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Soil carbon in tropical savannas mostly derived from grasses

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Tropical savannas have been increasingly targeted for carbon sequestration by afforestation, assuming large gains in soil organic carbon (SOC) with increasing tree cover. Because savanna SOC is also derived from grasses, this assumption may not reflect real changes in SOC under afforestation. However, the exact contribution of grasses to SOC and the changes in SOC with increasing tree cover remain poorly understood. Here we combine a case study from Kruger National Park, South Africa, with data synthesized from tropical savannas globally to show that grass-derived carbon constitutes more than half of total SOC to a soil depth of 1 m, even in soils directly under trees. The largest SOC concentrations were associated with the largest grass contributions (>70% of total SOC). Across the tropics, SOC concentration was not explained by tree cover. Both SOC gain and loss were observed following increasing tree cover, and on average SOC storage within a 1-m profile only increased by 6% (s.e. = 4%, n = 44). These results underscore the substantial contribution of grasses to SOC and the considerable uncertainty in SOC responses to increasing tree cover across tropical savannas.

Tropical and subtropical savannas are increasingly being targeted as areas where carbon storage can be promoted by increasing tree cover[1,2]. Tree-for-carbon projections assume that increasing tree cover universally enhances the carbon stored, both in woody biomass and in soils[1,3]. The first assumption is uncontroversial, at least above ground: increasing tree cover, for example, from an increase in density, cover or biomass of woody plants (a.k.a. woody encroachment) can substantially increase the carbon stored in above-ground biomass[4,5]. However, this response is not necessarily mirrored by below-ground biomass[6]. Tree-for-carbon projections also make the widespread assumption that afforestation of savannas will lead to increased soil organic carbon (SOC) storage in proportion with the increasing tree cover[1,7]. However, the formation and persistence of SOC involve an interplay of biological, chemical and physical processes[8]. Therefore, the evidence is mixed: some studies have shown increases in SOC storage[4,9], whereas others have demonstrated no overall effects on[10] or even declines[11] in SOC storage following woody encroachment.

Several factors suggest that this variation in SOC with increasing tree cover could be real. First, changes in grass productivity with increasing tree cover[11] may depend on site characteristics (for example,

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rainfall and soil texture), which together influence organic matter inputs, decomposition and therefore carbon accumulation in soils[11–13]. Grasses in tropical savannas are often highly productive[14], with substantial carbon allocation to roots, which contribute to SOC formation and pool size[15,16]. In arid and semiarid savannas (<700 mm in rainfall), trees may facilitate grass productivity[16,17], enhancing the overall productivity of the system and carbon allocation below ground[11,16], whereas in mesic savannas (>700 mm in rainfall), grass productivity instead decreases with increasing tree cover[17–19]. If decreases in grass-derived carbon inputs into soils are substantial enough to offset increases in tree-derived carbon inputs, then SOC might experience a net decrease with increasing tree cover[11], although this also depends on the decomposition of different carbon sources[20].

Second, how changes in carbon inputs affect total SOC depends on the size of those changes and soil properties[21]. The protection of soil organic matter (SOM) from microbial decomposition is associated with the physicochemical binding between SOM and soil minerals (including primary organo–mineral complexes)[22,23]. Clay soils generally afford more protection[21] and therefore have higher carbon storage capacity than sandy soils, increasing both the amount of carbon that can accumulate in soils at their long-term equilibrium and the rate at which carbon accumulates on shorter timescales. Testing this hypothesis is complicated by soil influences on vegetation dynamics. For example, sandy soils also promote faster water infiltration, facilitating woody encroachment in savannas[24,25].

Despite expectations that grass contributions to SOC may be substantial and vary across environments, our current understanding of the contribution of grass-derived carbon to SOC and how this contribution changes with increasing tree cover comes mostly from small-scale and site-based studies[16,26,27], resulting in substantial uncertainties and constraining generalization across tropical savannas. Disentangling these uncertainties requires a regional or global perspective, either via large-scale sampling or via data synthesis across broad geographical and environmental gradients.

Most grasses across the tropics employ C_4 photosynthesis, whereas trees (and forbs) in those same regions use C_3 photosynthesis. Plants with C_3 versus C_4 photosynthetic pathways have unique stable carbon isotope ratios that are largely preserved in soils[28], allowing the proportional contribution of each functional group to SOC to be estimated using a simple mixing model[20] (Methods). In this Article we use soil $\delta^{13}C$ analysis to differentiate C_4 grass-derived carbon from C_3 tree-derived carbon. First, we evaluated factors driving total SOC concentration (g C kg^{-1}) and grass-derived carbon (in units of %, where grass-derived carbon + tree-derived carbon = 100%) in surface soils (0–20 cm) at a regional scale in a semiarid savanna (mean annual rainfall of ~460–700 mm) in Kruger National Park (hereafter, Kruger), South Africa (Fig. 1), which spans broad gradients in grass biomass, tree cover and soil sand content[29]. Second, we compiled a dataset of 148 soil profiles with both $\delta^{13}C$ and SOC measurements to a depth of 1 m across tropical and subtropical savannas (Fig. 1), allowing us to quantify the contribution of grass-derived carbon to SOC across broader gradients in rainfall (180–2,500 mm) and tree cover across different savanna regions. Finally, we compiled a dataset of changes in SOC storage (Mg C ha^{-1}) within the 1-m soil profile following woody encroachment into tropical savannas and grasslands (Fig. 1), allowing us to quantify the SOC response to increasing tree cover and its variation with rainfall and soil texture.

Variation in SOC and grass-derived carbon

Across Kruger, on average, grass-derived carbon comprised 76% (s.e. = 1.6%, n = 98) of the total SOC within the 0–20-cm soil layer (Fig. 2a). Across tropical savannas, more than half of the total SOC within the 1-m soil profile was grass-derived (57.7%, s.e. = 2.4%, n = 148), even directly under trees or woody patches (51.4%, s.e. = 4.1%, n = 33) (Fig. 2d,e). Our data suggest that grasses contribute substantially to the SOC pool across tropical savannas. Both regionally from Kruger and more broadly from tropical savannas, we found that, when grass contributions were >70% of the total SOC, SOC concentration increased substantially with increasing grass-derived carbon (Fig. 2b,f). This pattern aligns with results from Kruger savannas (Table 1 and Extended Data Fig. 1) showing that SOC concentration increased with increasing grass biomass but decreased with increasing soil sand content. Grasses are generally able to compete better than trees for limited water and nutrient resources on more clayey soils[25], which also have a higher capacity to preserve SOC compared to sandy soils[21]. However, the lack of global grass biomass data and the poor performance of soil sand content predictions (Extended Data Fig. 2) prevented a similar analysis for soil profiles across tropical savannas. Nevertheless, our results suggest that savanna soils with exceptionally high grass-derived carbon may maintain higher SOC[26].

Interestingly, our tree-related parameters, including tree cover, stem density and basal area, had no explanatory power for SOC concentration or grass-derived soil carbon across Kruger (Table 1 and Fig. 2c). The major reason for this may be the relatively small contribution of tree-derived carbon (24.0 ± 1.6%, n = 98) in this system, which may be insufficient to override the influence of grass biomass and soil texture on SOC concentration (Table 1 and Extended Data Fig. 1). Surprisingly, more broadly across tropical savannas with tree cover ranging from open to closed-canopy, tree cover did not explain SOC concentration (Table 1, Fig. 2g and Extended Data Fig. 3), although we found a large variation in both SOC concentration and grass-derived SOC across the entire gradient of tree cover (Fig. 2g). However, we qualify this finding by noting that satellite-based remote-sensing-derived tree cover has a low accuracy for classifying heterogeneous vegetation structure such as savannas[30], which may obscure the observation of any underlying relationship.

Geographically, savannas in South America had the lowest grass-derived SOC within the 1-m soil profile compared with other continents (Table 1 and Extended Data Fig. 3). One possibility is that grasses in cerrado are less productive than their African and Australian counterparts due to nutrient-poor soils[31]. C_3 forbs may also make larger contributions to cerrado herbaceous productivity than in African or Australian savannas[32]. Alternatively, South American savannas receive more rainfall (Extended Data Fig. 4), so trees can have denser canopies[33] and thus may limit grass productivity via shading[17], especially where woody encroachment has been widespread[34]. Overall, tree-derived carbon is rarely the dominant carbon source for total SOC in semiarid savannas, aligning with the results from Kruger; however, trees can contribute substantially to SOC in humid savannas in South America (Extended Data Fig. 4).

SOC storage responses to increasing tree cover

Irrespective of whether ecosystems were encroached or not, SOC first increased and then decreased with rainfall (Fig. 3a), decreased with increasing soil sand (Fig. 3b) and increased substantially once grass-derived carbon reached ~70% (Fig. 3c). More measurements of SOC from humid savannas are needed to validate the response of SOC to rainfall, but the results are robust and consistent across Kruger and tropical savannas (Fig. 2 and Extended Data Figs. 2 and 3). On average, woody encroachment into grassy ecosystems increased SOC (by 5.75 Mg C ha^{-1}, s.e. = 5.42 Mg C ha^{-1}, n = 44) within the 1-m soil profile (Fig. 3d), but both large SOC gains and losses (from −65.0 to 105.3 Mg C ha^{-1}) were observed (Fig. 3d and Supplementary Table 1). Overall, relative increases (6.02%, s.e. = 4.04%) were negligible compared to SOC without woody encroachment (not different from zero; P = 0.25). Changes in SOC following woody encroachment were more pronounced in the upper 30-cm soil profile (4.04 Mg C ha^{-1}, s.e. = 2.29 Mg C ha^{-1}) than in the lower profile (1.71 Mg C ha^{-1}, s.e. = 3.94 Mg C ha^{-1}) (Fig. 3d), corroborating past work showing that the influence of decadal woody encroachment on SOC is constrained to

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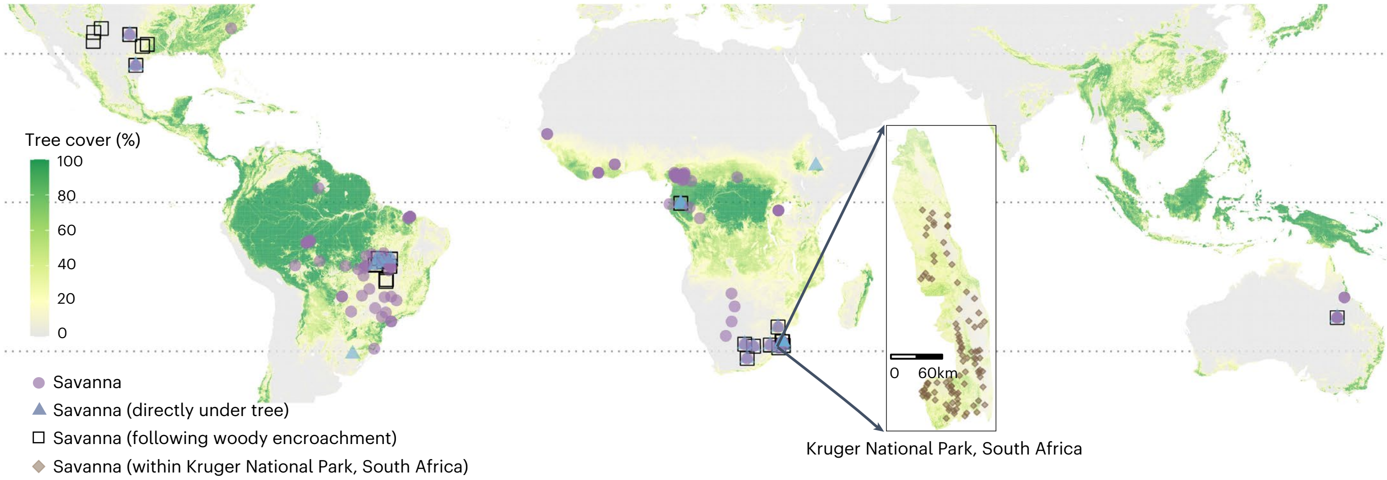

Fig. 1 | Geographic locations of soil samples across tropical and subtropical savannas. Soil samples were collected from studies (1) that measured $\delta^{13}C$ (‰) and SOC concentration (g C kg^{-1}) throughout the 1-m soil profile within savannas (circles) or within savannas and directly under trees (triangles) and (2) that measured changes in SOC storage (Mg C ha^{-1}) throughout the 1-m soil profile following woody encroachment into grassy ecosystems, including grasslands and savannas (squares). In addition, the inset shows soil samples with measurements of $\delta^{13}C$ and SOC concentration within the 0–20-cm soil layer across Kruger National Park, South Africa (diamonds). Tree canopy cover across the global tropics is derived from ref. 54. Tree canopy cover across Kruger National Park is derived from ref. 55. The base map is modified from Natural Earth.

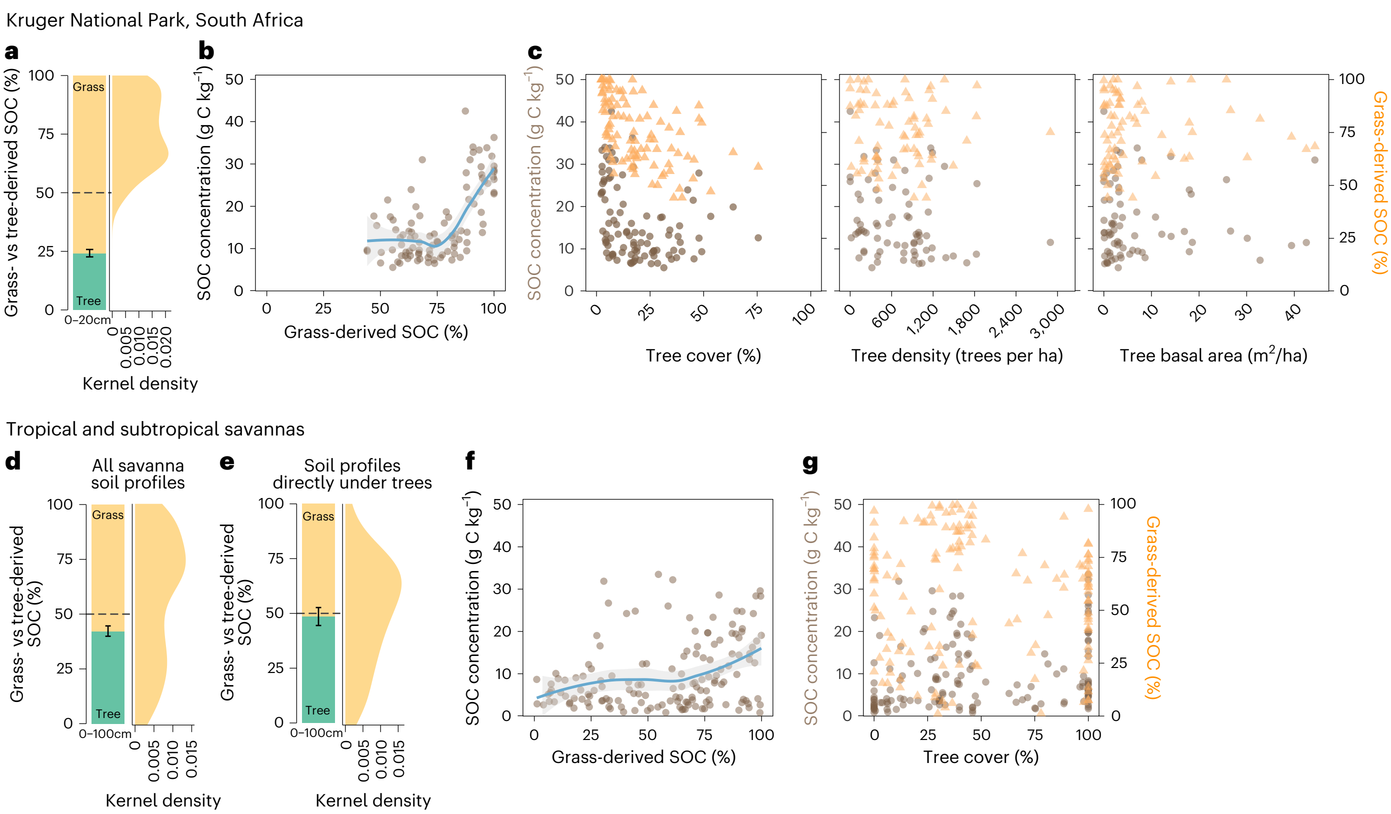

Fig. 2 | Contributions of grass-derived SOC to total SOC across tropical and subtropical savannas. a, Grass- versus tree-derived SOC within the 0–20-cm soil layer across Kruger National Park, South Africa. The kernel density plot indicates the density distribution of grass-derived SOC ($N = 98$). **b**, SOC concentration as a function of grass-derived SOC across Kruger ($N = 98$). **c**, Responses of SOC concentration (circles) and grass-derived SOC (triangles) to tree cover ($N = 98$), tree density ($N = 72$) and tree basal area ($N = 72$) across Kruger. **d**,**e**, Grass- versus tree-derived SOC within the 1-m soil profile across tropical and subtropical savannas (**d**) or across savannas with soil profiles sampled directly under trees/woody patches (**e**). The kernel density plots indicate the density distribution of grass-derived SOC ($N = 148$, **d**, and $N = 33$, **e**). **f**, SOC concentration as a function of grass-derived SOC across tropical and subtropical savannas ($N = 148$). **g**, Responses of SOC concentration (circles) and grass-derived SOC (triangles) to tree cover across tropical and subtropical savannas ($N = 148$). Error bars indicate mean values ± s.e. ($N = 98$, **a**; $N = 148$, **d**; $N = 33$, **e**). A loess smoother was used to fit relationships between SOC concentration and grass-derived SOC in **b** and **d**. Shaded areas indicate the 95% confidence intervals on the fit.

Table 1 | Model results to explain variation in SOC concentration (in g C kg^{-1}) and grass-derived SOC (in %) across tropical savannas

	Kruger National Park		Tropical and subtropical savannas	
Explanatory variables	**Standardized coefficient (SOC)**	**Standardized coefficient (grass-derived SOC)**	**Standardized coefficient (SOC)**	**Standardized coefficient (grass-derived SOC)**
Continent	NA	NA	+	+
Elephant density	–	−0.283	NA	NA
Elevation	–	–	–	–
Grass biomass	0.277	0.474	NA	NA
Fire frequency	–	–	-	-
Mean annual rainfall	–	−0.236	0.199	0.253
Slope	–	–	0.322	–
Soil sand content	−0.571	−0.315	NA	NA
Tree basal area	–	–	NA	NA
Tree cover	–	–	–	−0.164
Tree stem density	–	–	NA	NA

NA indicates that the explanatory variable is not available. – indicates that the explanatory variable is not selected for the best-fitted model. + indicates that a categorical variable was selected by the preferred model.

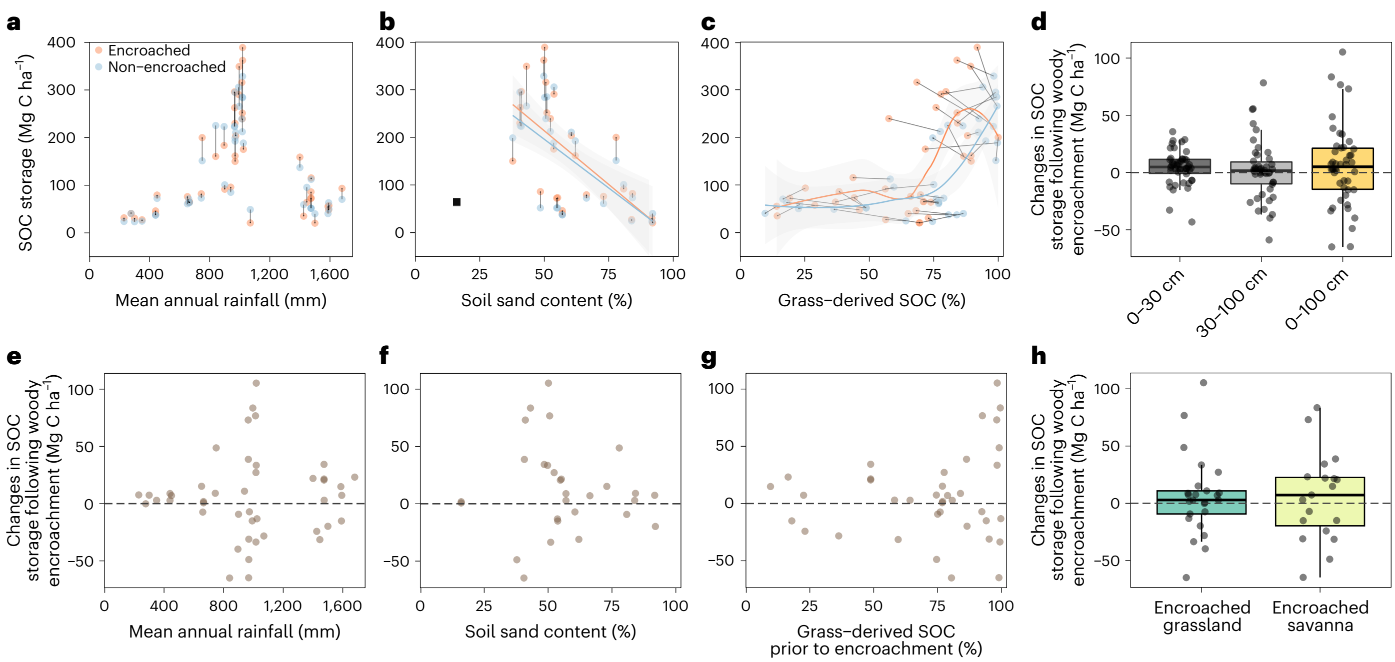

Fig. 3 | Changes in SOC storage following woody encroachment across tropical and subtropical grassy ecosystems. a–**c**, SOC storage throughout the entire 1-m soil profile within encroached or non-encroached grassy ecosystems as a function of mean annual rainfall (N = 44) (**a**), soil sand content (R^2 = 0.40, P < 0.001 and R^2 = 0.41, P < 0.001 for encroached and non-encroached systems, respectively; N = 29) (**b**) and grass-derived SOC (N = 38) (**c**). The black square in **b** is not included in the linear regressions. A loess smoother was used to fit the relationship between SOC storage and grass-derived SOC in **c**. Shaded areas in **b** and **c** indicate the 95% confidence intervals. **d**, Changes in SOC storage (Mg C ha^{-1}) within the upper (0–30 cm), lower (30–100 cm) and whole (0–100 cm) soil profile following woody encroachment (N = 44). **e**–**h**, Changes in SOC storage following woody encroachment as a function of mean annual rainfall (N = 44) (**e**), soil sand content (N = 29) (**f**) and grass-derived SOC prior to woody encroachment (N = 38) (**g**), and whether the encroached systems are grasslands (N = 25) or savannas (N = 19) (**h**). Box plots in **d** and **h** display medians (that is, 50th percentile), 25th and 75th percentiles, and 95% confidence intervals. Dashed lines in **d**–**h** indicate no net changes in SOC storage following woody encroachment.

surface soils[9]. However, because surface litter and SOM are susceptible to fires[35,36], increasing tree cover from fire abatement or afforestation may result in soil carbon loss when fire occurs.

Curiously, changes in SOC within the 1-m soil profile following woody encroachment were not explained by rainfall, soil sand, grass-derived SOC before encroachment, or ecosystem initial condition (grasslands versus savannas; Fig. 3e–h). Despite this, our results highlight that a large variation in changes in SOC following woody encroachment occurred in grassy ecosystems with intermediate rainfall (~800–1,000 mm), on less sandy soils (<50% sand) and with extremely high contributions of grass-derived carbon to total SOC (>70%) (Fig. 3e–g). Additionally, changes in SOC were relatively similar in encroached systems that were initially grasslands versus savannas (Fig. 3h).

Implications for carbon dynamics across tropical savannas

Our results suggest that grasses dominate the contribution of carbon to total SOC across tropical savannas, especially in arid and semiarid regions (annual rainfall of <700 mm). Grasses are well known to be highly productive across the tropics[14], but their productivity response to increasing tree cover has long been debated[16,17,19,37]. In arid and semi-arid savannas, our results suggest that increasing tree cover is unlikely to exclude grasses (see also refs. 16,17, which suggest that trees can even facilitate grass productivity), but also conclusively suggest that grass-derived carbon, not tree-derived carbon, will continue to dominate the SOC pool in these ecosystems (Fig. 2). Although increasing tree cover may lead to incremental gains in soil carbon sequestration in arid and semiarid savannas[9,11,12,38] (Fig. 3e), total SOC was not well-explained by tree cover, which suggests caution in the face of other management considerations including scarce water resources[39] and biodiversity conservation[4,40].

Meanwhile, in humid savannas, responses of SOC to tree cover were more varied (Fig. 3e). We found no easy explanation for this variation, with SOC gains and losses across soil texture gradients (Fig. 3f), in different ecosystems (Fig. 3h) and on different continents[11,38,41,42]. We speculate that several interacting dynamics may be involved. In humid savannas, large changes in ecosystem structure, especially increased tree canopy cover, can result from the suppression of fire and herbivory[33], which in turn excludes grasses through light interception and nutrient competition[17,37]. On the one hand, grass roots turn over more quickly compared to tree roots, making them important for SOC formation[43]. The loss of grass-derived carbon with decreasing grass productivity may lead to an overall reduction in SOC storage, as has been observed in some humid savannas[11,38,41]. On the other hand, woody plants sometimes produce more root biomass and exploit deeper portions of the soil profile than grasses, and both above-ground and below-ground carbon inputs from trees are generally more resistant to decay than those of grasses[44]. These dynamics can lead to increases in the amount of tree-derived carbon that are substantially larger than accompanying losses from grass-derived carbon, therefore enhancing SOC formation and storage with increasing tree cover[4,42]. Net changes in SOC probably result from the interplay between losses of grass-derived carbon and gains in tree-derived carbon, with both the sign and magnitude of change depending on their relative magnitudes and their retentions during the evolution of SOC.

Despite uncertainties, our findings challenge the assumption that increasing tree cover invariably leads to substantial additional carbon sequestration in soils[1]. Widely used estimates of the global carbon sequestration potential of tree planting assume that tropical savanna and grassland soils will gain 84 Mg C ha^{-1} on average from afforestation[1,7]. By contrast, the synthesis of field data presented here suggests that carbon accumulation in soil may be negligible (6% increase, s.e. = 4%), in line with other syntheses[45,46]. We also find especially large uncertainties in SOC changes with increasing tree cover in humid savannas, which is also where tree planting is likely to be most successful. Although not specific to savannas, dynamic global vegetation models[47] replicate this large variation in whole-ecosystem responses to avoided deforestation and afforestation/reforestation, with estimates ranging between −33 and +57 Gt C. In the model context, this large range comes from the susceptibility of vegetation biomass to rapid losses from droughts or fires[48], even though models suggest SOC is the larger and less active reservoir[49,50]. Thus, model and real-world mechanisms still differ substantially, which emphasizes the urgent need to explicitly and systematically disentangle how SOC storage and dynamics respond to increasing tree cover, especially in humid savannas.

Future research directions

Although our study provides compelling evidence of grasses making a substantial contribution to savanna SOC, we found that none of the parameters we examined could account for the observed variations in SOC change in response to an increase in tree cover. Here, we offer some ideas for next steps. First, soil texture did not explain how SOC would change under encroachment or afforestation, but responses were more variable in grassier ecosystems on more clayey soils. Further insights may come from measuring not only soil clay content, but also different clay minerals and their associated primary organo–mineral complexes, which may strongly influence physiochemical protection, microbial decomposition and the stabilization of organic matter[21–23]. A second possible source of variation not examined here is the length of time since woody encroachment[9,27], which could have variable effects resulting from heterogeneity in the rates of SOC accumulation and loss across different soils. Long-term monitoring of soil carbon inputs from trees versus grasses, organic matter formation, decomposition and persistence with afforestation at the same site can also overcome the variation from the commonly used space-for-time substitution approach[51]. Third, differences in SOC responses to encroachment could result from differences in composition and function of the grass community and of invading woody species[52], which can be tested with more nuanced comparative studies. Finally, savannas host a diverse assemblage of herbivores that impact SOC; increasing tree cover may interact with browsers and grazers and influence SOC, a dynamic that remains to be evaluated broadly across tropical savannas[16].

In summary, despite the existing knowledge gaps, our study suggests that savanna SOC cannot be simply predicted by tree cover. Furthermore, increasing tree cover may have minimal benefits when it comes to enhancing the potential for carbon sequestration in tropical savanna soils. This challenges the widespread assumption that afforestation universally enhances SOC storage across tropical savannas. The inaccuracy of this assumption incentivizes tree-for-carbon projects that we already know will be ineffective, with large unintended costs to biodiversity and ecosystem functions in tropical and subtropical savannas[4,53]. Their false promise distracts from the urgent business of reducing fossil-fuel emissions and associated policy development and diverts efforts and resources needed to conserve intact ecosystems and increase their adaptation to climate change.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41561-023-01232-0.

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Methods

In this study, we aimed to evaluate the variation and drivers of grass-derived carbon to SOC as well as SOC in response to increasing tree cover across tropical and subtropical savannas. To achieve this, we first examined a semiarid savanna in Kruger National Park, South Africa. The advantage of this regional-scale study is that savannas in Kruger have been extensively studied, with long-term monitoring of vegetation characteristics and environmental conditions, enabling a full test of the drivers of SOC concentration and grass-derived carbon. However, the rainfall of savannas in Kruger is only 460–700 mm. To generalize the findings from Kruger and to cover a broader rainfall gradient, we synthesized available data that have measured both soil carbon stable isotopic ratios and SOC values across tropical and subtropical savannas around the globe. However, the resolution of the vegetation characteristics and environmental conditions of these sites across tropical and subtropical savannas is low. Therefore, the regional study in Kruger complements the constraints of the broader study on testing the drivers of variation in SOC concentration and grass-derived carbon across tropics. Finally, to extend the scope of this study, we also compiled a dataset of changes in SOC storage for a 1-m soil profile following woody encroachment into tropical savannas and grasslands, allowing quantification of how SOC accumulates with increasing tree cover, and providing implications for the widespread assumption that afforestation universally and substantially enhances SOC storage across tropical savannas.

SOC dynamics across Kruger

We extensively sampled soil cores across a semiarid savanna in Kruger National Park to explore factors that influence C_4-derived carbon (that is, grass-derived carbon) and SOC concentration at the regional scale. Kruger covers nearly 20,000 km^2 (22° 20′ to 25° 30′ S, 31° 10′ to 32° 00′ E) and consists of tropical and subtropical savannas. Mean annual rainfall increases from 350 mm in the north to 750 mm in the south, with most precipitation during the period November to April. Elevation ranges from 260 to 839 m above sea level. Based on long-term fire records, the average fire return interval for Kruger is ~3.5 years, but fire regimes vary spatially across the park, ranging from one fire per year to one every 34 years[56]. Kruger is dominated by two underlying parent materials, granite and basalt, which strongly influence the soil and vegetation properties. The flora of Kruger includes over 400 woody species and 200 herbaceous species[57]. The herbaceous layer is dominated by the C_4 graminoids, including *Aristida congesta*, *Digitaria eriantha* and *Panicum maximum*. The most dominant woody encroachers are *Dichrostachys cinerea* and *Combretum apiculatum*[29].

To monitor grass biomass to inform fire management, Kruger established 533 Veld Condition Assessment (VCA) sites throughout the park in 1989. At each VCA site, grass biomass was measured with a calibrated disc pasture meter every April from 1989 to 2008 within a plot of 50 m × 60 m (ref. 58). Plot-level grass biomass estimates were averaged from measurements taken every 2 m along four 50-m transects (that is, 100 measurements in total), running at 0, 20, 40 and 60 m along the length of the plot. In 2008, a one-time woody plant survey was performed[29]. Plot-level stem density and basal diameter were averaged from two measurements located along each transect (that is, eight measurements in total). Measurements for the woody plant survey were located at 30 and 50 m along the first and third transects, and 20 and 40 m along the second and fourth transects. Woody cover for each VCA site was extracted from a 10-m-resolution remote sensing product across Kruger based on the Sentinel-1 time series for 2016–2017 and LiDAR data[55] (Fig. 1).

During the rainy seasons of 2010 and 2011, soil samples were collected to a depth of 20 cm from 98 VCA sites that were easy to access (Fig. 1). At each site, soil samples were collected at each of four corners and in the middle of the 50 × 60 m plot, and those five samples were then homogenized and subsampled. All soil samples were dried at 60 °C and sieved through a 2-mm sieve. A subset of each soil sample (~50 g) was used to measure soil texture using a hydrometer[59], with soil sand, silt and clay content adding up to 100%. Another subset was ground to a fine powder, acid-washed and used to analyse SOC concentrations and stable carbon isotopic ratios using a Costech ECS 4010 Elemental Analyzer interfaced via a ConFlo III device with a Delta V Advantage isotope ratio mass spectrometer at the Yale Analytical and Stable Isotope Center. The stable carbon isotopic value was expressed as deviations of soil samples from an international standard (Vienna Pee Dee Belemnite) in parts per thousand (‰) using the δ-notation (that is, $\delta^{13}C$).

SOC dynamics across tropical and subtropical savannas

Soil samples from Kruger only covered a narrow rainfall gradient (460–700 mm) and were constrained to surface soils. To obtain a fuller picture of grass-derived SOC across a full gradient of rainfall and to a soil depth of 1 m across global savannas, we used the key words '*savanna* AND *soil* AND *13 C* OR *stable carbon isotope*', to search relevant literature on Google Scholar on 17 July 2021. We used the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) protocol to screen and identify publications to be included in this analysis[60]. Briefly, the title and abstract of each publication were initially screened for eligibility based on whether the publication included soil stable carbon isotopic measurements within savanna soils. Eligible publications were further filtered based on (1) whether the herbaceous layer was dominated by C_4 grasses and (2) whether the publication included at least one soil profile where both soil $\delta^{13}C$ and SOC values were measured to up to a depth of 1 m. Overall, a total of 148 soil profiles met these criteria. Among these soil profiles, 33 were sampled directly underneath individual tree canopies or woody patches within savannas. The geographic locations of the soil profiles are shown in Fig. 1.

For each soil profile we recorded locations (latitude and latitude), continents (Africa, Australia, North America and South America), climatic variables (mean annual rainfall (MAP) and temperature (MAT)), elevation, soil sand content, tree cover, soil bulk density, SOC concentration (or storage), soil $\delta^{13}C$ and end members for calculating C_3- versus C_4-derived carbon if reported. When the results were presented graphically, we used WebPlotDigitizer 4.4 to digitize the data. If these data were not reported, we contacted the corresponding authors for additional information. Otherwise, MAT and MAP were extracted from the WorldClim database[61] (https://www.worldclim.org/); soil sand contents were extracted from the SoilGrids database[62] (https://soilgrids.org/); elevation was extracted from the Global Multi-resolution Terrain Elevation Data 2010 (https://earthexplorer.usgs.gov/); fire frequency (2000–2019) was extracted from the MODIS Burned Area Product[63] (https://lpdaac.usgs.gov/products/mcd64a1v006/); and tree cover was extracted from the Global Tree Cover 2010[54] (https://glad.umd.edu/dataset/global-2010-tree-cover-30-m).

SOC storage following woody encroachment

To quantify changes in SOC storage following woody (or forest) encroachment throughout the whole 1-m soil profile across tropical and subtropical grassy ecosystems, we used the key words '*woody encroachment* OR *woody thickening* OR *woody invasion* AND *soil profile* OR *soil column* OR *deep soil* AND *carbon*' to search the relevant literature on Google Scholar on 18 October 2021. Similarly, we used the PRISMA protocol to screen and identify publications to be included in this analysis[60]. Eligible publications were identified based on (1) whether SOC storage was measured from woody encroached or non-encroached sites, including the conversion of grasslands to woodlands/forests (hereafter encroached grasslands) and the thickening of savannas to woodlands/forests (hereafter encroached savannas) and (2) whether SOC storage was measured throughout the whole 1-m soil profile. Overall, 44 paired-soil profiles with and without woody encroachment were collected across tropical savannas and grasslands (Supplementary Table 1). Similarly, we extracted SOC storage from encroached and non-encroached sites, and all the other information outlined in the previous section. The geographic locations of soil profiles related to woody encroachment are shown in Fig. 1.

Data analyses

Because the herbaceous layer of these tropical and subtropical savannas is dominated by C_4 grasses, we calculated the relative proportion of SOC derived from C_4 vegetation using soil $\delta^{13}C$ values in a simple mass balance mixing model:

$$\delta^{13}C_{soil} = f \times \delta^{13}C_{C4} + (1-f) \times \delta^{13}C_{C3}$$

where $\delta^{13}C_{soil}$ is the measured $\delta^{13}C$ value for the soil samples, $\delta^{13}C_{C4}$ is the mean $\delta^{13}C$ value for C_4 vegetation, $\delta^{13}C_{C3}$ is the mean $\delta^{13}C$ value for C_3 vegetation, and f is the proportion of carbon derived from C_4 vegetation. For Kruger National Park, we used −26.7‰ (n = 49 species) and −12.5‰ (n = 93 species) as end members for C_3 vegetation and C_4 vegetation[64], respectively. For tropical and subtropical savannas, if studies have reported end members, we used reported values; if not, we used the global average for C_3 species (−27.1‰) and C_4 species (−13.1‰)[28].

However, it should be noted that this simple mass balance mixing model may underestimate or overestimate the proportion of carbon derived from C_4 vegetation. On the one hand, $\delta^{13}C$ generally becomes enriched with depth in the soil profile (~1–3‰) via several previously proposed mechanisms (for example, the Suess effect and microbial isotope discrimination during decomposition) that are independent of vegetation change, resulting in an overestimation of the proportion of carbon derived from C_4 vegetation[65,66]. On the other hand, there is evidence suggesting that SOC inputs from C_4 vegetation decompose more rapidly than those derived from C_3 vegetation[20,67], potentially resulting in lower soil $\delta^{13}C$ values that may underestimate the proportion of carbon derived from C_4 vegetation. However, the collected soil $\delta^{13}C$ values do not allow us to evaluate the influence of these factors on estimates of the proportions of carbon derived from C_3 versus C_4 vegetation. In addition, although we restricted our data collection to savannas with a herbaceous layer dominated by C_4 grasses, the presence of sparse C_3 grasses may underestimate the carbon derived from grasses. Nonetheless, this simple mass balance mixing model still provides us with a robust comparison of carbon derived from trees versus grasses across tropical and subtropical savannas.

We applied a linear regression model to relate changes in SOC concentration and grass-derived soil carbon to environmental determinants across Kruger National Park. The environmental variables include mean annual rainfall (1980–2010), tree basal area, stem density, tree cover, fire frequency (1980–2010), grass biomass (1989–2008), elephant density (1985–2008), soil sand content, slope and elevation. All variables were first centred and tested for collinearity (all correlation coefficients <0.7; Extended Data Fig. 1). The best-fit linear regression model was selected using Akaike's information criterion (AIC; Extended Data Table 1). Conditional regression plots for the linear regression model between changes in SOC concentration, grass-derived soil carbon, and selected explanatory variables were generated accordingly (Extended Data Fig. 1).

To estimate the proportion of grass-derived SOC within the 1-m soil profile across tropical and subtropical savannas, we first calculated the proportion of grass-derived soil carbon for each reported soil layer based on the simple mass balance mixing model as mentioned above. We then weighted the proportion of grass-derived soil carbon at each soil layer based on SOC concentration. Because surface soils generally have higher SOC concentration than deep soils, this weighted proportion of grass-derived soil carbon based on SOC concentration accounts for differences in SOC concentration throughout the soil profile. The proportion of grass-derived soil carbon within the whole soil profile was then averaged from all soil layers. We also estimated the SOC concentration within the 1-m soil profile by weighting the SOC concentration with soil depth. Similarly, we used a linear regression model to relate changes in weighted SOC concentration and grass-derived soil carbon to environmental variables across the tropical and subtropical savannas, including continent, tree cover, mean annual rainfall, fire frequency, elevation and slope. Unfortunately, no grass biomass data were available for these soil profiles, and we excluded soil sand content extracted from SoilGrid due to the poor performance of this global prediction product (Extended Data Fig. 2). The best-fitted linear regression model was selected using AIC (Extended Data Table 2).

To quantify how SOC storage responds to woody encroachment across tropical and subtropical grassy ecosystems, we used paired measurements of reported SOC storage throughout the entire 1-m soil profile between woody encroached and non-encroached sites. If the individual study reported SOC storage within the whole 1-m soil profile and separated into the upper (0–30 cm) and lower (30–100 cm) soil profile, we used their original measurements. If not, we fitted the SOC storage to soil depth for each soil profile with different models, including linear regression, second- and third-order polynomial regressions, exponential function, loess regression and spline regression. We used the middle point as the soil depth for each soil layer (for example, 5 cm for the 0–10-cm soil layer). We selected the best-fitted model with the smallest residual standard error. Once the best-fit model was determined, we predicted SOC storage within the 1-m soil profile and averaged the SOC storage for upper (0–30 cm), lower (30–100 cm) and the whole (0–100 cm) soil profile. Changes in SOC following woody encroachment were calculated using SOC storage in the encroached minus the non-encroached site. We also evaluated changes in SOC storage following woody encroachment as a function of rainfall, soil sand content, the initial amount of grass-derived soil carbon prior to encroachment, and whether the encroached ecosystems were grasslands or savannas.

Data availability

Data supporting the results can be found at Dryad Digital Repository (https://doi.org/10.5061/dryad.c59zw3rbg). Source data are provided with this paper.

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Author contributions
Y.Z. and A.C.S. conceived this study. A.C.S. conducted field sampling in Kruger National Park, and Y.Z. performed laboratory analyses. B.B., W.J.B., T.W.B., M.F.C., C.C., A.B.D., E.C.F., E.F.G., L.C.R.S. and J.L.W. contributed to conceptualization and data curation. Y.Z. collected data from the literature, performed data analysis and drafted the paper with substantial inputs from A.C.S. All authors provided paper feedback.

Competing interests
The authors declare no competing interests.

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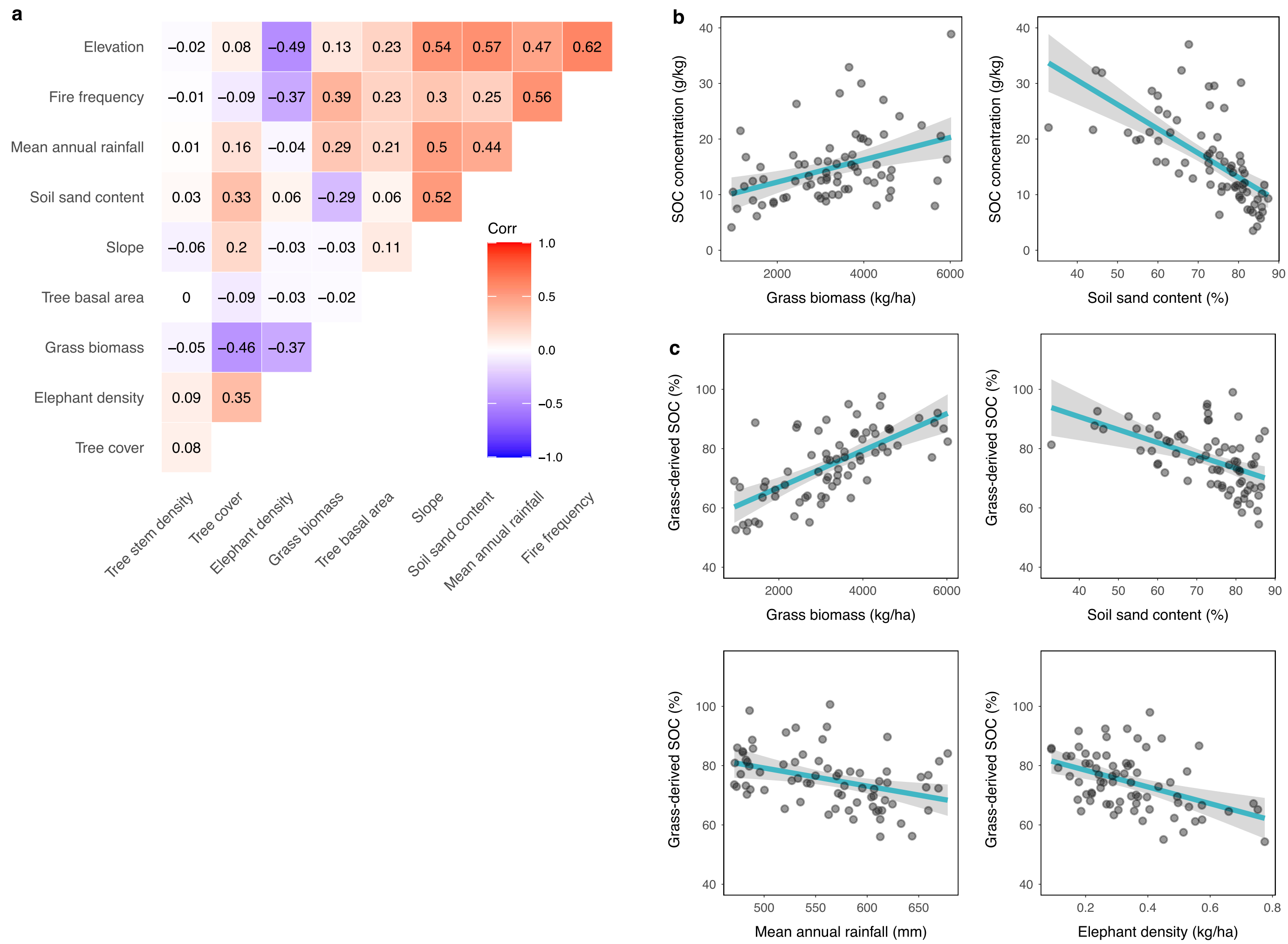
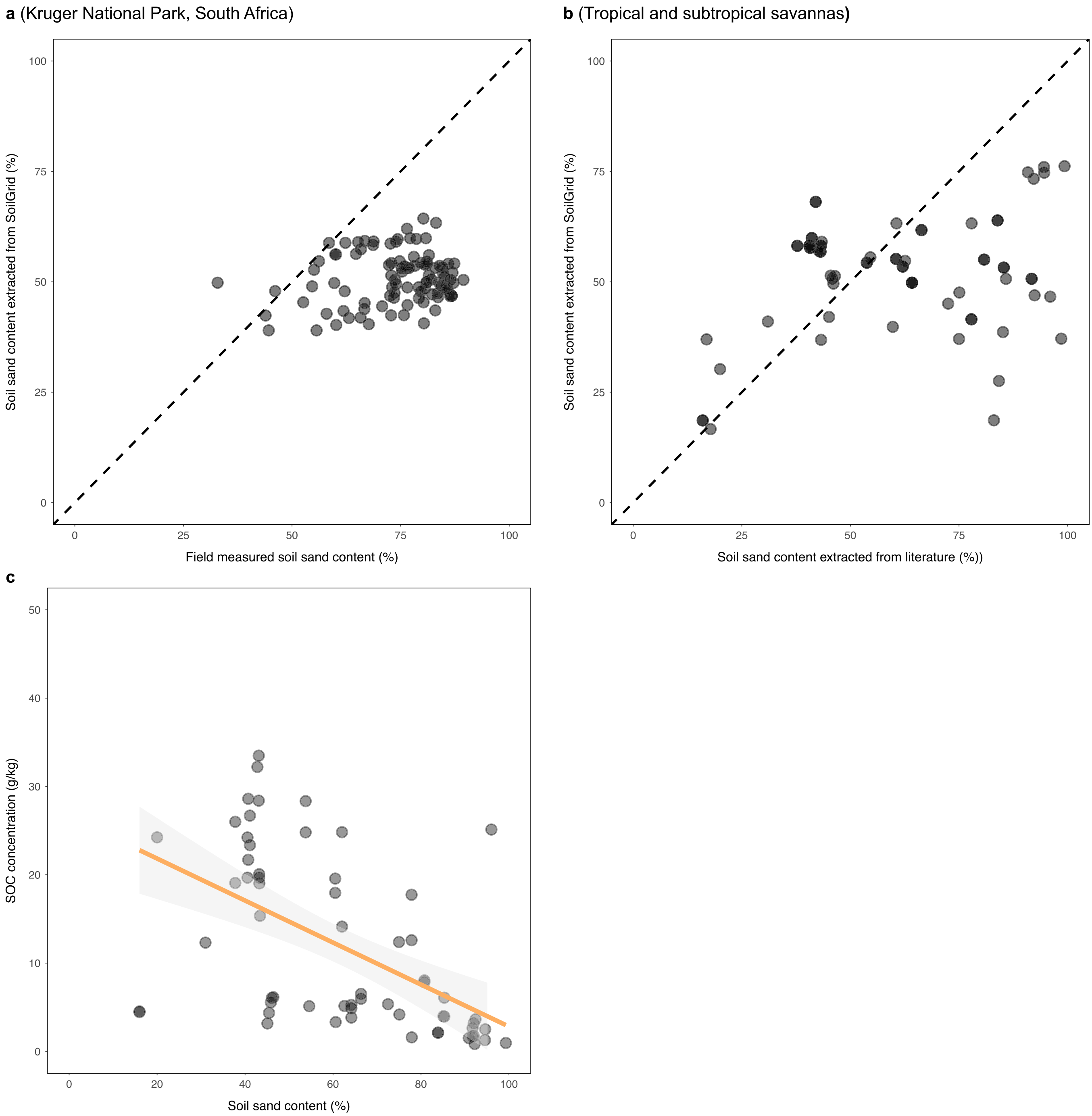


Extended Data Fig. 1 | Model predictors for soil organic carbon (SOC) concentration (g C/kg) and grass-derived SOC (%) across Kruger National Park, South Africa. (**a**) The correlation coefficient matrix among predictors used to model SOC concentration and grass-derived SOC. (**b**) Conditional regression plots from the best fitted linear model of changes in SOC concentration in response to grass biomass (kg/ha) and soil sand content (%). (**c**) Conditional regression plots from the best fitted linear model of changes in grass-derived soil C in response to grass biomass (kg/ha), soil sand content (%), mean annual rainfall (mm), and elephant density (kg/ha). All plots in panel (**b**) and (**c**) represent 72 sites across Kruger National Park (*that is*, n = 72). Shaded areas represent 95% confidence intervals. See Extended Data Table 1 for more details on model specifications.



Extended Data Fig. 2 | Comparison of field measured soil sand content with soil sand content extracted from soil Grid. (**a**) A scatter plot between field measured soil sand content (%) from Kruger National Park and soil sand content (%) extracted from SoilGrid ($R^2 = 0.03$, $p = 0.08$, n = 98). (**b**) A scatter plot between soil sand content extracted from literature across tropical/subtropical savannas and soil sand content extracted from SoilGrid ($R^2 = 0.09$, $p = 0.015$, n = 72). Dashed lines in panels (**a**) and (**b**) indicate the 1:1 ratio line. Soil organic carbon (SOC) concentration (g/kg) throughout the entire 1-m profile across tropic and subtropical savannas as a function of soil sand content (%) extracted from the related literature (**c**). Regression line indicates a linear fit ($R^2 = 0.29$, $p < 0.0001$, n = 72). Shaded areas indicate the 95% confidence intervals of the fit.

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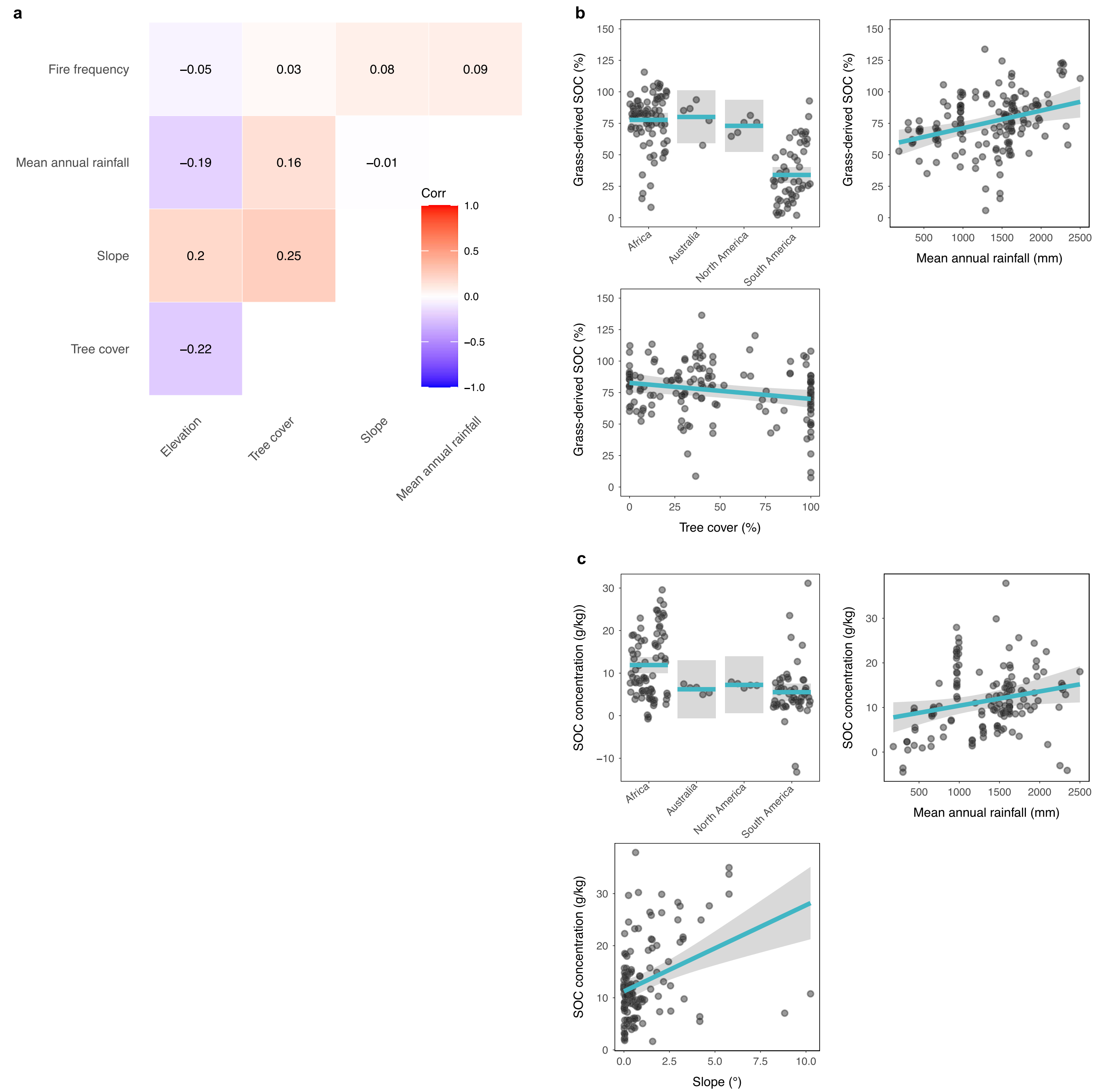

Extended Data Fig. 3 | Model predictors for soil organic carbon (SOC) concentration (g/kg) and grass-derived SOC (%) across tropical and subtropical savannas. (**a**) The correlation coefficient matrix among predictors used to model SOC concentration and grass-derived SOC. (**b**) Conditional regression plots from the best fitted linear model of changes in grass-derived soil C in response to different continent, mean annual rainfall (mm), and tree cover (%). (**c**) Conditional regression plots from the best fitted linear model of changes in SOC concentration in response to different continent, mean annual rainfall, and slope (∘). All plots in panel (**b**) and (**c**) represent 148 sites across tropical and subtropical savannas (*that is*, n = 148). Box plots display medians (*that is*, 50th percentile), 25th and 75th percentiles. Shaded areas represent 95% confidence intervals. See Extended Data Table 2 for more details on model specifications.

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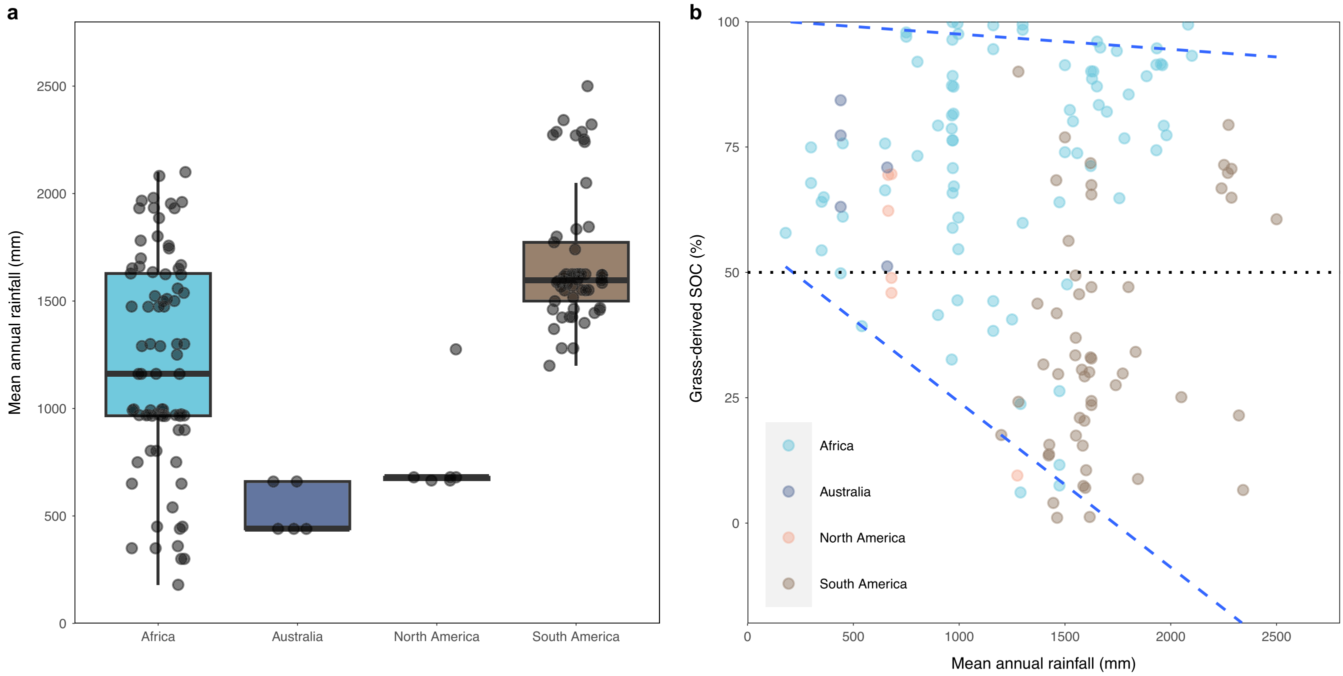

Extended Data Fig. 4 | Grass-derived SOC as a function of mean annual rainfall across tropical and subtropical savannas. (**a**) Boxplot distribution of mean annual rainfall (mm) for tropical and subtropical savanna sites across different continents (n = 81 for Africa, n = 5 for Australia, n = 6 for North America, and n = 56 for South America). Box plots display medians (that is, 50th percentile), 25th and 75th percentiles, and 95% confidence intervals. (**b**) Grass-derived SOC (%) throughout the 1-m soil profile as a function of mean annual rainfall (n = 148). The dotted black line indicates where grass- and tree-derived C contributed half of the total SOC (*that is*, 50%). Dashed blue lines indicate the upper bound and lower bound of the 95% quantile regressions.

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Extended Data Table 1 | Model specifications and model selections for soil organic carbon (SOC) concentration (g C/kg) and grass-derived SOC (%) across Kruger National Park, South Africa

Intercept	Basal area	Elephant density	Elevation	Fire frequency	Grass biomass	Rainfall	Soil sand	Slope	Stem density	Tree cover	df	logLik	AICc	delta	weight
SOC concentration															
-0.044					0.271		-0.568		-0.163		5	-71.63	154.20	0.00	0.04
-0.046				-0.117	0.329		-0.521		-0.163		6	-70.76	154.80	0.64	0.03
-0.036		0.107			0.308		-0.563		-0.171		6	-70.85	155.00	0.81	0.03
-0.043					0.323	-0.123	-0.501		-0.161		6	-70.87	155.00	0.86	0.03
-0.038					0.284		-0.513	-0.098	-0.170		6	-71.00	155.30	1.12	0.03
-0.033		0.121			0.374	-0.141	-0.486		-0.170		7	-69.84	155.40	1.26	0.02
-0.042			-0.100		0.302		-0.504		-0.165		6	-71.16	155.60	1.43	0.02
-0.044					**0.277**		**-0.571**				**4**	**-73.77**	**156.10**	**1.95**	**0.02**
-0.044	0.051				0.271		-0.571		-0.163		6	-71.42	156.10	1.96	0.02
-0.046	0.084			-0.142	0.342		-0.516		-0.163		7	-70.21	156.20	1.99	0.02
-0.030		0.105			0.320		-0.509	-0.096	-0.177		7	-70.23	156.20	2.03	0.02
Grass-derived SOC															
-0.049		**-0.283**			**0.474**	**-0.236**	**-0.315**				**6**	**-58.82**	**130.90**	**0.000**	**0.057**
-0.046		-0.200	0.164		0.468	-0.269	-0.398				7	-57.69	131.10	0.180	0.052
-0.046		-0.166	0.186		0.417	-0.243	-0.401			-0.119	8	-56.55	131.40	0.430	0.046
-0.050		-0.264			0.433	-0.209	-0.307			-0.100	7	-58.02	131.80	0.850	0.037
-0.049	0.083	-0.277			0.488	-0.262	-0.305				7	-58.07	131.90	0.940	0.036
-0.036			0.308		0.438	-0.272	-0.448			-0.154	7	-58.17	132.10	1.150	0.032
-0.050		-0.167	0.251	-0.120	0.435	-0.199	-0.416			-0.128	9	-55.64	132.20	1.240	0.031
-0.049		-0.204	0.220	-0.107	0.487	-0.233	-0.411				8	-56.99	132.30	1.320	0.030
-0.046	0.061	-0.208	0.139		0.479	-0.284	-0.378				8	-57.29	132.90	1.920	0.022
-0.039			0.372	-0.118	0.456	-0.230	-0.462			-0.164	8	-57.33	132.90	2.000	0.021

Predictor variables included tree basal area (m^2/ha), elephant density (kg/ha), elevation (m), fire frequency (fires/year), grass biomass (kg/ha), rainfall (mm), soil sand content (%), slope (∘), tree stem density (stem/ha), and tree cover (%) across Kruger National Park, South Africa. The preferred model (simplest model with ΔAIC < 2) is highlighted in bold and red. The values of R^2 for the preferred models for SOC concentration and grass-derived SOC are 0.54 and 0.69, respectively.

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Extended Data Table 2 | Model specifications and model selections for soil organic carbon (SOC) concentration (g/kg) and grass-derived SOC (%) across tropical and subtropical savannas

Intercept	Continent	Elevation	Fire frequency	Rainfall	Slope	Tree cover	df	logLik	AICc	delta	weight
SOC concentration											
0.332	**+**			**0.199**	**0.322**		**7**	**-177.1**	**369.0**	**0.00**	**0.302**
0.326	+			0.191	0.307	0.060	8	-176.7	370.6	1.61	0.135
0.346	+	-0.045		0.199	0.326		8	-176.9	370.9	1.91	0.116
0.334	+		-0.008	0.200	0.321		8	-177.1	371.2	2.24	0.099
Grass-derived SOC											
0.580	**+**			**0.253**		**-0.164**	**7**	**-161.3**	**337.4**	**0**	**0.245**
0.559	+		0.079	0.244		-0.157	8	-160.6	338.3	0.81	0.164
0.569	+			0.254	0.066	-0.181	8	-160.8	338.7	1.3	0.128
0.596	+	-0.041		0.254		-0.173	8	-161.1	339.4	1.91	0.094
0.547	+		0.080	0.245	0.067	-0.174	9	-160.1	339.5	2.1	0.086

Predictor variables included continent, elevation (m), fire frequency (number of times burned), rainfall (mm), slope (∘), and tree cover (%). The preferred model (simplest model with ΔAIC < 2) is highlighted in bold and red. The values of R^2 for the preferred models for SOC concentration and grass-derived SOC are 0.28 and 0.42, respectively.