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% ± 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 Mg C ha^{-1} yr^{-1} and -14.5 kg N ha^{-1} yr^{-1}; $P < 0.001$ for both) and broadleaf forests (-0.57 Mg C ha^{-1} yr^{-1} and -24.3 kg N ha^{-1} 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 ($+18.4$ kg N ha^{-1} 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 N[20].

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-GUESS[21] 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 CO_2 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 area[7] (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

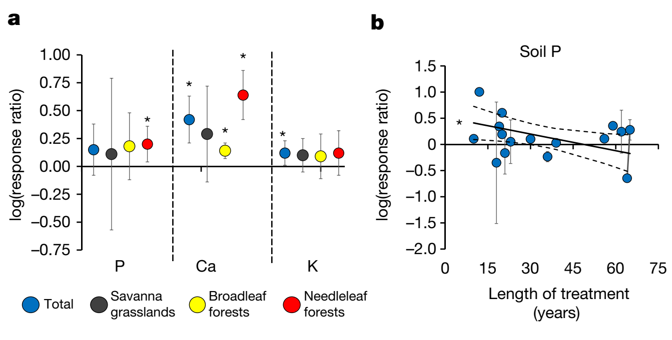

Figure 3 | Responses of P, Ca and K to changes in fire frequency. **a**, Logarithmic response ratios of the concentrations of P ($n = 16$), Ca ($n = 16$) and K ($n = 18$) for the total dataset compiled and partitioned into different ecosystem categories. The response ratio is defined as the concentration 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.