Conservation with elevated elephant densities sequesters carbon in soils despite losses of woody biomass

Alexandra Sandhage-Hofmann1 | Anja Linstädtter2,3 | Liana Kindermann2,3 | Simon Angombe4 | Wulf Amelung1

1Institute of Crop Science and Resource Conservation, Soil Science and Soil Ecology, University of Bonn, Bonn, Germany
2Institute of Crop Science and Resource Conservation, Section Grassland Ecology and Management, University of Bonn, Bonn, Germany
3Institute of Biochemistry and Biology, Biodiversity and Systematic Botany, University of Potsdam, Potsdam, Germany
4Faculty of Agriculture & Natural Resources, Neudamm Campus, University of Namibia, Windhoek, Namibia

Correspondence
Alexandra Sandhage-Hofmann,
Institute of Crop Science and Resource Conservation, Soil Science and Soil Ecology, University of Bonn, Nußallee 13, 53115 Bonn, Germany.
Email: sandhage@uni-bonn.de

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Abstract
Nature conservation and restoration in terrestrial ecosystems is often focused on increasing the numbers of megafauna, expecting them to have positive impacts on ecological self-regulation processes and biodiversity. In sub-Saharan Africa, conservation efforts also aspire to protect and enhance biodiversity with particular focus on elephants. However, elephant browsing carries the risk of woody biomass losses. In this context, little is known about how increasing elephant numbers affects carbon stocks in soils, including the subsoils. We hypothesized that (1) increasing numbers of elephants reduce tree biomass, and thus the amount of C stored therein, resulting (2) in a loss of soil organic carbon (SOC). If true, a negative carbon footprint could limit the sustainability of elephant conservation from a global carbon perspective. To test these hypotheses, we selected plots of low, medium, and high elephant densities in two national parks and adjacent conservancies in the Namibian component of the Kavango Zambezi Transfrontier Area (KAZA), and quantified carbon storage in both woody vegetation and soils (1 m). Analyses were supplemented by the assessment of soil carbon isotopic composition. We found that increasing elephant densities resulted in a loss of tree carbon storage by 6.4 t ha⁻¹. However, and in contrast to our second hypothesis, SOC stocks increased by 4.7 t ha⁻¹ with increasing elephant densities. These higher SOC stocks were mainly found in the topsoil (0–30 cm) and were largely due to the formation of SOC from woody biomass. A second carbon input source into the soils was megaherbivore dung, which contributed with 0.02–0.323 t C ha⁻¹ year⁻¹ to ecosystem carbon storage in the low and high elephant density plots, respectively. Consequently, increasing elephant density does not necessarily lead to a negative C footprint, as soil carbon sequestration and transient C storage in dung almost compensate for losses in tree biomass.

Key words
carbon sequestration, conservation, elephants, soil organic carbon, woody biomass
INTRODUCTION

Nature conservation is one of the dominant land uses currently shaping Africa’s ecosystems. Southern Africa in particular contributes to international conservation targets (Naidoo et al., 2018; Ramutsindela, 2007): the protected area almost doubled within the period from 1970 to the 2000s (Newmark, 2008), covering nowadays 22% of the total land surface in sub-Saharan Africa (WDPA, 2021). An important aspect of conservation efforts in southern Africa is to increase wildlife numbers, especially those of megaherbivores like elephants, giraffes, or rhinoceroses (i.e., animals exceeding 1000 kg body weight; Owen-Smith, 2013). This effort is envisioned to compensate for the dramatic decrease of megaherbivore numbers during the past 100 years (Bocherens, 2018; wwf.org, 2018), and because megaherbivores fulfill multiple ecological functions, which cannot be replaced by smaller herbivores (Owen-Smith, 2013). These functions include cascading positive effects on biodiversity due to opening of the vegetation (Asner et al., 2016), followed by changes in fire patterns, seed spreading (Bunney et al., 2017), redistribution of nutrients (Wolf et al., 2013), and accompanied increases in other herbivore species (de Boer et al., 2015).

Increasing numbers of megaherbivores impact ecosystem functioning at different spatial and temporal scales (Dirzo et al., 2014; Fullman & Bunting, 2014; Hempson et al., 2017). Previous studies have often outlined effects on vegetation characteristics such as on aboveground biomass (Guldemond et al., 2017) including vegetation structure and composition (Cromsigt et al., 2018; O’Connor & Page, 2013; Teren et al., 2018). Those studies found that browsing megaherbivores typically exerts strong negative effects on woody aboveground biomass, for example, by increasing the mortality rates within tree and shrub populations, thus also reducing the amount of carbon stored in aboveground biomass (Smit & Putman, 2011). A particular damage can occur from elephants (Loxodonta africana). Due to their large size, treefall considerably increases with increasing elephant densities, thus raising public concern about potentially detrimental impacts on woody biomass in protected areas where elephant populations are increasing rapidly (Asner et al., 2016). Nevertheless, elephants are keystone species in savanna ecosystems (du Toit et al., 2014; Owen-Smith, 1988), and as such a priority for conservation measures in Sub-Saharan Africa. As elephants prefer nutrient-rich trees over nutrient-poor ones (Skarpe et al., 2014), they modulate both biodiversity and spatial structure of savanna ecosystems (Teren et al., 2018; Thornley et al., 2020) toward tree species with higher disturbance tolerance and reseedability ability (Neke et al., 2006; Quédraogo et al., 2015). Related changes in fire frequency (Pellegrini et al., 2017), droughts, and other herbivore populations accompany this process (Zyambo, 2016).

As trees usually store more than 90% of the carbon in savanna ecosystems (Pellegrini et al., 2014), changes in tree density affect the atmospheric CO₂ balance. However, large amounts of carbon are also stored in soils (Lal, 2016). For Australian savannas, it is even estimated that 84% of the total carbon is stored in the soil (Chen et al., 2003). This soil C pool ranges from less than 25 t C ha⁻¹ in the soil’s top 30 cm in dry savannas (Alam et al., 2013) to more than 80 t C ha⁻¹ in the tropical savanna forests of Brazil (Leite et al., 2014). Yet, we are still lacking a mechanistic understanding of the degree to which increasing densities of megaherbivores change the soil system from a carbon sink to a source or vice versa (Andriuzzi & Wall, 2018), and how this affects the carbon storage in the entire ecosystem (Hempton et al., 2017). In general, it is assumed that shifts in the woody biomass in savannas over time shift the carbon stored in the soils in the same direction (Pellegrini et al., 2014), that is, a reduction of woody biomass should finally result in lower soil C stocks.

Nevertheless, a recently published study showed opposite effects in Kenya: Megaherbivores reduced adult tree densities, but increased the size of the soil carbon pool (Sitters et al., 2020).

Surprisingly, little is known on how elephants affect soil properties (Andriuzzi & Wall, 2018; Cromsigt et al., 2018; Sitters et al., 2020). Similar to other mammal herbivores such as cattle (Munjonji et al., 2020), elephants likely exert direct and indirect effects on soils and related carbon stocks and nutrient balances. Direct effects result from trampling, which could lead to soil compaction, for example by changing soil aggregate structure (Kotzé et al., 2013; Lobe et al., 2011), and consequently infiltration capacity. Trampling also destroys aggregates, rendering the carbon stored therein vulnerable to degradation. In addition, the megaherbivores may directly affect soil C by depositing dung and urine. In this way, megaherbivores also redistribute carbon and nutrients from one place to another (Wolf et al., 2013). The passage time in an elephant’s gut is usually one or two days (Beirne et al., 2019); hence, dung deposition usually occurs at places different from where the tree was originally browsed. This process increases spatial soil heterogeneity and plant nutrient availability, as also known for grazers (Veldhuis et al., 2018), but likely with different degree of material redistribution.

Indirect effects of megaherbivores on soils can include changes in vegetation composition toward a greater dominance of grasses, which finally affects soil organic matter (SOM) content, and its composition (Cromsigt et al., 2018). Stable 1³C isotopic tracing in soils may help to unravel this imprint. As grasses and woody plants in tropical savannas have different photosynthetic pathways, the δ¹³C values of C₄ grasses are higher (~−13‰) than those of C₃ trees (~−26‰), which is mirrored in the soils (Liao et al., 2006; Sandhage-Hofmann et al., 2020). Thus, tracking the δ¹³C isotope composition of SOM may help to reconstruct changes in the relative abundances of trees and grasses (Bai et al., 2013; Boulton et al., 1999). Extending these analyses to δ¹⁵N stable isotope composition may provide additional indications on the overall ecosystem N use efficiency (Bai et al., 2013; Peri et al., 2012).

The Zambezi Region in north-eastern Namibia lies in an area where land conservation has increased with aspirations for higher wildlife numbers and related socio-economic development (Kalvelage et al., 2020). The region includes several national parks and community-based natural resource management (CBNRM) schemes in close vicinity. Its savanna ecosystems are representative for many other protected areas, where increasing numbers of
wildlife are a prominent goal (Asner et al., 2016). Conservation is particularly promoted within the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA), which was established in 2011. With a size of 520,000 km², it is the largest terrestrial transboundary conservation zone in the world. Elephant numbers rose from around 5000 in 1995 to more than 19,500 in 2018 (Stoldt et al., 2020). The effects of these rising numbers on the carbon stocks in soils are not known, particularly not for the subsoil, which may comprise more than half of ecosystem carbon storage (Batjes, 1996; Duarte-Guardia et al., 2018). Nature-based solutions are increasingly considered as important add-ons to climate change mitigation (Amundson & Biardeau, 2018), for example, via afforestation in respective climate-mitigation-related monitoring programs such as REDD+ (Quijas et al., 2018), by increasing C input into agricultural soil (Amelung et al., 2020; Smith et al., 2020; Sykes et al., 2020), or by protecting carbon in sensitive ecosystems (Goldstein et al., 2020). To our knowledge, there is no study that has investigated carbon stocks down to 1 m soil depth in relation to increasing elephant numbers outside experimental setups.

The main aim of the present study was to quantify the effects of increased elephant numbers on savanna soil characteristics, particularly on soil carbon stocks, and to assess how observable changes in the soil are related to changes in the carbon storage of woody vegetation. We test the hypotheses that higher elephant numbers (1) reduce tree cover, biomass, and the C stored therein, which (2), in turn, may reduce soil carbon stocks. This is highly relevant, as carbon removal by wild herbivores would present a trade-off between climate mitigation through increased carbon storage, and addressing the biodiversity crisis through rewilding, including the reintroduction of large herbivores to help restore self-regulating ecosystems. A rejection of this hypothesis would strengthen ideas of synergies from rising biodiversity with increased C storage (Flores-Rios et al., 2020). Hence, we sampled sites with low, medium, and high elephant density in two national parks and conservation zones of two communal conservancies. The study included the analysis of C and N storage in soils down to 1 m soil depth, together with studies on the tree layer and the C stored therein, and an assessment of the C pools in elephant dung. To unravel changes in past vegetation composition and N cycling, we also recorded soil δ¹³C and δ¹⁵N isotopes.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in Namibia’s Zambezi Region (Figure 1), a central part of the KAZA TFCA (Stoldt et al., 2020). Climate is moist semiarid, with temperatures ranging from a maximum average of 10°C or over in winter, and 36°C or above in summer. Mean annual rainfall ranges between 550 and 600 mm (Mandelsohn, 2007) and falls highly variable during summer, between October and March. The study region is relatively flat, with an average elevation of about 940 m a.s.l.

The Zambezi Region is part of the Kalahari Basin and covered by thick deposits of Kalahari sand, on which sandy, infertile soils have developed. They are shaped by perennial rivers that formed more fertile soil along the river channels. Approximately half of the Zambezi region is dominated by soils with sand contents of more than 90%, another >10% has sand contents between >70% and 90%. On these deep, nutrient-poor Kalahari sands, Arenosols developed (FAO, 2015). The present study focused on these Arenosols in the western area of the region (Figure 1). The Zambezi Region falls in the Mombo ecoregion, an area of savanna woodlands and dry open forests in south-central Africa (Frost, 1999). Our study area is classified as ‘Kalahari woodland’ (Mandelsohn, 2007), where the tree layer is dominated by species such as Terminalia sericea, Pterocarpus angolensis, and Baikiaea plurijuga.

Approximately 21% of the Zambezi Region is covered by three national parks: Bwabwata (3.137 km²), Mudumu (737 km²), and Nkasa Rupara (337 km²). As in all parts of KAZA TCFA, the main aim of these national parks is to increase biodiversity and wildlife numbers with free migration between countries (Stoldt et al., 2020). In Namibia, this is combined with models for socio-economic development of communities, which aim to involve local people in the management of natural resources and benefit by generating income for them, for example through tourism. Communal conservancies have designated conservation zones (core areas), which are intended for wildlife only. Ranging and settlements are not allowed, but in reality, activities such as grazing by livestock could occur. Population densities of elephant and other mammal herbivore species such as giraffe, buffalo, hippo, impala, wildebeest, zebra, and springbok have increased considerably in the Namibian part of KAZA since the 1960s (Stoldt et al., 2020), with elephant numbers being close to 20,000 animals now. Further increases are envisioned for the future. In the core areas of the conservancies, wildlife numbers are highly variable, but still low (Mashi-Report, 2019; Wuparo-Report, 2018).

2.2 | Study design

To assess the impact of increasing numbers of elephants on the two ecosystem compartments “soil” and “woody vegetation”, the sampling was stratified into three elephant density classes: low, medium, and high population densities. Sites with medium and high elephant densities were located in the national parks Mudumu and Bwabwata, while sites with low densities were placed in the core areas of the conservancies Mashi and Wuparo (Figure 1), adjacent to the national parks. Sampling took place in September/October 2018 and in April to June 2019. In all, 10 independent observation plots (25 x 40 m) were selected per site (60 in total). Plots had a minimum distance of 200 m. All sites had a similar (flat) topography, and were located on Arenosols. They also showed no visible signs of recent fires, and displayed a comparatively homogeneous vegetation structure and composition. As elephant densities are a function of distance to water, plots with higher elephant densities were located in closer...
distance to the river than those with medium densities. Minimum distance to water was 1.5 km to minimize inundation effects.

2.3 Estimation of herbivore densities and elephant dung

For an expert assessment of recent elephant abundances on our plots, three physical indicators for elephant activities (trampling, dung deposition, and fresh damages of woody plant individuals) were combined (Linstädter et al., 2014). Elephant spoors (tracks and dung deposits) were recorded together with recent signs of elephant browsing activity (freshly broken branches, peeled barks, and torn off leaves). These three proxies were combined into an indicator for recent elephant abundance in and around the plot. Values ranged from zero (no elephants) to five (>80% of biomass lost due to elephant browsing). Separate assessments were performed for trees and shrubs, and for old losses (>2 years) and recent losses (≤2 years), following O’Connor and Page (2013). The four values were then summed, resulting in values on an ordinal scale of 0–20. We treated ordinal data as quasi-numerical in further analyses.

Our overall approach allowed us to reach indirect conclusions about elephant densities on the plot level. In the nearby Chobe National Park (<100 km distance), it was found that, in the dry season, 4–7.7 elephants km\(^{-2}\) occurred directly at the riparian riverfront, whereas only 0.9–1.1 elephants km\(^{-2}\) occurred in the Kalahari woodlands far away from the river (Chase, 2013; du Toit et al., 2014). These values, together with our indirect density assessments, indicate for the plots under study that the average elephant densities on the investigated areas are also in this order of magnitude; that is, between <1 elephant km\(^{-2}\) in the low-density plots to >4 elephants km\(^{-2}\) in the high-density plots.
To estimate transient C pools in elephant dung, we performed visual estimations of herbivore dung cover on our plots (dung area m$^{-2}$) and estimated the relative contribution of elephant dung to total dung cover at each plot. We focused on elephant dung because contribution in area and size was highest. Additionally, dung of other herbivores varies widely in size and C content (Sitters et al., 2014), rendering these materials less reliable for estimating transient C pools.

$$\text{Dung C kg ha}^{-1} = \text{Dung cover (m}^2\text{ha}^{-1}) \times \text{height of bolus (dm)} \times \text{density of bolus (kg dm}^{-3}\text{)} \times \text{dry weight (kg)} \times \text{C content (\%)} \times \text{corr}, \quad (1a)$$

with bolus height set at 1.4 dm, bolus density set at 0.5 kg dm$^{-3}$ (Morrison et al., 2005), dry bolus dry weight at 20% (Anderson & Coe, 1974)*C content of dry weight set at 39% (Stanbrook, 2018) and a volume correction factor corr ($1/6\pi$, to correct for the cubic shape of a bolus). To check the plausibility of our calculations, we used an alternative method to estimate average dung C pools for the sites situated in the two national parks Bwabwata and Mudumu, based on elephant densities in the two parks, and defecation rates (Equation 1b)

$$\text{Dung C kg ha}^{-1} = \frac{\text{Park size (ha)} \times \text{elephant numbers} \times \text{fresh dung per elephant (kg day}^{-1}\text{)}}{\text{bolus dry weight (kg)} \times \text{C content (\%)} \times 365 \text{ days}}. \quad (1b)$$

Data for the national parks were obtained from landscapes.namibia.org, fresh dung deposition set at 150 kg dm$^{-3}$ (Haynes, 2012), bolus dry weight set at 20% (Anderson & Coe, 1974), and C content of dry weight set at 39% (Stanbrook, 2018).

### 2.4 Assesment of carbon stocks in woody vegetation

To accurately estimate carbon stocks in woody vegetation for our disturbance-prone study ecosystems, we developed a novel methodology to estimate biomass of heavily damaged woody individuals and stands; see Kindermann et al. (2020). We recorded tree and shrub individuals growing on the plots with their species identity and with a suite of dendrometric parameters. To keep sampling efforts in reasonable limits, we used a flexible sampling strategy with a nested plot design; for methodological details, see Kindermann et al. (2020). In brief, we stratified our sampling effort according to tree size. Small, sub-adult individuals with a height <50 cm and a basal stem diameter <5 cm were only sampled on 100 m$^2$ subplots, while adult individuals (height ≥50 cm, basal stem diameter ≥5 cm) were recorded on the whole plot area of 1000 m$^2$. For intermediate growth classes (including individuals heavily damaged by elephant browsing), intermediate plot sizes were sampled (see Kindermann et al., 2020). Canopy dimensions were recorded for sub-adult individuals while stem circumferences were additionally recorded for adult individuals. For estimating aboveground biomass (AGB) from these dendrometric proxies, we chose two different allometric models. For adult, comparatively undamaged trees, we used the updated, stem-based model by Chave et al. (2014), which is based on an exceptionally large dataset across all types of tropical forests, including African dry forests. As shrubs and shrub-like growth forms could not be covered with the stem-based model by Chave et al. (2014), we instead deployed a canopy-based shrub model calibrated in close vicinity to our study region, which shared dominant species with our dataset (Meyer et al., 2013). We estimated individuals’ belowground biomass (BGB) using a root-to-shoot ratio (RS ratio). As the RS ratio decreases nonlinearly with tree size (Mugasha et al., 2013), we used an equation developed by Rachambak et al. (2016) for Miombo woodlands to determine individual RS ratios and estimate individual BGB. The AGB and BGB values were then upscaled and expressed as stand-level total woody biomass (BM$_{tot}$). Carbon stocks in woody vegetation (t ha$^{-1}$) were subsequently calculated as 47% of BM$_{tot}$ (Brown, 1997; Ryan et al., 2011).

### 2.5 Soil sampling and analyses**

To capture differences in soil carbon stocks across different microsites that are typical for dryland ecosystems (Ochoa-Hueso et al., 2018), we distinguished between three habitat types (following Gaitán et al., 2019), and sampled under trees (subcanopy), between trees (interscapopy, mostly grass), and in bare soil without any visible vegetation cover. For each habitat type, we visually estimated their ground cover on the 1000 m$^2$ plots, with the three estimations summing up to 100%. We took one soil core in each of the three habitat types per plot (three cores per plot), with sampling concentrated on the 100 m$^2$ subplots. To analyze the effects of habitat characteristics on soil organic carbon, soil samples were treated separately; for site-level estimates, soil data obtained in the three habitat types were scaled up according to the percentages of the habitat cover. For the majority of habitat patches (153 out of 180), sampling was done to 100 cm depth, using an electrical soil auger of 6 cm in diameter. A smaller part of the plots was sampled with a hand auger up to a soil depth of 50 cm. The auger cores were divided into six depth classes (0–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm).

Each soil sample was weighted for fresh and dry weight. Dry bulk density was determined by weighing the air-dried subsamples and dividing the weight by the respective soil volume in the auger (Walter et al., 2016). Particle-size analyses were performed using the sieve-pipette method (The Non-Affiliated Soil Analysis Work Committee, 1990) according to (FAO, 2015). The concentrations of total C and N were determined by dry combustion using a CHNS analyzer (Elementar-Analysensysteme GmbH). There was no detectable inorganic C, which meant that total C was equal to organic C, hereafter SOC. The $^{13}$C and $^{15}$N values were analyzed using an isotope ratio mass spectrometer (Delta V Advantage IRMS, Thermo Electron Corporation) according to Equation (2)

$$\delta = \frac{R(\text{sample}) - R(\text{standard})}{R(\text{standard})} \times 1000, \quad (2)$$

where $R(\text{sample})$ is the $^{13}$C/$^{12}$C and $^{15}$N/$^{14}$N isotope ratio of the sample and $R(\text{standard})$ is the $^{13}$C/$^{12}$C and $^{15}$N/$^{14}$N isotope ratio of the standard with respect to the V-PDB standard for carbon isotopes and the atmospheric dinitrogen standard for nitrogen isotopes (Coplen et al., 2006).
We used the $\delta^{13}C$ values of soils and plant material (woody and grass biomass, from leaves of trees and tufts of grass) to estimate the relative proportion of SOC derived from $C_3$ photosynthetic pathways using the following equation (Boutton et al., 1998).

$$FC3 = \frac{\delta^{13}C_{soil} - \delta^{13}C_4}{\delta^{13}C_3 - \delta^{13}C_4},$$

with $\delta^{13}C_{soil}$ being the measured $\delta^{13}C$ value of the soil sample, $\delta^{13}C_4$ the average $\delta^{13}C$ value of mixture of grass species ($-14.3\%$),, and $\delta^{13}C_3$ the average $\delta^{13}C$ value of woody plant material from *Terminalia sericea* vegetation ($-27.1\%$).

Carbon stocks were calculated according to Equation (3)

$$C_{stock} = SOC \times BD \times D/10,$$

where $C_{stock}$ is soil organic carbon stocks (t ha$^{-1}$), SOC is soil organic carbon concentration (g kg$^{-1}$); BD is soil bulk density (g cm$^{-3}$); and D is soil depth (cm) (Deng et al., 2016).

### 2.6 Statistical analyses

The statistical analyses were performed using the R statistic package (Version 3.6.3.; lm package). All data had to be transformed with Tukey’s Ladder of powers on a vector of values to achieve normality according to the Shapiro–Wilks test. To analyze the impact of different elephant densities on carbon storage in tree biomass, soil C, and N stocks, FC3, and dung, we used linear mixed models with the three elephant densities as fixed factors and site as the random effect. Tukey post-hoc tests were performed for multiple comparisons.

### 3 RESULTS

#### 3.1 Biomass and carbon stocks in woody vegetation and dung

As expected, woody biomass losses increased significantly in the order of low < medium < high elephant density (Table 1). These changes coincided with a decline in woody tree cover in the same direction, with the differences between sites with low and high elephant densities being significant ($p = 0.045$; Table 1). Herbaceous cover was significantly elevated at medium-density plots ($p = 0.016$), while bare ground seemed to be elevated at high animal densities, but these differences were not significant (Table 1).

According to our hypothesis, total woody biomass (AGB plus BGB) decreased with increasing elephant density (Table S2). Accordingly, the C stored in woody biomass decreased in the same direction, and plots with high elephant density contained approximately 20 t ha$^{-1}$ less woody biomass than plots with low elephant density (Figure 2). Differences between low and high elephant density plots were significant ($p = 0.021$), despite high variability.

Elephant dung contributed to at least 70%–75% to total dung cover on all plots (individual data not shown). The quantity of carbon stored in elephant dung (calculated with Equation 1a) ranged between 24 and 328 kg C ha$^{-1}$ (Table 2a; Figure 4) with no significant differences between plots of different elephant densities. Calculations with elephant densities per park and dung deposition (Equation 1b) resulted in comparable values of 224 kg ha$^{-1}$ year$^{-1}$ in Bwabwata, and 266 kg in Mudumu National Park (Table 2b).

#### 3.2 Carbon storage in soils

The Arenosols showed the typical predominance of sand (95.4% ± 2.6) and low contents of silt (2.5% ± 2.1) and clay (1.7% ± 1.1; F = 6.5, Table S3). Texture composition did not change among sites and, thus, also not with variations in elephant densities. Soil texture also hardly changed with soil depth (data not shown). The bulk density of all plots averaged 1.48 g cm$^{-3}$ in the topsoil (0–10 cm) and increased to 1.7 g cm$^{-3}$ in 70–100 cm soil depth. There was no significant compaction in the surface soil due to animal trampling. Overall, different densities of elephants had only small effects on bulk densities in this sandy environment (Table S4).

As is also typical for Arenosols, all sites showed low concentrations of SOC, which decreased steeply with increasing soil depth from an average of 4.6 g kg$^{-1}$ C in 0–10 cm to 1.2 g kg$^{-1}$ C in 70–100 cm (Table S4). Higher wildlife densities resulted in higher carbon concentrations within the top 50 cm of soil. This effect was significant for the first 30 cm of soil ($p = 0.011$) except for 0–10 cm but still visible in the subsoil. Overall, carbon concentrations in the

| Table 1 Evidence for the presence and impact of elephants at the plot level (0.1 ha) in the three elephant density classes |
|-----------------------------------------------|
| Elephant density class | Woody biomass losses | Recent elephant abundances | Subcanopy (%) | Intercanopy (%) | Bare soil (%) |
|-------------------------|---------------------|--------------------------|--------------|----------------|-------------|
| Low                     | 4 ± 1.2 a           | 1.4 ± 0.7 a              | 46.6 ± 18.8 a | 12.7 ± 15.1 a | 40.7 ± 18.4 a |
| Medium                  | 7 ± 3.3 b           | 2.2 ± 0.6 ab             | 36.2 ± 19.1 ab | 23.9 ± 17.3 b | 39.9 ± 19.6 a |
| High                    | 11 ± 2.4 c          | 4.1 ± 0.6 b              | 32.6 ± 15.3 b | 13.4 ± 20.9 a | 54.0 ± 19.4 a |

Note: Given are woody biomass losses due to elephant browsing (scale 0–20, where 0 is no loss and 20 is severe losses); recent elephant abundances according to physical signs of elephant presence on the plots (trampling, dung deposition, and visible damages of woody vegetation due to browsing; scale 0–5, where 0 is no animals, and 5 is very high animal abundances); and percent cover of habitat types on plots (subcanopy, intercanopy, and bare soil patches). Shown are mean values ± standard deviations. Different letters show significant differences ($p < 0.05$) for comparisons between elephant density classes.
low-density plots were up to 21% and 18% lower than in high- and medium-density plots, respectively.

Total nitrogen concentrations followed the patterns of SOC, but differences between sites were more pronounced (Table S4; significant for the top 20 cm). The plots with low elephant density stored only a quarter of the nitrogen than plots with high elephant density (top 20 cm). Hence, C/N ratios also showed significant differences among sites, with the highest values measured in plots with medium and low density.

The stratification of the soil sampling according to habitat types allowed us to differentiate SOC and N storage in three different types: woody vegetation patches, grass vegetation patches, and bare soil patches. The highest SOC concentration was found under subcanopy woody vegetation patches, grass vegetation patches, and bare soil (4.1 g C kg⁻¹). The differences were not significant but indicated potential differences in SOC storage of up to 2 t C ha⁻¹ across different patch types (Table S5).

When habitat-level soil organic carbon stocks were upscaled to the plot-level based cover on each plot (Table 1), we found that half of the SOC was stored in the top 30 cm of the soil. Intriguingly, SOC stocks were highest in the plots with high elephant density (30.8 t ha⁻¹), followed by those with medium (28.8 t ha⁻¹), and low impact of elephants on woody vegetation (26.6 t ha⁻¹). The differences in SOC storage between plots with low and high elephant densities were significant (F = 6.5, p < 0.002; Figure 3). Differences in total N storage followed the same directions as those in SOC (Figure S1), again with significant differences in element storage between sites of low and high elephant densities (F = 5.12, p < 0.005).

Overall, our results point to losses of 6.4 t C ha⁻¹ in woody biomass at sites with high elephant density relative to the low-density sites with least impact of elephants. In contrast, SOC stocks increased by 4.7 t C ha⁻¹ with increasing numbers of elephants. Hence, there was still an apparent loss of 1.7 t C ha⁻¹ (Figure 4).

### 3.3 | Origin of soil organic matter

The stable carbon isotope composition (δ¹³C) of the plant litter reflected the differences in photosynthetic pathways between the C₄ grasses (δ¹³C = −14.3‰) and the C₃ woody vegetation component (δ¹³C = −27.1‰ Terminalia sericea). All sites sampled showed a slight dominance of C input from C₃ plants into the soils, resulting in higher proportions of SOC (FC3) derived from woody vegetation (Table S5). Averaged values showed only small differences between the three levels of elephant density. However, differences became apparent when differentiating among the three habitat types: The portions of wood-derived carbon (FC3) in soil increased in intercanopy and bare soil when elephant density increased (Figure 5; Table S5), indicating an increased input of woody components into the soil.

The δ¹⁵N isotopic composition of the topsoils (0–10 cm) showed also clear, significant differences among sites with different elephant densities: the site with the largest elephant impact revealed the highest soil δ¹⁵N values (Figure S2). As elephant densities declined, also soil δ¹⁵N values declined, both in the topsoil as well as in the subsoil (Figure S2).

### 4 | DISCUSSION

The results of our study showed that a shift from low to high elephant numbers reduced the amount of tree biomass and that of carbon stored therein by 6.4 t ha⁻¹. Contrary to our second hypothesis, though, SOC stocks increased with higher elephant densities by 4.7 t ha⁻¹. Consequently, soil carbon gains almost offsets woody carbon losses. We assume that two carbon input sources are responsible for this compensation: (i) the formation of SOC from decaying tree and shrub biomass, such as elephant toppled trees and broken branches lying on the ground, and decomposing tree roots and (ii) the deposition of dung

![Figure 2](https://example.com/figure2.png)

**Figure 2** Carbon storage in woody vegetation (t ha⁻¹) at sites with different elephant densities. Different letters indicate significant differences (p < 0.05) between elephant densities

| Elephant density class | Total dung cover (m² ha⁻¹) | Elephant dung cover (m² ha⁻¹) | C stocks in elephant dung (C kg ha⁻¹) |
|------------------------|-----------------------------|-----------------------------|-------------------------------------|
| Low                    | 1.3 ± 2.4                   | 0.8 ± 1.4                   | 24.2 ± 42                           |
| Medium                 | 8.3 ± 9.2                   | 5.9 ± 6.8                   | 167 ± 194                           |
| High                   | 15.0 ± 11.7                 | 11.5 ± 9.0                  | 328 ± 276                           |

Note: There were no significant differences for comparisons between elephant density classes.
from megaherbivores in plots with high elephant density. In the high elephant density plots, the dung-derived C amounted 328 kg C ha\(^{-1}\). Adding this amount to the C gains in soils reduced the offset of C losses from browsed woody vegetation to ≤1.4 t C ha\(^{-1}\) (Figure 4).

In the KAZA TCFA area, elephant numbers are a main indicator for the success of nature conservation. In this respect, conservation measures of recent decades have been successful, because elephant numbers have increased in Namibia’s Zambezi Region (Stoldt et al., 2020). Megaherbivores play an important role in structuring natural ecosystems and their biodiversity (Estes et al., 2011; Ripple et al., 2014). However, also negative impacts of elephants have been reported, due to the decline of woody biomass, depending on elephant numbers, sex, rainfall, and distance to river (Davies & Asner, 2019; Pellegrini et al., 2017; Skarpe et al., 2014; Tanentzap & Coomes, 2012). Our results of 33% losses are in line with these studies, and support our first hypothesis that higher elephant densities lead to substantial loss of woody biomass and related C stocks. Apart from the direct impacts of elephants also other drivers such as fire, a selective browsing of nutrient-rich trees (Teren et al., 2018) and the potential interactions of these drivers with elephants may have contributed to the losses of aboveground woody biomass (Pellegrini et al., 2017). In this study, we cannot decipher the contribution of each individual factor, but following Davies and Asner (2019) we consider the impact of elephants to be the dominant one.

While the effects of elephants on woody biomass have been studied before, their effects on soil characteristics remained largely unknown. This study filled this gap. Bulk densities measured in our study were similar to those reported for other sandy soils in southern Africa (Hartemink & Huting, 2008), Yet, we did not find any indication that increasing numbers of elephants compacted the soils (Table S3). Such compaction has been observed, though, for other African savanna ecosystems under the impact of cattle grazing (Kotzé et al., 2013; Schrama et al., 2013), or high wildlife numbers (Holdo & Mack, 2014). The latter study found higher bulk densities in areas with herbivores (including elephants with a stocking density of 0.8–1.2 elephants km\(^{-2}\)) than in exclusion areas without wildlife (sandy and loamy soil). Cumming and Cumming (2003) reported that trampling pressure was highest in elephant dominated wildlife areas compared with areas that lacked elephants or which were used for livestock grazing only (stocking density of elephants 1.2–3 km\(^{-2}\)), which is in line with the general assumption that trampling pressure rises with rising body mass (Cromsigt et al., 2018). Yet, increased mechanical pressure is frequently associated with the breakdown of aggregates (Kotzé et al., 2013; Lobe et al., 2011). The sandy Arenosols hardly contain aggregates (Sandhage-Hofmann et al., 2015). Possibly, elephant numbers in the Zambezi Region (Table 2b) are still too low to lead to a significant compaction of Arenosols.

### 4.1 Soil carbon sequestration

Many studies have observed a positive correlation between the loss of aboveground biomass and the loss of soil organic carbon, both in...
agricultural fields (Lobe et al., 2005), as well as in forests (Achat et al., 2015). Our second hypothesis was in accordance to these findings, however, our results showed the opposite. In general, soil carbon concentrations and stocks were low, reflecting the poor nutrient status of the Arenosols, but they were in line with slightly higher C stocks measured in adjacent parts of the Zambezi Region, where woodlands indicated SOC concentrations in the topsoil of 6.9 g kg⁻¹ and SOC stocks for 100 cm soil depth of up to 47.9 t C ha⁻¹ (de Blécourt et al., 2018). Here, we found elevated SOC stocks at sites with high and medium elephant densities (Figure 3), opposing the C storage in woody vegetation (Figure 2). Overall, in plots with higher numbers of elephants and associated megaherbivores SOC stocks increased by 4.7 t C ha⁻¹, with almost 3.2 t C ha⁻¹ stored in the top 30 cm of soil (Figures 3a and 4). The remaining gain in SOC occurred in the subsoil. This finding is different from Holdo and Mack (2014), who found similar SOC concentrations in and outside a fenced area that excluded wildlife like elephants, but dissimilar bulk densities: possibly, the elevated bulk densities in wildlife-influenced areas impaired increased SOC input. However, our results are consistent with a recent experiment conducted in Kenya. Here, the composition of the animals (cattle and wildlife) was manipulated by fences. More than 20 years after the experiment started, the plots with mega- and mesoherbivores exhibited elevated SOC stocks by up to 14% (upper 15 cm) relative to plots that did not have these animals or that were grazed by cattle (Sitters et al., 2020).

Stable ¹³C isotope tracing allows to identify the origin of the C gain. Browsing megaherbivores like elephants can change vegetation structure from a comparatively closed woodland to an open savanna (Skarpe et al., 2014). On the one hand, this can leave more space for C₄ grasses, forming SOC that has higher δ¹³C values than that formed by the C₃ shrubs or trees (Bai et al., 2012; Boutton et al., 1998; Sandhage-Hofmann et al., 2020). On the other hand, toppling of trees by elephants, remaining browsing material, and decomposition of roots could result also in an even higher input of C₃-derived C into the soils. In our study, the higher elephant densities were associated with an opening of the vegetation (Table 1), but we did not detect significant changes in overall soil δ¹³C values (−21.4‰), indicating a mixing of C₃- and C₄-derived vegetation remnants for SOC formation (Bai et al., 2012; Boutton et al., 1998; Liao et al., 2006). But we did detect changes in the origin of SOC in different habitat types: in intercanopy and bare soil habitats portions of wood-derived C increased with rising levels of elephant densities, whereas the woody vegetation patches contained elevated portions of wood-derived C already (Figure 5; Table S5). The results are in line with those in the manipulation experiments by Sitters et al. (2020), where the authors also observed a substantial input of C₃-derived C into the soils induced by megaherbivores. Obviously, tree toppling and broken parts of trees do not necessarily lead to net carbon losses from the savanna ecosystem, as significant portions of this C was transferred into the soil.
In addition, there appears to be a C transfer within the ecosystem, which is directly mediated by the elephants. An adult African elephant defecates 20–30 times a day, releasing up to 100 boluses of 1–2 kg (Haynes, 2012; Stanbrook, 2018) per day, summing up to 150 kg fresh dung or 30 kg dry weight dung day\(^{-1}\). With the given elephant numbers for the national parks (Table 2b), this makes 223–250 kg C ha\(^{-1}\) year\(^{-1}\) (Table 2b). These are maximum estimates assuming that all elephants were adults; younger elephants may defecate less than 150 kg dung day\(^{-1}\) (Coe, 1972). Hence, true total average dung deposition is likely a bit lower in the park, but will remain well in the range between our low and high elephant density plots. Our calculations based on dung cover estimates were in the same range (2a) and showed dung input values of 328 kg C ha\(^{-1}\) year\(^{-1}\) for the plots with high elephant density. Elephants accounted approximately for three quarters of the dung found on the plots. An additional input of C originates from other herbivores, where the mass of their dung typically accounts for only 2%–13% of the mass of elephant dung, and thus the carbon deposited by them (Sitters et al., 2014). This dung from other large megaherbivores, such as giraffe, zebra, and impala, megaherbivores might thus further reduce the gap between C losses and gains by another 45 kg C ha\(^{-1}\) year\(^{-1}\).

Overall, transient storage of C in the dung of animals reduced the gap between aboveground C loss from browsing and SOC accrual to ≤1.4 t C ha\(^{-1}\) (Figure 4). The mean residence time of C storage in the dung may vary depending on habitat type, climate, nutrient stoichiometry (Sitters et al., 2014), and lignin contents (Chaudhary et al., 2020). At the dry climate of KAZA, the C loss from the dung will largely occur as CO\(_2\), or it is taken away by small animals such as beetle and termites (Andriuzzi & Wall, 2018). Yet, there are also continued dung-C reimports, constantly replenishing the pool and compensating the losses (Zhu et al., 2020), that is, under steady-state conditions the amount of C in the dung is withdrawn from the atmosphere irrespectively of the dung turnover time. Future studies should thus include the amount of dung C into climate change mitigation calculations, because even this labile dung C may add to climate change mitigation if the decomposing dung is continuously replaced by fresh one.

Dung does not only concentrate C but also N. The N-input via dung was 0.8 kg ha\(^{-1}\) for the low, 6 kg ha\(^{-1}\) for the medium, and 11 kg ha\(^{-1}\) for the high elephant densities. Notably, both soil N and soil \(\delta^{15}\)N values were thus larger at sites with higher elephant densities (Figure S2). Apparently, there was no selective browsing of N fixing trees to a degree that it would have lowered the overall soil \(\delta^{15}\)N signatures. Codron et al. (2005) observed that urine and feces from browsers were generally \(\delta^{15}\)N enriched compared to grazers, which is in support of our findings. The authors attributed this to more concentrated urine (and feces), and protein intake, which appears to have the primary influence on herbivore feces \(\delta^{15}\)N. As N losses primarily affect lightweight N isotopes (Högberg, 1997), elevated \(\delta^{15}\)N values frequently indicate lower N use efficiencies (Bai et al., 2013). Significant N losses may occur, for example, during feces formation (Masunga et al., 2006). The degree at which increasing elephant numbers also affects \(\mathrm{N}_2\mathrm{O}\) greenhouse gas emissions thus warrants further attention.

### 4.2 Carbon storage in woody biomass, dung, and soil

Woody biomass and soils together stored 43.4–45.5 t C ha\(^{-1}\) in the savanna woodlands of the Zambezi Region. These values were in the range of savanna systems in Brazil, where between 20 and 84 t C ha\(^{-1}\) were stored in topsoils (20 cm; Abreu et al., 2017). However, the study underestimated total SOC storage across whole profile depth by up to 50% (Table S3; see Kothandaraman et al. (2020)). In general, herbaceous biomass comprises usually only between 0.5% and 10% of the carbon storage of the aboveground savanna biomass (Abreu et al., 2017; Kothandaraman et al., 2020; Pellegrini et al., 2014). The total amount depends on woody cover. Taking this low carbon storage in herbaceous vegetation into account, our estimation of aboveground and belowground carbon stored in woody vegetation captured the majority of the carbon stored in the vegetation component of the savanna ecosystem.

In our study, we found that elephants caused up to 6.4 t C ha\(^{-1}\) losses of woody biomass. However, increases in soil carbon due to rising elephant densities largely compensated for these carbon losses due to woody biomass removal (Figure 5), leaving a gap of only 1.7 t C ha\(^{-1}\) in sites with high elephant densities. Generally, SOC sequestration

**FIGURE 5** Proportion of woody biomass (FC3%) in soils under grass and bare soil patches in plots with different elephant densities and in different soil depth. Different letters indicate significant differences (p < 0.05) between elephant densities.
is facilitated by an increase in C input (Amelung et al., 2020). Hence, the presence of animals affected the C balance of the savanna system much less than hypothesized. Even in the subsoil, a substantial part of carbon was sequestered. Obviously, the loss of woody biomass does not necessarily entail losses of SOC, and the general observation that shifts in savanna woody biomass alter carbon stocks in the same direction (Pellegrini et al., 2017) have to be reconsidered if megaherbivores are involved.

Our results should be of major interest for future biodiversity conservation measures including (trophic) rewilding. This increasingly popular approach aims to restore ecosystems through trophic rewilding by repopulating them with mega-herbivore species; increasing biodiversity and combating the extinction crisis (Bakker & Svenning, 2018). Aboveground carbon removal by wild herbivores presents a trade-off between climate mitigation through increased carbon storage and addressing the biodiversity crisis through rewilding. But, as current data show, restoring elephant densities does not necessarily lead to a pronounced negative carbon footprint. A major fraction of woody biomass C is merely redistributed into soil during decomposition. Including soil into ecosystem assessment could therefore help to better align climate mitigation measures with those of biodiversity conservation, thereby linking two large scientific directions with the aim of potentially reducing joint coordination efforts for reaching the sustainable development goals. Future studies might also be needed to test these findings for soils other than the dominating Arenosols, such as well-structured soils with potential risk of aggregate disintegration. Besides, there is a research need to clarify to what extent increasing numbers of megaherbivores can be coupled to the restoration of other ecosystem services (Bakker & Svenning, 2018; Flores-Ríos et al., 2020).

5 | CONCLUSION

Our study for the first time provides data of carbon stocks for the most important ecosystem compartments in relation to different elephant densities in Sub-Saharan conservation areas. Our assessments included not only C pools in woody vegetation but also in soil down to a depth of 1m and elephant dung. Conservation in Sub-Saharan Africa is inextricably linked to wildlife numbers and as such, it is also one of the major aspirations of the KAZA. Since 2011, wildlife numbers have increased steadily, with largely unknown impacts on specific ecosystem compartments such as soils. The effects of elephants on vegetation structure have often been seen as initiating a decline in carbon storage of woody vegetation (Davies & Asner, 2019). Our study confirms a loss of carbon stored in woody biomass but reports an unexpected gain of carbon stored in soils. To date, the role of soils for carbon storage has been neglected in the vivid debate on ecological effects of conservation and the rising numbers of wildlife, which is surprising given that soils are a much larger terrestrial carbon reservoir than vegetation. The present study showed that increases in SOC from decaying woody material and dung inputs largely offset C losses in woody biomass.

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CONFLICT OF INTEREST

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the database of TRR228. https://www.trr228db.uni-koeln.de/, http://dx.doi.org/10.5880/TRR228DB.4.

ORCID

Alexandra Sandhage-Hofmann https://orcid.org/0000-0002-1766-8002
Anja Linstädter https://orcid.org/0000-0003-0038-9557
Liana Kindermann https://orcid.org/0000-0002-8126-2576
Simon Angombe https://orcid.org/0000-0002-5144-1370

REFERENCES

Abreu, R. C. R., Hoffmann, W. A., Vasconcelos, H. L., Pilon, N. A., Rossatto, D. R., & Durigan, G. (2017). The biodiversity cost of carbon sequestration in tropical savanna. Science Advances, 3(8), e1701284. https://doi.org/10.1126/sciadv.1701284
Achat, D., Fortin, M., Landmann, G., Rengevink, B., & Augusto, L. (2015). Forest soil carbon insthreatened by intensive biomass harvesting. Scientific Reports, 1–10. https://doi.org/10.1038/srep15991
Alam, S. A., Starr, M., & Clark, B. J. F. (2013). Tree biomass and soil organic carbon densities across the Sudanese woodland savannah: A regional carbon sequestration study. Journal of Arid Environments, 89, 67–75. https://doi.org/10.1016/j.jaridenv.2012.10.002
Amelung, W., Bossio, D., de Vries, W., Kögel-Knabner, I., Lehmann, J., Amundson, R., Bol, R., Collins, C., Lal, R., Leifeld, J., Minasny, B., Pan, G., Paustian, K., Rumpel, C., Sanderman, J., van Groenigen, J. W., Mooney, S., van Wesemael, B., Wander, M., & Chabbi, A. (2020). Towards a global-scale soil climate mitigation strategy. Nature Communications, 11(1), 5427. https://doi.org/10.1038/s41467-020-18887-7
Amundson, R., & Biardeau, L. (2018). Soil carbon sequestration is an elusive climate mitigation tool. Proceedings of the National Academy of Sciences of the United States of America, 115, 11652–11656. https://doi.org/10.1073/pnas.1815901115
Anderson, J. M., & Coe, M. J. (1974). Decomposition of elephant dung in an arid environment. Oecologia, 14, 111–125.
Andriuzzi, W. S., & Wall, D. H. (2018). Soil biological responses to, and feedbacks on, trophic rewilding. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 373(1761). https://doi.org/10.1098/rstb.2017.0448
Asner, G. P., Vaughn, N., Smit, I. P. J., & Levkiv, S. (2016). Ecosystem-scale effects of megafauna in African savannas. Ecosphere, 39(2), 240–252. https://doi.org/10.1002/ecs2.1640

Bai, E., Boutton, T. W., Liu, F., Wu, B., & Archer, S. R. (2013). δ13C in a subtropical savanna parkland: Spatial-temporal perspectives. Ecosphere, 4, 1–17.

Bai, E., Boutton, T. W., Liu, F., Wu, X. B., Hallmark, C. T., & Archer, S. R. (2012). Spatial variation of soil δ15N and its relation to carbon input and soil texture in a subtropical lowland woodland. Soil Biology and Biochemistry, 44(1), 102–112. https://doi.org/10.1016/j.soilbio.2011.09.013

Bakker, E. S., & Svenning, J. C. (2018). Trophic rewilding: Impact on ecosystems under global change. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 373(1761). https://doi.org/10.1098/rstb.2017.0432

Batjes, N. H. (1996). Total carbon and nitrogen in the soils of the world. European Journal of Soil Science, 47, 151–163. https://doi.org/10.1111/j.1365-2389.1996.tb01386.x

Beirne, C., Nuñez, C. L., Baldino, M., Kim, S., Knorr, J., Minich, T., Jin, L., Xiao, S.,Mbamy, W., Obiang, G. N., Masseloux, J., Ngkoge, T., Ebanea, M. O., Rundel, C., Wright, J. P., & Poulsen, J. R. (2019). Estimation of gut passage time of wild, free roaming forest elephants. Wildlife Biology, 2019(1), https://doi.org/10.2981/wlb.00543

Bocherens, H. (2018). The rise of the anthroposphere since 50,000 years: An ecological replacement of megaherbivores by humans in terrestrial ecosystems? Frontiers in Ecology and Evolution, 6. https://doi.org/10.3389/fevo.2018.00003

Boutton, T. W., Archer, S. R., & Midwood, A. J. (1999). Stable isotopes in ecosystem science: Structure, function and dynamics of a subtropical savanna. Rapid Communications in Mass Spectrometry, 13(13), 1263–1277.

Boutton, T. W., Archer, S. R., Midwood, A. J., Zitzer, S. F., & Bol, R. (1998). δ13C values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem. Geoderma, 82(1–3), 5–41. https://doi.org/10.1016/S0016-7061(97)00095-5

Brown, S. (1997). Estimating biomass and biomass change of tropical forests: A primer. FAO Forestry Paper (Vol. 134). Food and Agriculture Organization of the United Nations.

Bunney, K., Bond, W. J., & Henley, M. (2017). Seed dispersal kernel of the African elephant (Loxodonta africana). The South African Journal of Wildlife Research, 24(5), 1368–1382. https://doi.org/10.1111/gcb.14585

de Blécourt, M., Röder, A., Gröning, A., Baumann, S., Frantz, D., & Eschenbach, A. (2018). Deforestation for agricultural expansion in SW Zambia and NE Namibia and the impacts on soil fertility, soil organic carbon- and nutrient levels. Biodiversity & Ecology, 6, 242–250. https://doi.org/10.7809/b-e.000330

de Boer, W. F., Van Oort, J. W. A., Grover, M., & Peel, M. J. S. (2015). Elephant-mediated habitat modifications and changes in herbivore species assemblages in Sabi Sand, South Africa. European Journal of Wildlife Research, 61(4), 491–503. https://doi.org/10.1007/s10344-015-0919-3

Deng, L., Zhu, G.-Y., Tang, Z.-S., & Shangguan, Z.-P. (2016). Global patterns of the effects of land-use changes on soil carbon stocks. Global Ecology and Conservation, 5, 127–138. https://doi.org/10.1016/j.gecco.2015.12.004

Dirzo, R., Young, H., Galetti, M., Ceballos, S., Isaac, N., & Collen, B. (2014). Defaunation in the Anthropocene. Science, 345, 401–406. https://doi.org/10.1126/science.1251817

du Toit, J., Moe, S., & Sarke, C. (2014). Elephant-mediated ecosystem processes in Kalahari-sand woodlands. In C. Sarke, J. du Toit, & S. Moe (Eds.), Elephants and savanna woodlands ecosystems, A study from Chobe National Park, Botswana. (pp. 30–41). Wiley Blackwell.

Duarte-Guardia, S., Peri, P. L., Amelung, W., Shel, D., Laflan, S. W., Borchard, N., Bird, M. I., Dieleman, W., Pepper, D. A., Zutta, B., Jobbagy, E., Silva, L. C. R., Bonser, S. P., Berhongaray, G., Piñeiro, G., Martinez, M.-J., Cowie, A. L., & Ladd, B. (2018). Better estimates of soil carbon from geographical data: a revised global approach. Mitigation and Adaptation Strategies for Global Change, 24(3), 355–372. https://doi.org/10.1007/s11027-018-9815-y

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoeno, T. W., Wardle, D. A. (2011). Trophic downgrading of planet Earth. Science, 333, 301–306. https://doi.org/10.1126/science.1205106

FAO. (2015). World reference base for soil resources 2014. International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Report 106 (pp. 1–193). Food and Agriculture Organization of the United Nations.

Flores-Rios, A., Thomas, E., Peri, P. P., Amelung, W., Duarte-Guardia, S., Borchard, N., Lizarraga-Travaglini, A., Vélez-Azañero, A., Shel, D., Tscharntke, T., Steffan-Dewenter, I., & Ladd, B. (2020). Co-benefits of soil carbon protection for invertebrate conservation. Biological Conservation, 252. https://doi.org/10.1016/j.biocon.2020.108859

Frost, P. G. (1999). Fire in southern African woodlands: Origins, impacts, effects and control. Proceedings of an FAO Meeting on Public Policies Affecting Forest Fires. FAO Forestry Paper 138, 14.

Fullman, T., & Bunting, E. (2014). Analyzing vegetation change in an elephant-impacted landscape using the moving standard deviation index. Land, 3(1), 74–104. https://doi.org/10.3390/land3010074

Gaitan, J., Maestre, F. T., Buono, G., Bran, D., Dougill, A. J., Garcia-Martinez, G., & Oliva, G. (2019). Biotic and abiotic factors controlling soil organic carbon content have similar effects in regional and global drylands. Ecosystems, 4, 1141–1151. https://doi.org/10.1007/s10021-019-00348-y
Pellegrini, A. F. A., Pringle, R. M., Govender, N., Hedlin, L. O., & Wardle, D. (2017). Woody plant biomass and carbon exchange depend on elephant-fire interactions across a productivity gradient in African savanna. *Journal of Ecology*, 105(1), 111-121. https://doi.org/10.1111/1365-2745.12668

Peri, P. L., Ladd, B., Pepper, D. A., Bonser, S. P., Laffan, S. W., & Amelung, W. (2012). Carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) stable isotope composition in plant and soil in Southern Patagonia's native forests. *Global Change Biology*, 18(1), 311–321. https://doi.org/10.1111/j.1365-2486.2011.02494.x

Quijas, S., Boit, A., Thonincke, K., Murray-Tortarolo, G., Mwampamba, T., Skutsch, M., Simeos, M., Ascarunzn, N., Peña-Claro, M., Jones, L., Arets, E., Jaramillo, V. J., Lazos, E., Toledo, M., Martorano, L. G., Ferraz, R., & Balvanera, P. (2018). Modelling carbon stock and carbon sequestration ecosystem services for policy design: A comprehensive approach using a dynamic vegetation model. *Ecosystems and People*, 15(1), 42–60. https://doi.org/10.1002/26395908.20181542413

Ramutsindela, M. (2007). *Transfrontier conservation in Africa: At the confluence of capital, politics and nature*. In M. Ramutsindela (Ed.), CABI.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Seidemann, A., Wurland, M., Ballard, C., Caro, T. M., Dallas, A., Field, J. C., Ford, N. V., Furman, J. C., Geck, J. A., Giacalone, A., et al. (2014). Reversing historical declines of megaherbivores. In R. Putman, M. Apollonio, & R. Andersen (Eds.), *Ungulate management in Europe*. *Problems and practices* (pp. 260–283). Cambridge University Press.

Smith, P., Soussana, J.-F., Angers, D., Schipper, L., Chenu, C., Rasse, D. P., Batjes, N. H., Egmond, F., McNeill, S., Kuhnert, M., Arias-Navarro, C., Olesen, J. E., Chihrinda, N., Formara, D., Wollenberg, E., Álvaro-Fuentes, J., Sanz-Cobena, A., & Klumpp, K. (2020). How to measure, report and verify soil carbon change to realize the potential of soil carbon sequestration for atmospheric greenhouse gas removal. *Global Change Biology*, 26(1), 219–241. https://doi.org/10.1111/gcb.14815

Stanbrook, R. (2018). Assessing the nutrient status of elephant dung in the Aberdare National Park, Kenya. *Pachyderm*, 59, 5.

Stoldt, M., Gottert, T., Mann, C., & Zeller, U. (2020). Transfrontier conservation areas and human-wildlife conflict: The case of the Namibian component of the Kavango-Zambesi (KAZA) TFCA. *Scientific Reports*, 10(1), 7964. https://doi.org/10.1038/s41598-020-64537-9

Sykes, A. J., Macleod, M., Eory, V., Rees, R. M., Payen, F., Myrgotis, V., Williams, M., Sohi, S., Hillier, J., Moran, D., Manning, D. A. C., Goglio, P., Seghetta, M., Williams, A., Harris, J., Dondini, M., Walton, J., House, J., & Smith, P. (2020). Characterising the biophysical, economic and social impacts of soil carbon sequestration as a greenhouse gas removal technology. *Global Change Biology*, 26(3), 1085-1108. https://doi.org/10.1111/gcb.14844

Tanentzap, A. J., & Coomes, D. A. (2012). Carbon storage in terrestrial ecosystems: Do browsing and grazing herbivores matter? *Biological Reviews of the Cambridge Philosophical Society*, 87(1), 72–94. https://doi.org/10.1111/j.1469-185X.2011.00185.x

Teren, G., Owen-Smith, N., Erasmus, B. F. N., & Ward, D. (2018). Elephant-mediated compositional changes in riparian canopy trees over more than two decades in northern Botswana. *Journal of Vegetation Science*, 29(4), 585–595. https://doi.org/10.1111/jvs.12638

Thornley, R., Spencer, M., Zitzer, H. R., & Parr, C. L. (2020). Woody vegetation damage by the African elephant during severe drought at Pongola Game Reserve, South Africa. *African Journal of Ecology*, 58(4), 658–673. https://doi.org/10.1111/aie.12736

Veldhuis, M. P., Gomers, M. I., Olf, H., Berg, M. P., & Gomez-Aparicio, L. (2018). Spatial redistribution of nutrients by large herbivores and dung beetles in a savanna ecosystem. *Journal of Ecology*, 106(1), 422–433. https://doi.org/10.1111/1365-2745.12874

Walter, K., Don, A., Tiemeyer, B., & Freibauer, A. (2016). Determining soil bulk density for carbon stock calculation: A systematic method comparison. *Soil Science Society of America Journal*, 80, 579–591.

WDPA. (2021). World data base on protected area. https://www.iucn.org/theme/protected-areas/our-work/world-database-protected-areas

Wolf, A., Doughty, C. E., & Malhi, Y. (2013). Lateral diffusion of nutrients by mammalian herbivores in terrestrial ecosystems. *PLoS ONE*, 8(8), e71352. https://doi.org/10.1371/journal.pone.0071352

Wuparot-Report. (2018). *Wuparot audit report*. http://www.nacco.org.na wwf.org. (2018). The status of African elephants. *World wildlife magazine*. Zhu, Y., Merbold, L., Pelster, E. P., Abwanda Okoma, S., Ngetich, F., Anyango Onyango, A., Pellikka, P., & Butterbach-Bahl, K. (2020). The effects of climate on decomposition of cattle, sheep and goat manure in Kenyan tropical pastures. *Plant and Soil*, 451, 325–343. https://doi.org/10.1007/s11104-020-04528-x

Zyambo, P. (2016). Woodyland conversion by elephants in Africa: The search for causal factors, processes, mechanisms and management strategies. *Open Journal of Ecology*, 06(02), 93–101. https://doi.org/10.4236/oje.2016.62010