effect on the $Fe_d + Al_d$ content (Figure 2d−f). Additionally, Ca-associated C content significantly increased only in SY organic horizons in the sixth month postfire (Figures 2b and S4).

Recalcitrant C content significantly increased in XC mineral horizons in the one year postfire and in XC organic horizons in the first and third months postfire (p < 0.05; Figures 2g and S4). The E4/E6 ratio and Δlog K significantly decreased in XC organic horizons in the one year postfire, and the E4/E6 ratio in XC mineral horizons decreased in the sixth and 12th months postfire (p < 0.05; Figures 2h, S4). These results indicate a lower substrate quality postfire in XC organic horizons. However, substrate quality at SY exhibited pronounced temporal variations; it increased in the third month postfire and declined in the sixth month postfire (p < 0.05; Figure S4).

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Microbial Properties. Wildfires generally reduced the microbial α diversity (both bacteria and fungi) in the one year postfire at XC, but increased α diversity at SY ($p < 0.05$; Figure S5). For the bacterial community, wildfire significantly increased the rrn copy number in organic horizons at both sites, whereas there was no apparent change in mineral horizons ($p < 0.05$; Figure 3a). For the fungal community, wildfire decreased the relative abundance of ECM fungi and increased that of saprotrophic fungi ($p < 0.05$; Figure S5). However, this trend was reversed in the third month postfire in both soil horizons at SY. Similarly, wildfire reduced the ECM-to-saprotrophic fungi ratio in most samples, but enhanced this ratio in the third month postfire in both soil horizons at SY ($p < 0.05$; Figures 3b and S5). These results suggest that wildfire induces a shift in the life strategies of microbial communities (bacteria and fungi) from K-strategy to r-strategy. Additionally, wildfire significantly increased soil pH by 1.22 (XC-O), 1.07 (SY-O), and 0.60 (SY-A) units, particularly in organic horizons ($p < 0.05$; Figures 3c and S5).

Main Environmental Factors Regulating Q_{10}. Based on the heat map and linear regression analysis, we found that Q_{10} was regulated by complex factors, including significant positive correlations of substrate quantity and substrate quality with Q_{10}, whereas a significant negative correlation was found for soil pH, mineral protection and microbial r/K strategy with Q_{10} ($p < 0.05$; Figures 4a, S6, and S7). The random forest model indicated that DOC, pH and rrn copy number were the most important environmental factors affecting Q_{10}, explaining 16%, 13% and 12% of the variation, respectively (Figure 4b). The variance decomposition analysis further revealed that substrate (16%) and microbial (10%) characteristics had significant individual effects on Q_{10}, as well as a significant interactive effect (15%) (Figure 4c). Finally, the structural equation model demonstrated that the standardized total effect coefficient for substrate quantity (e.g., DOC) was the highest at 0.39, primarily through a direct effect on Q_{10} (Figure 4d, e). Soil pH had an indirect effect (−0.28) on Q_{10} while microbial characteristics had a significant direct effect (0.18) on Q_{10}.

■ DISCUSSION

To document postfire initial changes of forest ecosystems, we collected soil samples from four points-in-time within one year following stand-replacing wildfires (Figure S1). Given the limited number of sampling times, this study focuses on identifying stable phenomena rather than detailed temporal dynamics within the one year postfire period. If wildfire-induced changes of C efflux are consistently observed within one year, it suggests robust results and may have significant implications for forest C sequestration. Therefore, we used linear mixed-effect models with sampling time as a random factor and wildfire treatment as a fixed factor to parse the overall response of soil C efflux to wildfire during the initial recovery period (Figures 1−3).

Wildfire-Induced Soil C Efflux Buffered by Thermal Compensatory Response. An essential thesis of forest C sequestration is that the reduction in C efflux from postfire soil can offset a portion of combustion loss.[1,4,59,60] This aligns with our observed depletion in substrate quantity and microbial biomass in organic horizons following wildfire (Figures 1 and S3). However, wildfires also led to an increase in soil R_h and the C pool in mineral horizons, likely due to ash leaching and DOC migration from surface soils, as well as the mortality of fine roots and microbes.[5,61] Standardizing the R_h with MBC

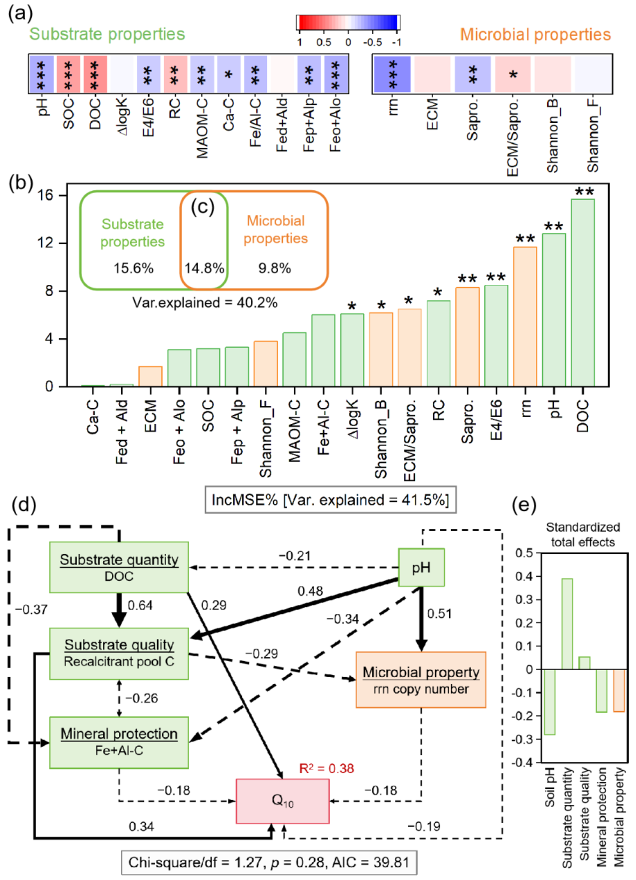

Figure 4. Effects of abiotic and biotic factors on Q_{10} related to overall soil properties. Standardized regression coefficients for Q_{10} (a), random forest model for Q_{10} (b), variation partitioning analysis for Q_{10} (c), and structural equation model (d) and their standardized total effects of five environmental factors (e) for Q_{10}. In (a), the color indicates the strength and sign of the relationship. In (b), IncMSE% indicates the increase of mean square error (%). In (c), numbers in the overlapping area of the two circles are the shared effects of the two factors, and values within each circle are the unique effects of the corresponding factor. In (d), black lines indicate the significant relationships at $p < 0.05$ level. Solid and dotted lines represent positive and negative relationships, respectively. Arrow width is proportional to the strength of the relationship. Numbers adjacent to arrows denote standardized path coefficients. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$. AIC, Akaike information criterion.

reveals that wildfires substantially enhanced the qCO_2 within the first year after wildfire (Figure 1c). This phenomenon is common in postfire soils[43] and is primarily attributed to more fast-growth taxa within the microbial community.[40] Wildfire can initially decimate most soil microorganisms (Figure 1b), thereby creating new ecological niches. These ecological niches were rapidly occupied by selected survivors with fast-growth traits, and these pioneers were especially active in the postfire environment with less competition, thereby increasing qCO_2.[39−41]

Given that soil R_h increases rapidly with temperature,[7] there is concern regarding whether the strong metabolic capacity (qCO_2) of postfire microorganisms could inhibit C sequestration under climate warming.[59,60] Namely, it raises questions about whether climate warming stimulates the C release capacity of individual microorganisms, thereby increasing the total C emissions after wildfire. A critical parameter determining the likelihood of this scenario is the temperature dependence of R_h.[27,28] We found that wildfire generally reduced the Q_{10} of soil R_h in both soil horizons within the first year after wildfire (Figure 1), which is consistent with previous studies.[14−17] This thermal compensatory response of soil R_h in postfire soils suggests that fire-induced C release is buffered by stable soil C pools, therein playing an important role during ecosystem recovery from wildfires even under climate warming.[1,4−6,62] We next explore the mechanisms driving this thermal compensatory response.

Dual Roles of Soil C Properties in Regulating Q_{10}. Wildfire prominently decreased soil C availability by modifying substrate quantity and mineral protection, thereby imposing changes in Q_{10} dynamics (Figures 1 and 2). Regarding substrate quantity, wildfire consumed a substantial amount of OM in surface soils at both sites, especially in organic horizons (SOC and DOC; Figure 1).[32,33] During the combustion process, a considerable amount of metal oxides was liberated from aboveground vegetation, litterfall, and SOM that subsequently entered the mineral horizon.[63] Wildfires notably enhanced the mineral-associated C content in XC mineral horizons but showed no significant change at SY (Figure 2). This difference can be attributed to the higher Fe/Al (hydr)oxide contents in XC resulting from greater soil chemical weathering associated with higher air temperatures and basalt parent material (Figure S2). The increase in Fe/Al-associated C was primarily driven by the $Fe_p + Al_p$ and $Fe_o + Al_o$ components (Figure 2).[62] These Fe/Al components form organic-mineral complexes and stable soil aggregates via adsorption (mainly including ligand-exchange and cation-bridging interactions), coprecipitation with soil organic C, and as a binding agent to promote physical protection of SOM in soil aggregates, all of which facilitate long-term C storage.[52,64,65] This may also explain why only the XC mineral horizon showed an increase in the soil C pool after wildfire (Figure 1). After the rainy season, the $Fe_o + Al_o$ and $Fe_p + Al_p$ in minerals horizons of XC (six months postfire) and SY (three months postfire) were partially leached and showed a decrease in their contents (Figures S4). This indicates that mineral protection may vary seasonally due to leaching dynamics. Overall, the depletion of C content and strong mineral protection by Fe/Al components reduced substrate availability after wildfire.

We conducted further investigations into the relationships between substrate availability and Q_{10} and found that Q_{10} displayed a significant positive correlation with SOC and DOC and a negative correlation with mineral-associated C content (Figure S6). This suggests that the decrease in substrate availability induced by wildfires inhibits Q_{10}. Several energy-consuming processes affect the relationship between microbial C demand and substrate C supply, including enzyme investment to acquire substrate, activation energy to initiate substrate decomposition, adenosine triphosphate (ATP) required for substrate intake, and cellular reduction equivalents involved in substrate assimilation.[29] The decline in postwildfire C availability exacerbates the imbalance between supply and demand, which could force microorganisms to reduce their activity and Q_{10}, and dedicate more resources to substrate acquisition.[20,21,29,66]

The Q_{10} is influenced not only by substrate availability but also by substrate quality, with these two factors potentially playing contrasting roles in different soil environments.[23] Hence, we investigated the response of substrate quality to wildfire and its regulation of Q_{10}. We found that SOC at XC displayed higher aromatization and recalcitrance in both soil horizons within the first year after wildfire, whereas SY SOC showed only minor changes (Figure 2). The increase in Q_{10} correlated with more recalcitrant components (Figure 4), consistent with the C quality-temperature (CQT) hypothesis.[22] The CQT hypothesis posits that recalcitrant C requires a higher activation energy to induce decomposition than labile C due to its more complex chemical structures and thermodynamically stable molecular configurations.[23,67−69] This implies that the CQT mechanism was more consistently observed at XC than at SY where the molecular composition of SOC in the burnt soils experienced less fluctuations in the first year following wildfire. Moreover, a recent study demonstrated that the CQT hypothesis plays a major role when the substrate is sufficient, otherwise, Q_{10} is primarily regulated by substrate availability.[23] Apparently, low substrate availability was responsible for the emergence of low Q_{10} in burnt soils at XC, while the low-quality C pool likely had a limited stimulating effect on Q_{10}, supporting DOC as the most important variable regulating Q_{10} (Figure 4).

We performed a confirmatory experiment by inoculating burnt and unburnt substrates with a uniform microbiome to isolate the relationship between substrate properties and Q_{10}. Incubation results demonstrated that burnt soils exhibited a lower Q_{10} compared to unburnt soils ($p < 0.10$; Figure 5a), thereby substantiating that wildfire-induced alterations in substrate properties contributed to the lower Q_{10}. The Q_{10} in SY soils was more susceptible to wildfire disturbance than XC soils, showing a consistent decrease in the first year after wildfire (Figure 5c). This can be explained by the pronounced decrease in substrate quantity (e.g., SOC and DOC) in postfire SY soils whereas the trade-off in fire-altered substrate quality was more important in XC soils (e.g., low quality and high quantity) (Figures 1 and 2). These result corroborates that substrate availability, particularly in substrate quantity, plays a more important role in shaping Q_{10} changes than that of substrate quality within the first year after wildfire.

Microbial Thermal Adaptation Dominated by r-Strategists. Environmental pressures from fire legacy effects determine which ruderal or fast-growing taxa may flourish, as dictated by their life strategies.[40] Wildfires drove a shift in microbial communities from K-strategy to r-strategy for both bacteria and fungi, as evidenced by the increased rrn copy number and decreased ECM-to-saprotrophic fungi ratio, respectively (Figure 3). Fast-growing microbes rapidly colonized ecological niches created by biological mortality and a postfire nutrient pulse, constituting a significant fraction of the overall community.[39−41] The proportion of r-/K-strategists in bacterial and fungal communities showed a positive relationship with Q_{10} across all samples (Figure S7). Additionally, we observed a recovery trend toward prefire levels for r-/K-strategists (rrn copy number) within the first year after wildfire, suggesting that microbial thermal adaptation might be lost at longer time scales (Figure S5).[70,71]

To further verify the relationship between intrinsic microbial traits and the apparent Q_{10} of respiration, we conducted an experiment by adding sufficient glucose (10 g C kg^{-1} soil) to eliminate substrate limitation. We found that wildfires generally diminished the Q_{10} under C-rich conditions only in organic horizons (XC from 2.54 to 2.19; SY from 2.96 to 2.48) (Figure 5). This phenomenon can be attributed to a change in survival strategies for the bacterial community in organic horizons after wildfire, based on the increase in bacterial r-/K-

https://doi.org/10.1021/acs.est.4c11833
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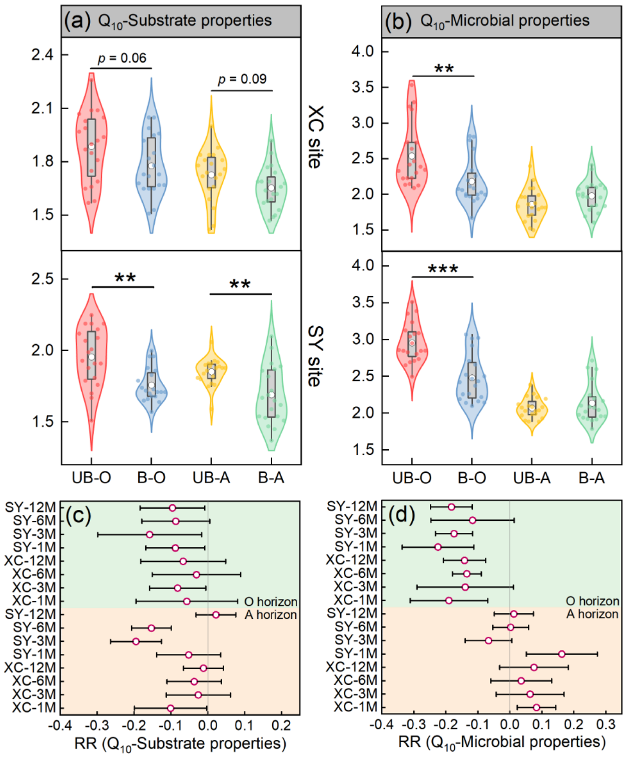

Figure 5. Comparison of temperature sensitivity (Q_{10}) between the unburnt (UB) and burnt (B) soils in organic (O) and mineral (A) horizons of two confirmatory experiments. Subpanels correspond to Q_{10} related to substrate properties (a, c) and microbial properties (b, d) utilizing uniform inoculation and glucose addition incubation, respectively. For figures a and b, the Q_{10} values at two forest sites within one year after undergoing a stand-replacing wildfire as an overall presentation including four points in time with five replicates (n = 20). Whiskers illustrate 5th and 95th percentiles, box ends represent the 25th and 75th quartiles (interquartile range), and white points represent the mean value. **, $p < 0.01$; ***, $p < 0.001$. For figures c and d, the response ratios (RR) for soil Q_{10} due to wildfire disturbance in O and A horizons in two forest sites at four points in time (1, 3, 6, and 12 months postfire). Error bars represent 95% confidence intervals (CIs). Significant responses ($p < 0.05$; n = 5) are recognized if the 95% CI does not overlap with zero.

strategists ($p < 0.001$; Figure 3) and the strong correlation with Q_{10} (rrn copy number, Figures 4 and S7). This finding was derived from a short-term incubation (12 h) with the addition of a simple C source (glucose). Although some studies suggest that a short-term incubation with glucose addition does not appreciably change the soil microbial community,[19,72] we recognize that such an approach inevitably amplifies the role of r-strategists over the longer term.[47] As such, this microcosm experiment was more inclined to confirm that the bacterial r-strategy populations drove microbial thermal adaptation.

The Role of Soil pH in Regulating Q_{10}. Soil pH is a master variable in soils that mediates a wide variety of soil biogeochemical processes/properties.[51,73] Following wildfire, soil pH significantly increased due to the presence of alkaline ash and pyrogenic charcoal particles ($p < 0.01$; Figure 3c).[33] According to structural equation modeling, soil pH had a direct effect on Q_{10} and exhibited complex interactions with other factors that indirectly affect Q_{10} (Figure 4). Soil pH was negatively correlated with substrate quantity and positively correlated with substrate quality. This reflects the fact that a substantial amount of OM was burned during wildfires, with some lost as CO_2 efflux and some transformed into alkaline and recalcitrant pyrogenic C or ash.[1,4] Soil pH also showed a significant negative correlation with mineral protection, attributed to the reduction in positive surface charge on Fe/Al (hydr)oxides as pH increases, which inhibits the adsorption of negatively charged SOM and facilitates its release from mineral surfaces.[74]

In the unburnt reference soils at both sites, soil pH was strongly acidic ranging from 3.6 to 5.5 (Figure 3). Microorganisms typically maintain intracellular pH and charge balance through a plasma membrane H-adenosine triphosphatase (H^+-ATPase) system, which expels protons by catalyzing ATP hydrolysis.[74] Genes expression for ATPase production consumes six times more ATP following a decrease in environmental pH compared to optimal pH levels.[75] The postwildfire increase in soil pH allowed microorganisms to allocate more energy and C sources toward growth (rrn copy number, $p < 0.001$) rather than compensating for an acidic environment,[76] thereby amplifying microbial thermal adaptation (Q_{10}, $p < 0.001$; Figure 4). This might explain why soil pH was negatively correlated with Q_{10} (R^2 = 0.078, $p < 0.001$; Figure S6a). Notably, soil pH explained the second most variability for Q_{10} after substrate availability (Figure 4), underscoring the critical role of soil pH in a cascade of abiotic−biotic interactions regulating Q_{10}.

Environmental Implications. The response of SOC stocks to climate warming remains one of the largest uncertainties in the global C cycle.[20,67,72] The initial stages (<1 year) of recovery from wildfires are susceptibly to potentially high soil C efflux from microbes (i.e., qCO_2); however, the thermal compensatory response will limit C losses under climate warming, thereby maintaining SOM stocks in forest soils experiencing periodic wildfires. We identified that the thermal compensatory effect was mainly associated with changes in two substrate properties (DOC and pH) and one microbial property (rrn copy number) (Figure 4). Although our analyses strongly confirmed the occurrence of multifactor regulation on Q_{10}, they explained only 38−42% of the variability in Q_{10}, thereby revealing a considerable level of uncertainty. Therefore, future studies must consider more factors and their interactions to ensure accurate and robust predictive models for Q_{10} regulation. These additional factors include soil aggregate dynamics, microbial C decomposition functions, clay mineral composition, climatic parameters, and salinity/heavy metal stress.[7] Moreover, this multifactorial regulation of Q_{10} exhibits dynamic temporal changes (Figures S3−S5). Hence, future work should employ a higher temporal resolution and a longer time scale to better understand the temporal dynamics following wildfire (i.e., seasonal and vegetation recovery dynamics). This study is the first to comprehensively reveal the multiple interacting mechanisms by which wildfires alter the temperature dependence of SOM decomposition. The results from this study can improve the accuracy of global CCF models in predicting future global climate change scenarios and inform postfire forest management activities to enhance forest ecosystem recovery.

■ ASSOCIATED CONTENT

Data Availability Statement

All sequences have been deposited in the NCBI Sequence Read Archive (SRA) database (accession numbers PRJNA1158506 and PRJNA1158531). Other data that support the findings of this study are provided in Supporting Information.

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acs.est.4c11833.

Measurement of forest biomass C loss from wildfire, soil C efflux and respiration quotient, Q_{10} related to substrate properties, Q_{10} related to microbial properties, substrate quality, mineral-protected organic matter, and microbial properties (Supplementary Methods); description of study site and experiments (Table S1, Figure S1); mean monthly temperature and precipitation during soil sampling (Figure S2); response ratios for soil C efflux, substrate properties, microbial properties, and soil pH to wildfire (Figures S3–S5); relationships between Q_{10}, substrate properties, and microbial properties (Figures S6 and S7) (PDF)

Basic data (XLSX)

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Author Contributions

J.X. acquired funding, developed the original idea, and designed the study. H.S. conducted laboratory experiments, statistical analyses, and wrote the first draft. H.S., Y.H., and S.Z. collected soil samples. J.L. performed microbial statistical analyses. J.X., Y.Z., Z.D., Y.L., and R.A.D. edited the paper and contributed to the discussion.

Notes

The authors declare no competing financial interest.

ACKNOWLEDGMENTS

This study was supported by the Science and Technology Program of Zhejiang Province (2022C02046), the National Natural Science Foundation of China (41721001) and the 111 Project (B17039).

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https://doi.org/10.1021/acs.est.4c11833
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