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

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.

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 century[3] 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 species[24] or redistribution of mobilized N during the smouldering of the thick forest floor that is characteristic of needleleaf forests[25]. 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

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 layer[26]. 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 climates[27]. More frequent slash-and-burn cycles, for example, have been shown to deplete soil C, N and P[28] 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 rainforests[29] 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