

Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity

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Fire frequency is changing globally and is projected to affect the global carbon cycle and climate^{1–3}. However, uncertainty about how ecosystems respond to decadal changes in fire frequency makes it difficult to predict the effects of altered fire regimes on the carbon cycle; for instance, we do not fully understand the long-term effects of fire on soil carbon and nutrient storage, or whether fire-driven nutrient losses limit plant productivity^{4,5}. Here we analyse data from 48 sites in savanna grasslands, broadleaf forests and needleleaf forests spanning up to 65 years, during which time the frequency of fires was altered at each site. We find that frequently burned plots experienced a decline in surface soil carbon and nitrogen that was non-saturating through time, having 36 per cent (± 13 per cent) less carbon and 38 per cent (± 16 per cent) less nitrogen after 64 years than plots that were protected from fire. Fire-driven carbon and nitrogen losses were substantial in savanna grasslands and broadleaf forests, but not in temperate and boreal needleleaf forests. We also observe comparable soil carbon and nitrogen losses in an independent field dataset and in dynamic model simulations of global vegetation. The model study predicts that the long-term losses of soil nitrogen that result from more frequent burning may in turn decrease the carbon that is sequestered by net primary productivity by about 20 per cent of the total carbon that is emitted from burning biomass over the same period. Furthermore, we estimate that the effects of changes in fire frequency on ecosystem carbon storage may be 30 per cent too low if they do not include multidecadal changes in soil carbon, especially in drier savanna grasslands. Future changes in fire frequency may shift ecosystem carbon storage by changing soil carbon pools and nitrogen limitations on plant growth, altering the carbon sink capacity of frequently burning savanna grasslands and broadleaf forests.

Fire regimes have been altered by changes in climate and land use, and are predicted to change further as temperatures rise and populations grow^{1–3}. In consequence, the response of ecosystems to long-term alterations in fire frequency—that is, either more frequent burning or fire suppression—will be essential to the future of the terrestrial carbon sink^{3,6}. Although carbon fluxes to the atmosphere from combusting plant biomass have been well characterized⁷, uncertainties remain concerning the responses of soil carbon and nutrient pools^{4,5}, which also regulate plant primary productivity⁸.

On the one hand, increased burning may decrease soil organic matter, as repeated burning reduces organic inputs to soils and leads to declines in soil carbon (C) and nutrients^{9–11}. On the other hand, increased burning may enrich C and nutrient concentrations in soils by promoting the establishment of more-productive plant species¹² and the leaching of ash downwards into soils¹³. Observations generally

illustrate that single fires deplete pools of C and nutrients in the surface litter layer and, in some cases, in shallow organic horizons^{14,15}. Critically, however, studies that document changes in soils over short timescales or in response to a single fire (see, for example, refs 13, 14) offer limited insight into long-term changes in the larger mineral soil pools as a result of shifting fire regimes, particularly in soils below the top few centimetres; such soils are generally not subject to direct consumption¹⁶ and are influenced more by fire-induced changes in plant inputs and microbial activity^{10,17}. Thus generalized long-term effects of changes in fire frequencies on soil C and nitrogen, and on their controlling mechanisms, remain unclear, with contrasting results observed in studies of different regions or ecosystems^{10,11,17}.

A lack of consensus on the long-term response of soils to fire limits our ability to predict how vegetation productivity may change as fire alters soil nutrient availability. Over the short-term, single fires can stimulate plant productivity¹⁸; however, over the longer-term, potential declines in soil nutrients with increased fire frequency^{9–11} have been hypothesized to suppress productivity, although long-term evidence for this effect is limited¹¹. These interactions may determine whether fire reduces ecosystem C storage by depleting soil C and nutrients, which may reduce plant growth and turnover, further constraining C storage in the ecosystem (Supplementary Fig. 1).

Here, we evaluate these interactions by examining how long-term differences in fire frequency alter soil C and nutrients and accompanying shifts in plant productivity, using three approaches. First, we use a meta-analysis of data from 48 sites worldwide (Fig. 1a) to test how frequent burning alters soil C and nutrients over time spans as long as 65 years. We then evaluate our results using an independent dataset from 16 additional field sites, which were not replicated at the site scale (and thus were not included in the meta-analysis), but collectively are valuable given the high number of sites and standardized data collection. Finally, we use our results to validate an individual-based dynamic global vegetation model (the DGVM LPJ-GUESS-BLAZE) for quantifying the effect of fire-driven nutrient losses on vegetation productivity and the degree to which soils contribute to ecosystem-level changes in C.

The sites included in the meta-analysis compared the effects of changes in long-term fire frequencies on C and nutrients in the upper soil layer (0–20 cm depth); the average treatment length was 30 years and ranged from 9–65 years. Sites generally contained plots that either experienced elevated fire frequency (4.3 ± 0.6 times more than the estimated historical mean for that ecosystem, calculated over the length of the study) or were protected from fire (complete fire exclusion in all but one case), which we refer to hereafter as ‘elevated’ and ‘protected’ treatments, respectively (see Supplementary Information). Sites covered

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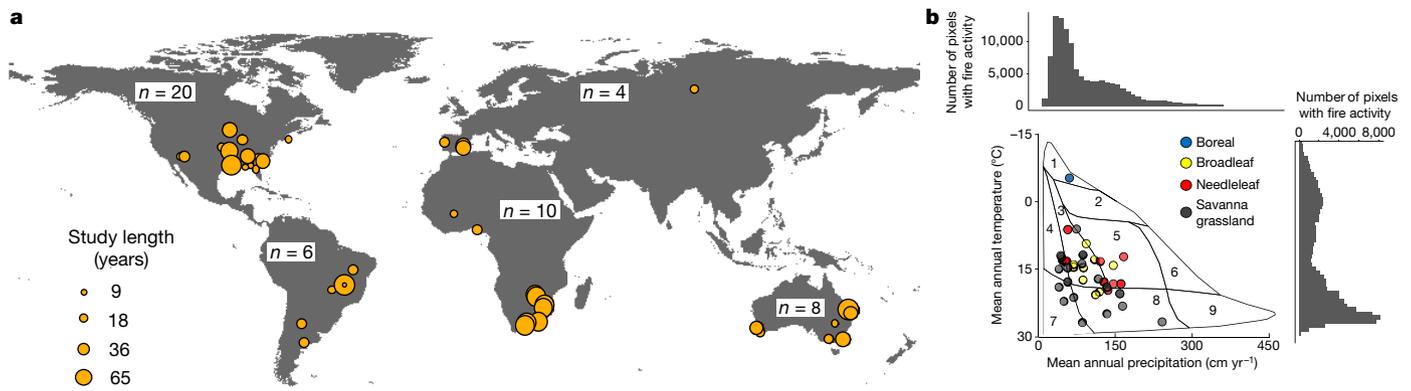


Figure 1 | Distribution of study sites. **a**, Geographical distribution of sites ($n = 48$), with dot size representing study duration. **b**, Climatic distribution of sites. Bottom left, vegetation types are indicated by different colours plotted over a modified diagram of Whittaker's biomes³⁰ (1, tundra; 2, boreal forest; 3, woodland/shrubland; 4, temperate grassland/desert; 5, temperate forest; 6, temperate rainforest; 7, subtropical desert;

8, tropical forest and savanna; 9, tropical rainforest). Dots are slightly transparent to allow overlap to be visualized. The histograms above and to the right illustrate the frequency distribution of global fire activity for a given climatic condition. Fire activity was determined using gridded maps of mean fire occurrence taken from the global fire emissions database 4 with small fires (GFED4s)⁷.

a broad range of mean annual temperature (-5 – 27 °C) and precipitation (410 – $2,410$ mm yr⁻¹) (Fig. 1b and Supplementary Fig. 2). To evaluate whether fire effects depended on plant communities, we categorized sites on the basis of the dominant plant functional type into savanna grasslands, broadleaf forests and needleleaf forests. Statistical significance was evaluated using mixed-effects models of the logarithmic response ratio (natural logarithm of the quotient between elemental concentration in elevated and protected plots), weighted by site replication and variance¹⁹ (Supplementary Fig. 3).

We found that elevated fire frequencies substantially decreased total soil C and nitrogen (N) concentrations globally, with the largest effects observed in broadleaf forests and savanna grasslands. Averaged across all sites, vegetation types, and treatment lengths, higher fire frequencies reduced the concentrations of total soil C and N concentrations by

12.1% (confidence interval $\pm 10.2\%$; $P = 0.02$) and 10.4% ($\pm 10.0\%$; $P = 0.04$), respectively, compared with plots protected from fire (Fig. 2a, b and Supplementary Table 1; 30-year mean treatment length). Within vegetation types, fires had strong depletion effects on soils in both broadleaf forests (27% less C and 25% less N in elevated versus protected plots; $P < 0.001$ and $P = 0.02$, respectively) and savanna grasslands (21% less C and N in elevated versus protected plots; $P < 0.001$ for each; Fig. 2a, b and Supplementary Table 1). By contrast, soil C and N in needleleaf forests increased by 26% and 21%, respectively, in elevated compared with protected plots ($P < 0.001$ for each; Fig. 2a, b and Supplementary Table 1). The different responses that we observed in needleleaf forests were unlikely to be caused by climatic variables or study design, given that, in our dataset, there were no differences between sites in temperate needleleaf forests and those in savanna

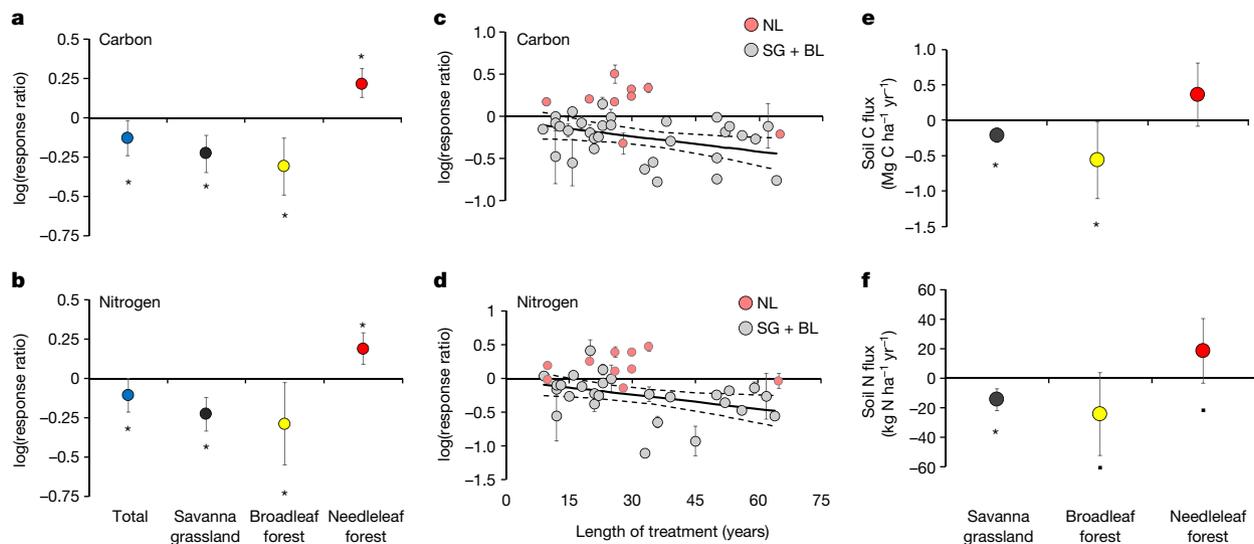


Figure 2 | Effects of fire on soil carbon and nitrogen across ecosystems and over time. **a**, **b**, Logarithmic response ratios of the concentrations of C (a, $n = 41$) and N (b, $n = 38$) for the total dataset compiled and partitioned into different vegetation types (see Supplementary Tables 1 and 2 for statistics). The response ratio is defined as the concentration of C or N in elevated plots divided by the concentration in protected plots. **c**, **d**, Regressions between the response ratios of C (c, $n = 31$) or N (d, $n = 27$) and the length of time during which plots experienced contrasting fire frequencies, fitted for savanna grasslands (SG) plus

broadleaf forests (BL) using a meta-regression. Pink dots represent data from needleleaf forests (NL), which were not used in the regression. **e**, **f**, Total fluxes of C (e) and N (f), determined as the absolute rate of change in soil C or N between the fire frequency treatments (negative values indicate losses under frequent burning). Dashed lines represent 95% confidence intervals (for c, d) and error bars represent either 95% confidence intervals (for a, b, e, f) or the variance around the logarithmic response ratio (for c, d; see ref. 19), with asterisks indicating significance at $P < 0.05$ and dots at $P < 0.10$ (Supplementary Tables 4 and 5).

grasslands and broadleaf forests in climatic conditions, sampling depths, or fire frequency in elevated plots (Supplementary Tables 2 and 3). The effect of fire in boreal needleleaf forests, which differ substantially in climate compared with the other vegetation types (Fig. 1b), was similar to its effect in temperate needleleaf forests (see Supplementary Information). N stocks in mineral soils tended to increase with more frequent burning ($r^2 = 0.24$, $P = 0.058$), whereas C stocks displayed no trend (Supplementary Fig. 4).

In savanna grasslands and broadleaf forests, the severity of fire-driven losses of soil C and N increased significantly with the length of time for which plots experienced altered fire frequencies. Soils in elevated plots were estimated to have 36% and 38% less C ($P = 0.026$) and N ($P = 0.022$), respectively, than those in protected plots after 64 years (the maximum duration in savanna grassland and broadleaf forest sites; Fig. 2c, d and Supplementary Table 4). Furthermore, for both C and N, the difference between elevated and protected plots differed significantly ($P < 0.05$) only after 18 years of contrasting fire frequencies, highlighting that effects emerge over decadal timescales. By contrast, the responses in needleleaf forests were unchanged with increasing duration of fire treatment ($P > 0.5$ for C and N; Fig. 2c, d).

To further evaluate the generality of our global meta-analysis, we analysed an independent dataset from a network of 16 additional field experiments across the southeastern United States (see Supplementary Information). Of those sites that experienced different fire frequencies for a duration sufficient to detect a potential effect, 83% showed declines in C and 67% showed declines in N with frequent burning; elevated sites had on average 13% and 11% lower C and N, respectively, than did protected plots (Supplementary Fig. 5). Considering the shorter average length of time that these plots experienced different fire frequencies (22 years), the mean responses are consistent with results from the global meta-analysis regression between C and N losses and study length ($17\% \pm 10\%$ for C and N; Supplementary Fig. 5).

To determine changes in total stocks of C and N in response to fire alterations, we combined elemental concentrations with soil bulk densities to a standardized depth of 10 cm, and normalized stock changes to an annual rate from the meta-analysis. The subset of studies that did not provide bulk density data required values to be extrapolated on the basis of soil texture or by using the mean value (see Supplementary Information). Plots exposed to elevated fire frequencies experienced large average losses of soil C and N stocks relative to protected plots in savanna grasslands ($-0.21 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and $-14.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$; $P < 0.001$ for both) and broadleaf forests ($-0.57 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and $-24.3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$; $P < 0.05$ and $P < 0.1$, respectively) (Fig. 2e, f and Supplementary Table 5). By contrast, there was no change in soil C stocks, and a marginally significant enrichment of soil N, in needleleaf forests in elevated plots ($+18.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$; $P < 0.1$) (Fig. 2e, f and Supplementary Table 5).

We found little evidence that increased fire frequencies depleted other elements besides C and N. Averaged across all sites, surface mineral soils in elevated plots showed no change in concentrations of phosphorus (P) relative to protected plots (Fig. 3a and Supplementary Table 6), but they were enriched in calcium ($+52\%$; $P < 0.0001$) and potassium ($+13\%$; $P = 0.02$) (Supplementary Table 6). The duration of fire frequency alterations influenced the direction and significance of results only for soil P. Concentrations of P were initially enriched in the elevated plots after a decade of burning ($+51\%$; $P = 0.01$), but this effect disappeared after about 30 years of frequency alterations (Fig. 3b and Supplementary Table 7). Longer-term studies are needed to determine whether exposure to fire will deplete soil P because of enhanced erosion; however, of the five sites in our analysis that experienced more than 50 years of altered fire frequencies, only one was depleted in P. The lack of P, potassium and calcium losses following long-term changes in fire frequency is consistent with the hypothesis that their higher oxidation temperatures and/or soil sorption capacities decrease losses during frequent burning compared with C and N²⁰.

Changes in fire frequency can also alter plant-available nutrients. Across the global dataset, elevated-frequency plots had 25% lower concentrations of inorganic N (the main form of N available to plants) relative to protected plots ($P < 0.0001$), with a positive correlation found between total N and inorganic N response ratios (Supplementary Fig. 6). By contrast, there was no significant effect of fire frequency on concentrations of inorganic P (the main form of P available to plants). The responses of inorganic P and total P were positively correlated (Supplementary Fig. 7). Our data clearly show that the observed significant increases in inorganic N immediately following fires (see, for example, ref. 14) are transient, and often reverse with repeated burning.

Given the importance of soil N for sustained productivity, we next evaluated the degree to which N losses might constrain plant net primary productivity (NPP), potentially restricting C uptake. To do so, we simulated the effect of fire on ecosystem C and N by using the DGVM LPJ-GUESS²¹ with the process-based fire module BLAZE (see Supplementary Information). For each study site, we simulated ecosystem dynamics for the period 1950–2013, using fire frequencies, climate, and N deposition specific to each site, as well as changes in global CO₂ concentrations (see Supplementary Information).

Like our empirical data, the model showed losses (albeit smaller ones) of total soil C and N in response to frequent burning in both broadleaf forests and savanna grasslands (Supplementary Figs 8 and 9). However, the model also simulated net losses of soil C and N from needleleaf sites, unlike the empirical data (Supplementary Fig. 10), illustrating the need for further model development and additional data. In broadleaf forests and savanna grasslands, simulated declines in total soil C were equivalent to 12% of the cumulative annual C fluxes by combustion of plant biomass and 30% of the decrease in the total plant biomass C in a plot. Comparing paired simulations at each site, either including or excluding N losses, illustrated that fire-driven N losses reduced cumulative NPP by about 5% over the entire 63-year period of the simulation on average across sites (Supplementary Fig. 8). The changes in NPP were of substantial magnitude relative to other C fluxes, with the total reduction in C drawdown from NPP being equivalent to 20% of the total annual C emissions from combustion of plant biomass summed over the simulation period, averaged across sites.

We next assessed the potential generality of fire-induced soil C and N losses changing ecosystem C storage and productivity by performing simulations across savanna grasslands globally; these ecosystems represent about 70% of actual global burned area⁷ (see Supplementary Information). When all locations were burned at a biennial frequency, declines in soil C stocks were equivalent to 40% of the changes in

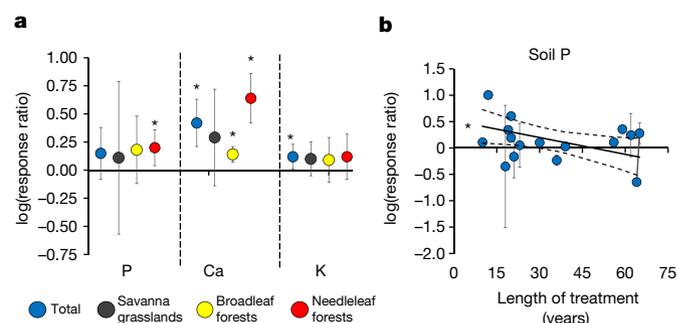


Figure 3 | Responses of P, Ca and K to changes in fire frequency. **a**, Logarithmic response ratios of the concentrations of P ($n = 16$), Ca ($n = 16$) and K ($n = 18$) for the total dataset compiled and partitioned into different ecosystem categories. The response ratio is defined as the concentration of P, Ca or K in elevated plots divided by the concentration in protected plots. **b**, Change in the logarithmic response ratio of soil P as a function of the length of time during which plots experienced contrasting fire frequencies. Error bars in **a** indicate the 95% confidence intervals and those in **b** indicate the variance around the response ratio and dashed lines in **b** are 95% confidence intervals, with an asterisk indicating significant effects ($P < 0.05$). See Supplementary Tables 6 and 7 for statistics.

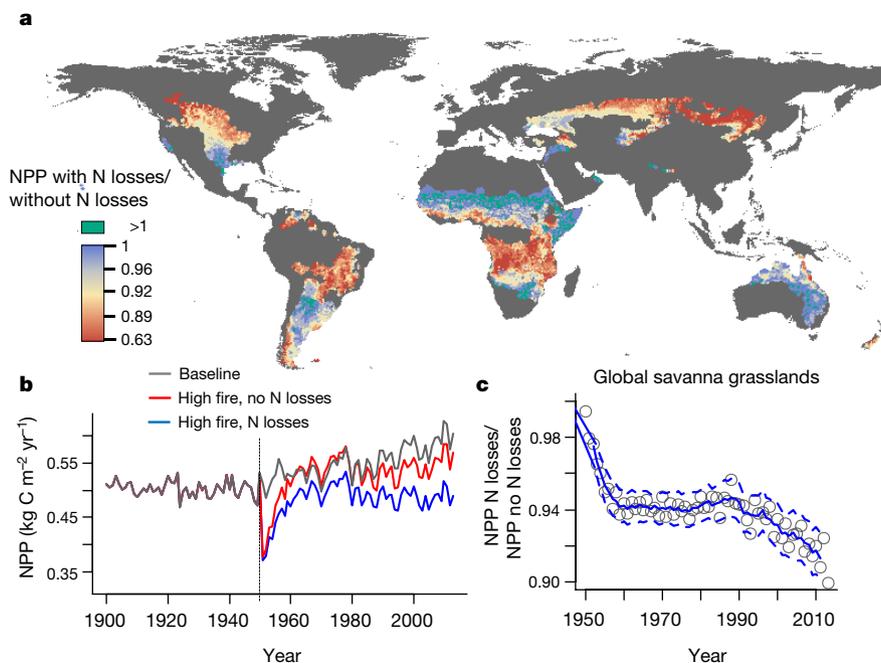


Figure 4 | Effect of N losses on net primary productivity (NPP) across savanna grasslands globally. Simulations were run by initiating a high fire frequency in 1950 (with grid cells burned every two years) and tracking NPP until 2013 with and without N losses. **a**, Relative ratio of cumulative NPP between the two scenarios, with the colour bar scaled by quantiles (values are minimum (0.63), first, second and third quantiles (0.89, 0.92 and 0.96), and maximum (1)). Green cells illustrate areas where N losses stimulated NPP (where the ratio is greater than 1). **b**, Mean NPP simulated across savanna grasslands, weighted by the area of a grid cell. The sharp reduction in NPP in 1950 (grey vertical line) is caused by the initiation of

plant biomass C stocks, on average, with the relative contribution of declines in soil C being greatest in driest locations (Supplementary Fig. 11; $r^2 = 0.45$). Furthermore, N losses resulted in widespread declines in NPP (Fig. 4a), with the largest effect on NPP seen in wet tropical regions, probably because of higher potential productivity and N demand. The effect of N losses on NPP increased through time (Fig. 4b, c), amounting to a 9% reduction of NPP in savanna grasslands globally when summed over the entire simulation period and area. Consequently, omitting the multidecadal changes in soil pools that result from shifting fire frequencies may substantially underestimate ecosystem C losses.

Our results reveal several factors that regulate how fire affects C and N in soils, and shed light on potential responses under future fire regimes. First, the effect of fire on both C and N strengthened through time and emerged only over multiple decades. The lack of a saturating response was surprising, and suggests that shifts in fire frequency during the twenty-first century³ may alter soil C and N over an extensive land area. Considering changes in soil C over longer time periods—especially through the formation of pyrogenic C, which can influence long-term C storage and nutrient dynamics^{22,23}—will provide additional insight into the stability of C in the soils and when effects may saturate.

Second, whether fire changed soil C and N and by how much depended on vegetation type across our analysis. The enrichment of N in needleleaf forest soils could be attributable to a number of processes, such as colonization by N-fixing plant species²⁴ or redistribution of mobilized N during the smouldering of the thick forest floor that is characteristic of needleleaf forests²⁵. Whether our results from needleleaf forests that primarily received frequent, low-intensity prescribed fires are representative of colder needleleaf forests that experience less frequent, but more intense, wildfires requires further evaluation, especially for boreal forests. Although we found qualitatively similar responses

the prescribed higher fire frequency scenarios, where N is lost by fire (blue line) or not lost by fire (red line). The grey line shows the evolution of NPP as predicted internally in the dynamic global vegetation model LPJ-GUESS with fires determined via BLAZE operating dynamically (for example, as for the period before 1950). **c**, Model simulations of the ratio between NPP with N losses versus without N losses through time, averaged across savanna grasslands globally (each circle is a global average within a year); the solid line represents a five-year rolling average and the dashed lines represent the standard errors across grid cells.

of boreal and temperate needleleaf forests, more boreal studies in particular are needed to test the generality in the response and application over longer fire-return intervals and for severe crown fires that can consume the soil organic layer²⁶. Studies of gradients in long-term fire frequencies are lacking at present and do not always examine changes in mineral soils (see, for example, ref. 26).

Further consideration is also needed for relatively wet ecosystems, such as some tropical rainforests, that are now experiencing more frequent burning because of human activities and drying climates²⁷. More frequent slash-and-burn cycles, for example, have been shown to deplete soil C, N and P²⁸ in tropical rainforests. Our observation that the initial P enrichment fades through time may be a critical component in determining the response of P-limited tropical rainforests²⁹ to changes in fire frequency.

Projecting the effect of changes in fire frequency on ecosystem C storage also needs better understanding of historical fire regimes. We compared historical fire frequencies to our elevated and protected fire treatments by using data from a subset of the locations included in the meta-analysis ($n = 25$) that had intermediate fire frequencies to approximate historical natural burning (see Supplementary Information). Compared with these intermediate fire frequencies, more frequent burning significantly decreased C and N concentrations (-13% C and N, $P = 0.007$ and $P < 0.001$, respectively), whereas less frequent burning significantly increased C and N concentrations ($+19\%$ C and $+18\%$ N, $P = 0.0005$ and $P < 0.0001$, respectively) in savanna grasslands (Supplementary Table 8 and Supplementary Fig. 12). Analyses of broadleaf forest sites had less statistical power, but suggested that differences occurred primarily because of greater losses in elevated-frequency relative to historical-frequency plots. In needleleaf forests, fire tended to enrich N in historical-frequency versus protected plots, but elevated versus historical-frequency plots were comparable. Consequently, the significant changes we observed when

comparing elevated-frequency versus protected plots are attributable both to C and N accumulation during fire protection, and to C and N loss during increased burning.

In conclusion, our results reveal the sensitivity of surface soils to fire and the substantial effects that changes in soil pools have on long-term ecosystem C exchange. The large empirical and conservative model-based estimates of soil C changes suggest that present estimates of fire-driven C losses⁷, which primarily consider losses from plant biomass pools, may substantially underestimate the effects of long-term trends in fire frequencies in savanna grasslands and broadleaf forests in particular. Our findings suggest that future alterations in fire regimes in savanna grasslands and broadleaf forests may shift ecosystem C storage by changing soil C levels and changing the N limitation of plant growth, altering the carbon-sink capacity of these fire-prone ecosystems.

Data Availability The datasets generated and analysed during this study are available from the corresponding author on request and in the corresponding papers cited in Supplementary Information.

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Supplementary Information is available in the online version of the paper.

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