



East African megafauna influence on vegetation structure permeates from landscape to tree level scales

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ARTICLE INFO

Keywords:

LiDAR
Elephants
Kenya
Land cover
Remote sensing
QSM

ABSTRACT

African savanna elephants (*Loxodonta africana*) can substantially modify their habitat through their interactions with woody vegetation. Nonetheless, the scale, intensity and characteristics of these relations are not yet fully understood. Consequently, it is unclear how vegetation-megafauna interactions can be disrupted by external factors, such as land management. This study attempted to quantify and characterize structural changes in vegetation caused by elephants, from landscape to tree level scales. We applied multi-scale geospatial tools, including airborne (ALS) and terrestrial laser scanning (TLS), to address the following questions: (1) How do elephants shape landscape level vegetation structure in conservation areas? (2) Are the impacts of elephants evident on individual tree architecture? Our study area was located at the Taita Hills Wildlife Sanctuary in South-eastern Kenya. The occurrence of elephants was estimated using elephant observation records and proximity to elephant tracks. Landscape level structure was assessed using tree density maps calculated based on individually detected treetops from ALS data. Next, TLS measurements of 72 trees were processed using quantitative structural modelling to characterize their architecture. Our results demonstrate a widespread influence of elephants on both landscape and tree level structural characteristics. This influence was strongly mediated by management, as we observed differences in vegetation structure inside and outside conservation areas. Tree density was up to 42% lower (5.84 trees/ha) in conservation areas than in non-conservation areas (10.17 trees/ha). Trees were relatively larger with closer proximity to elephant tracks, while smaller trees were more often observed in areas further away from elephants. At an architectural level, trees closer to elephant tracks had lower ratio between the crown length and the tree height, demonstrating a substantial influence of elephants on the morphological characteristics of trees. Our results highlight the importance of accounting for vegetation fauna interactions when planning conservation areas in African savannahs.

1. Introduction

The largest and heaviest living terrestrial animal, the African savanna elephant (*Loxodonta africana*), is a renowned “ecosystem engineer” (Howard, 2017; Jones et al., 1994). The title refers to the ability

of the species to alter woody ecosystems towards open grasslands by consuming and damaging woody vegetation cover (Laws, 1970). Elephants are proven to be major agents of adult tree mortality (Asner and Levick, 2012; Guldmond and Van Aarde, 2008).

Contrastingly, elephant behavior can aid the survival of certain plant

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<https://doi.org/10.1016/j.ecoinf.2023.102435>

Received 28 June 2023; Received in revised form 12 December 2023; Accepted 12 December 2023

Available online 17 December 2023

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species in their range as they can also shape their surrounding habitats by being “forest gardeners” dispersing seeds to long distances (Blake et al., 2009; Bunney et al., 2017; Campos-Arceiz and Blake, 2011; Cochrane, 2003). The species as a large herbivore may also enhance the carbon persistence of ecosystems by redistributing aboveground carbon to soil pools (Kristensen et al., 2022).

The general population of elephants has faced declines, which means that there is a need for conservation to avoid extinctions (Lemieux and Clarke, 2009; Thouless et al., 2016). However, elephant populations have increased in small invariably fenced reserves (Blanc et al., 2007; Chase et al., 2016; Gaugris and Van Rooyen, 2010; Grobler et al., 2001; Mackey et al., 2006; Thouless et al., 2016), where they are being protected from the illegal elephant ivory trade.

The conservation areas provide shelter from poaching and artificial water sources. This leads to a high reproductive success that can lead to high elephant population densities within the conservation areas due to limited dispersal opportunities. The long-term impact of the species on the surrounding ecosystem has been referred as to the “elephant problem” in the earlier scientific literature (Caughley, 1976; Glover, 1963), even though areas are enclosed to protect the species from poaching for ivory and to mitigate human-elephant conflicts.

Vegetation-elephant interactions are also affected by weather conditions. During droughts, elephants tend to form larger groups (Howes et al., 2020; Karvonen, 2018; Owen-Smith et al., 2006). The large herds tend to migrate to woody areas to browse on woody plants due to water scarcity (Loarie et al., 2009). The impacts of this process can be further intensified by habitat restriction of the wildlife reserves, presumably causing the elephants to forage in the same areas season after season, thus challenging the carrying capacities of their surrounding ecosystems. The outer borders of the conservation areas restrict the movement of the elephants with electric fences, even though the borders of adjacent parks are usually open.

The impacts of elephants on the structural characteristics of vegetation can be identified in multiple scales, from a tree level to regional levels. At regional scales, elephants can affect the structure of the landscape by modifying the density of trees and the connectivity of forest fragments, with subsequent effects on vegetation dynamics (Berzaghi et al., 2019). At the individual tree level, on the other hand, elephants can modify the architectural characteristics of trees, that is, the structure of the aboveground portion of a perennial woody plant, such as tree height, crown diameter, branching pattern, and branch orientation (Hollender and Dardick, 2014; Tomlinson, 1983; Valladares and Nii-nemets, 2007).

The architecture of individual trees determines how individuals compete for resources and cluster together, which controls the energy, water, and carbon fluxes at the ecosystem level (Enquist et al., 2009). Disturbances affect tree productivity directly (Foster et al., 2003; Reyer et al., 2017). This can happen when the ability of trees to capture resources becomes limited (e.g., due to a lower leaf area) or when the resource utilization ability decreases (Peters et al., 2013). Broken branches can make trees more susceptible to further herbivore damage, wind, and drought, while also reducing the growth rates (Fontes et al., 2018; Franklin et al., 1987). Since these factors elevate the mortality risk, alteration by elephants can cause tree mortality. One of the major causes of tree mortality is ringbarking by elephants, when the bark is stripped around the entire trunk or stem circumference (Anderson and Walker, 1974; Boundja and Midgley, 2010; Croze, 1974; O'Connor et al., 2007).

Although the effects of elephants cannot be completely separated from the effects of other herbivore species in scientific analysis, the elephant impacts have a greater scale than the impacts of smaller herbivores. The presence of smaller herbivores may constrain the recruitment of new trees, which is also affected by elephants that tend to browse on new trees once they grow into taller height classes, topple small trees to access foliage, and may consume saplings when large trees are less available (Caughley, 1976; Dublin et al., 1990; Berzaghi et al.,

2023). Higher parts of trees can be affected due to their size, allowing them to forage up to 8 m above the ground (Croze, 1974). Elephants also have a very high daily food intake about over 60 kg weighed as dry mass for a fully grown male (Owen-Smith, 1988), explaining their substantial effect on the vegetation. Elephants may cause death of mature trees by uprooting, felling, and removing the bark with their tusks (Barnes, 1982), unlike most other herbivore species (Asner and Levick, 2012; Guldemond and Van Aarde, 2008).

Despite substantial advances in understanding vegetation-elephant interactions during recent years, the characteristics and magnitude of structural changes in savannas caused by elephants has not yet been comprehensively quantified. One of the main reasons behind this knowledge gap has been the availability of and accessibility to suitable tools for measuring vegetation structure at multiple scales (Malhi et al., 2018). This limitation, however, has been largely overcome in recent years, with the advent of remote sensing methods that combine high resolution, portability and financial feasibility (Beland et al., 2019; Muumbe et al., 2021; Viergever et al., 2008).

Airborne laser scanning (ALS), for instance, has been successfully applied in multiple applications aiming at describing vegetation characteristics over large areas. Studies using ALS on savanna vegetation often focused on assessing biomass or carbon storage (e.g., Goldbergs et al., 2018; Pellikka et al., 2018; Wu et al., 2009; Zimbres et al., 2020). For instance, Davies and Asner (2019) used ALS to investigate the limiting effects of elephants on aboveground carbon gains in Africa. Amara et al. (2020) used aboveground biomass (AGB) derived from ALS data to demonstrate the impacts of fences and land use on landscape level carbon storage. ALS data have also been used to quantify the loss of large savanna trees (Levick and Asner, 2013).

Terrestrial laser scanning (TLS) is a ground-based Light Detection and Ranging (LiDAR) system that produces three-dimensional information as point clouds. Studies have demonstrated the large potential of TLS data for characterising vegetation complexity, as it can provide high precision measurements of vegetation structural components, including detailed description of the under canopy structure (Calders, et al., 2015; Maeda et al., 2022; Malhi et al., 2018; Newnham et al., 2015). TLS has rarely been used for studying savanna vegetation, as most studies were conducted in Europe, North America, and China (Muumbe et al., 2021). TLS data have been used to quantify tree architectural characteristics by generating quantitative structure models (QSM) of individual trees segmented from TLS point clouds (Raumonen et al., 2013; Raumonen et al., 2015). QSMs have not yet been extensively applied in savanna vegetation. To the best of our knowledge, currently there are no published studies on the effect of elephants on the architectural attributes of savanna trees using TLS.

TLS data have been used to quantify tree architectural characteristics by generating quantitative structure models (QSM) of individual trees segmented from TLS point clouds (Raumonen et al., 2013; Raumonen et al., 2015). Computer algorithms for constructing QSMs of individual trees have been considerably improved in recent years, providing comprehensive, automatic, and fast solutions (Raumonen et al., 2013; Raumonen et al., 2015). Nonetheless, QSMs have not yet been extensively applied in savanna vegetation. Previous studies on tree structure have typically covered tropical forests (e.g., Lau et al., 2019; Martin-Ducup et al., 2021) and temperate forests (e.g., Åkerblom et al., 2017; Potapov et al., 2017). In Africa, QSMs have been used to study vegetation in agroforestry areas (Reckziegel et al., 2022). To the best of our knowledge, currently there are no published studies on the effect of elephants on the architectural attributes of savanna trees using TLS.

Combining the advantages of ALS and TLS systems can thus provide detailed information on the characteristics and dynamics of ecosystems. While ALS systems allow for the assessment of landscape structure characterization over larger areas, TLS systems can provide high resolution of structural features of individual trees. When placed in the context of the study of vegetation-megafauna interactions, such information has the potential to provide unprecedented insights on the

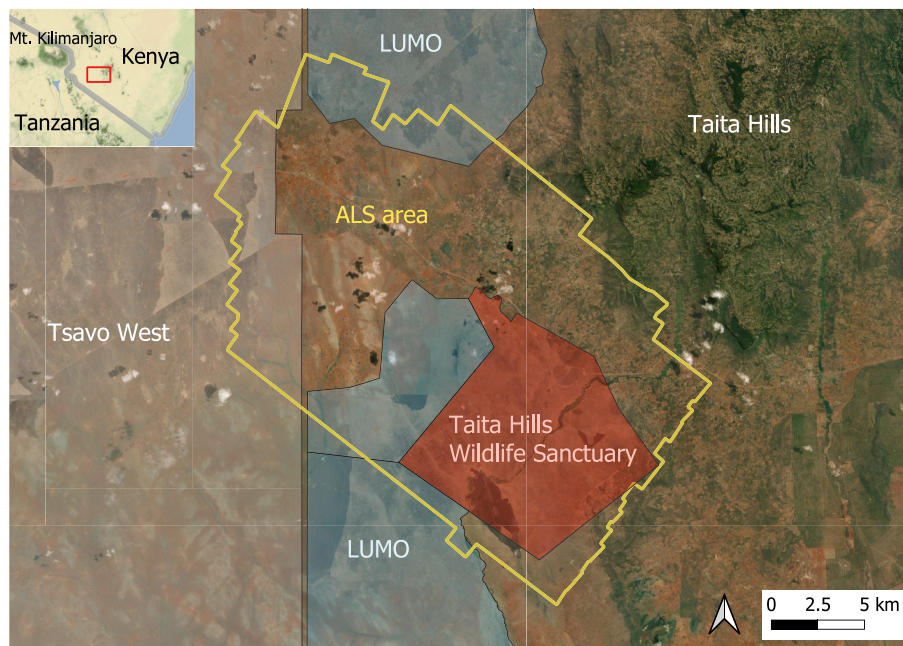


Fig. 1. The location of Taita Hills Wildlife Sanctuary and the area scanned with airborne LiDAR (ALS) in southern Kenya in relation to the Taita Hills, Tsavo West National Park, and LUMO Community Wildlife Conservancy.

impacts of fauna, as well as land management (e.g., protected areas), on the fate of African savannas.

In this study, we aimed at assessing the influence of elephants on multi-scale structural woody vegetation features in East African savannas. We applied multi-scale geospatial tools, including ALS and TLS measurements, as well as advanced tree structure modelling techniques, to address the following questions: (1) How do elephants shape landscape level vegetation structure inside and outside conservation areas? (2) Are the impacts of elephants evident at the level of individual tree architecture?

We expect to find a sparser vegetation structure consisting of mainly larger trees inside conservation areas compared to the outside areas. We also expect to see less intact individual trees in areas with higher elephant densities, near elephant tracks, and closer to the river. We hypothesize that the elephants could have reduced the canopy volume by browsing on and breaking the lower branches, therefore affecting the crown ratio, diameter, volume, and area. Undamaged trees would have relatively larger crowns compared to damaged trees.

2. Material and methods

2.1. Study area

The study area is the Taita Hills Wildlife Sanctuary (THWS), a small privately owned game reserve in southern Kenya (Fig. 1) that is a guarded conservation area for a high diversity of native African wildlife, including African savanna elephants. THWS is located in the plains southwest to the Taita Hills and covers an area of about 11,331 ha. It borders the community owned LUMO Community Wildlife Conservancy in the east, west and south, through which it is connected to Tsavo West National Park. THWS belongs to the Tsavo ecosystem, where there are large wildlife populations of e.g., elephants, lions, giraffes and buffaloes (Ogutu et al., 2016; Smith and Kasiki, 2000). The animals can migrate freely between the reserves, as there are no fences separating them.

While the THWS is exclusively managed for wildlife conservation and wildlife-based tourism, areas to the north and east are mixed use which includes livestock management, firewood collection from *Acacia-Commiphora* bushlands, and dryland agriculture. The most common woody species primarily include trees from the *Vachellia*-genus (e.g.,

V. tortilis and *V. xanthophloea*), *Acacia*-genus (e.g., *A. brevispica* and *A. elata*), the *Commiphora*-genus (e.g., *C. baluensis*, *C. schimperi*, and *C. trothe*), (Amara et al., 2020). The most common species of the grasslands (including most of THWS) is *Vachellia tortilis* (Amara et al., 2023). There is a gallery forest around the Bura river in the middle of THWS, maintained by the high water table level of the riverbed. Besides the widest part of the river, the Crocodile pond, the rest of the river is dry most of the year. The gallery forest is characterized by tall *Newtonia hildebrandtii* and *Vachellia xanthophloea* trees (Amara et al., 2020; Amara et al., 2023).

The soil type of the lowlands surrounding the Taita Hills is typically red and acidic sandy clay soil, while the elevation ranges between approximately 600 and 1000 m above sea level (Amara et al., 2020). The soil is porous, so it is not very fertile. The lowlands experience a bimodal rainfall pattern that maintains the savanna ecosystem. The seasonal rains occur twice in a year in THWS from March to May and from October to December (Pellikka et al., 2013). This means that there are also two dry seasons each year. The drier conditions shape the environment in many ways: the trees shed their leaves, the soil dries out, the grasses begin to brown, and seasonal fires occur.

The elephant population of the sanctuary tends to come from Tsavo West National Park and surrounding areas during the dry season to drink from the artificial waterholes that are replenished from boreholes. THWS is an important migratory corridor for elephants moving between the main conservation areas, Tsavo East and Tsavo West national parks, in the ecosystem. For instance, in 2013 there were 462 elephants recorded in the sanctuary during the dry season and 17 during the wet season road census (Muteti and Maloba, 2013). The whole Tsavo ecosystem has over 12,000 elephants (Ngene et al., 2017), most of which live within the protected areas (Karvonen, 2018). The protected areas include Tsavo West and East national parks, LUMO, and THWS. The sometimes-destructive pattern of the elephant overcrowding on the woody cover of the study area was already noted in the 1960's as the "elephant problem" that ended in 1970's due to poaching and drought (Glover, 1963; van Wijngaarden, 1985). The impact of fire also accelerated the destruction of the bushland. Examples of changes in the land cover characteristics arising from the creation of fences and protected areas are illustrated in Figs. S1-S3 in the supplementary material.

Trees have a key role in an African savanna ecosystem. They provide

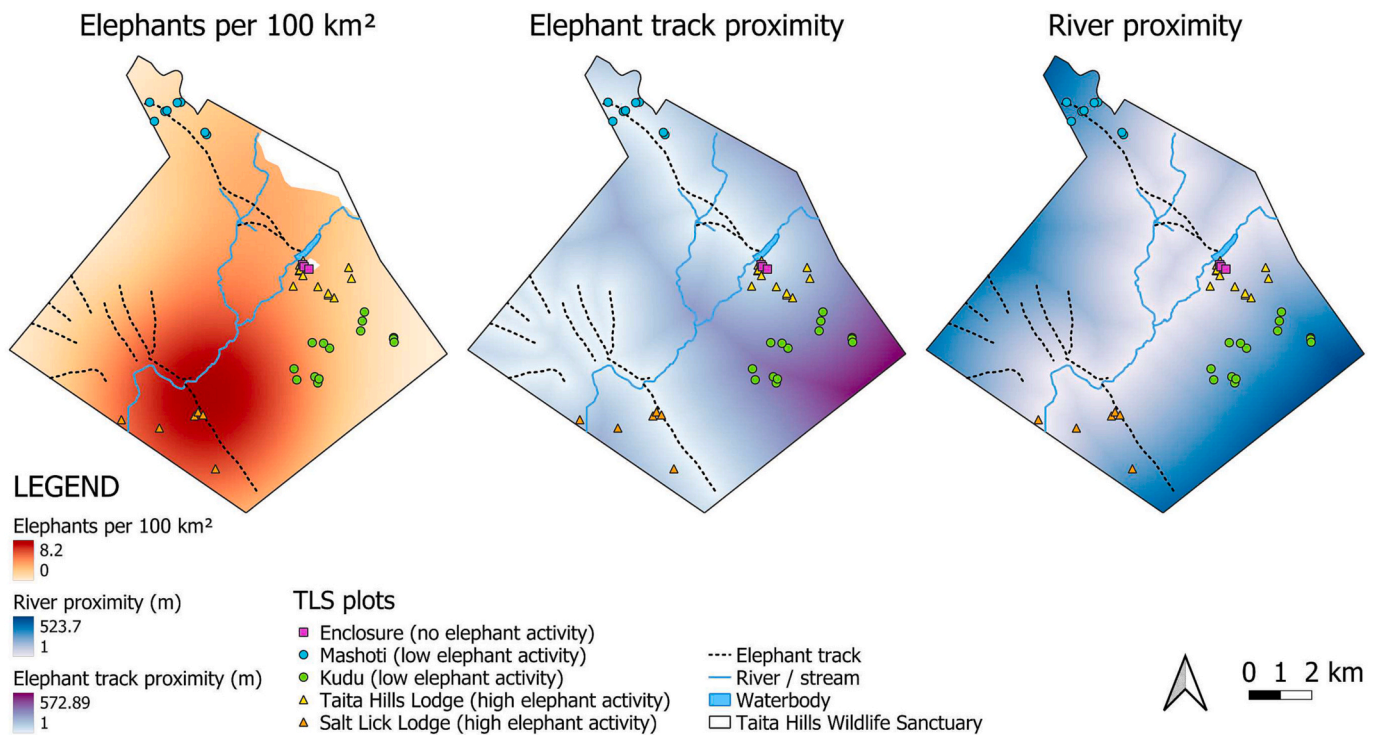


Fig. 2. Elephant density, elephant track proximity, and river proximity. TLS plot locations are displayed in the grayscale dots.

wildlife habitats, food for browsing herbivores, increase the soil nutrient concentrations, create favourable microenvironments, and provide shade, increasing the forage quality and grass productivity (Anderson et al., 2001; Belsky, 1994; Cruz et al., 1999; Ludwig et al., 2004; Ludwig et al., 2008; Scholes and Archer, 1997; Sebata, 2017). Trees also provide sustenance for wood-feeding termite species that can further increase the nutrient availability and forage quality (Grant and Scholes, 2006). Most of the termite mounds in THWS are abandoned unlike in the non-conservation areas in its surroundings, possibly due to the decreased tree cover.

2.2. Elephant activity and river distances

This study used two proxy datasets for elephant activity and one river distance dataset. The first elephant activity proxy used were geolocated points of elephant occurrence obtained from the Kenya Wildlife Service that were produced using elephant census counts from fixed-wing aircrafts (Ngene et al., 2013). The Tsavo-Mkomazi ecosystem was divided into counting blocks and each block was surveyed with a specific aircraft with multiple observers. The data are from four different years: 1999, 2005, 2008, and 2011 total elephant counts conducted in the Tsavo-Mkomazi ecosystem. The surveys were undertaken in January or February, depending on the year (Ngene et al., 2013; Ngene et al., 2017). All sighting points used in our analysis that fell within THWS were located in same areas near the main water sources. All points were combined for a large elephant density raster, including the points outside THWS. The large raster was then clipped using the extent of THWS.

The second elephant proxy was geolocated elephant tracks (GIS vector lines), which were produced using field observations and satellite image interpretation of the paths formed by elephant herds using them frequently (Boström, 2015). The tracks often seem to be the shortest paths between water holes and the river, meaning that it is likely that other large mammal species are using them as well. This data still helps to complement the elephant density data. Additionally, river data were also included in the study to assess how the distance from the Bura river

correlates with different variables. We also hypothesize that the distance of water sources could be the reason why the elephants visit certain areas less frequently, since those areas typically have the desired forage species, such as *Vachellia tortilis*.

The geolocated vector datasets were processed in QGIS to obtain raster maps (Fig. 2) (QGIS Development Team, 2023). The elephant count data were used for creating a map of elephant density as a heatmap that shows elephant individuals per 100 km². The elephant track and river proximity data were first rasterized. The results were used to obtain proximity maps as heatmaps.

2.3. Airborne laser scanning and landscape level vegetation structure

The ALS data covering an area of 433 km² were collected during a rainy season in late March 2014 with a Leica ALS60-sensor that recorded a maximum of 4 returns per a single laser pulse. The return density per square meter is 1.04. The data was pre-processed by Ramani Geosystems, the Kenyan data vendor, which included ground return filtering. The data were available for this study as a georeferenced point cloud in UTM/WGS84 coordinate system (Amara et al., 2020). The data have been acquired to cover the whole extent of THWS and LUMO Mramba, and a part of Tsavo West National Park. Additionally, some agricultural areas across the northern border of the reserves have been scanned since the differences in the tree cover between the conservation areas and its surroundings have been of interest. The data has also been used to assess the amount of aboveground biomass in the area (Amara et al., 2020).

A digital terrain model (DTM) and a digital surface model (DSM) at 1 m resolution were created based on the LAS-files using lidR package (Rousset et al., 2020) in R software. Based on their difference, a canopy height model (CHM) was calculated. Treetops were detected from the ground normalized CHM using lidR package's *find_trees*-function. The function detects trees as the highest points within the moving window. The diameter of moving window was set to 10 m after comparing different results visually to the details of the CHM.

The heights of the treetops were extracted from the CHM in QGIS

software. All trees in the point cloud were included. Points under 2 m were deleted and separate files were created for short (2–3 m) and tall (>7 m) trees. The smallest and largest trees were of interest, because the smallest trees represent the most fragile woody plants most prone to elephant damage and the largest trees represent the trees that were scanned with TLS. Mean tree density values were calculated for the entire area covered by the ALS data. A flowchart with the steps undertaken during data processing is presented in Fig. S4 of the supplementary material.

Exploratory analysis of the correlations between the tree densities and elephant track proximity, river proximity, and elephant density was done using Spearman's correlation. Given the high number points resulting from the rasters, the data were divided into classes and the distributions within each class assessed using violin plots. Lastly, a multiple regression model was fitted to evaluate how the elephant activity proxies and proximity to river can explain the spatial patterns of tree density (Fig. S5, Supplementary material).

2.4. Terrestrial laser scanning (TLS) data and tree level structural metrics

2.4.1. Tree species

Two tree species were chosen based on two criteria: 1) their abundance in the park and its surroundings, and 2) them being frequently consumed by elephants. The species were Umbrella thorn acacia (*Vachellia tortilis*) and Lebombo wattle (*Newtonia hildebrandtii*). The latter tends to favour proximity to water source. *Vachellia tortilis* is evenly distributed across the reserve.

Vachellia tortilis is a deciduous tree widespread in Africa, Israel, and southern Arabia, according to the Manual on taxonomy of Acacia species (FAO, 1983). While at times reaching the height of 21 m, the species usually grows from 1.5 to 18 m high (Brenan, 1959). The bark is described to be 'rough and fissured' (FAO, 1983), which may attract elephants to scratch themselves against it. In accordance with its common name "Umbrella thorn acacia", the shape of the species is cylindrical as the crown usually is flat and spreading. The *Vachellia tortilis* trees analysed in this study most likely belong to the subsp. *spirocarpa*. The species can be considered a primary food source for browsers in African savannas (Johnson and Ebersole, 2017). There are also multiple scientific studies concerning the dynamics between the species and elephants (e.g., Gandiwa et al., 2011; MacGregor and O'Connor, 2004; Pellew, 1983).

Newtonia hildebrandtii is a large deciduous tree native to East Africa and can reach a height of 25 m (Bingham et al., 2020; Brenan, 1959). The species was named after a German botanist Johannes Maria Hildebrandt (1847–1881), who collected plants in East Africa and Madagascar (Beetje, 1998; Bingham et al., 2020). The species occurs often in riverine forests, in areas where the water table is high, and in bushlands. The bark is usually rough, but it can sometimes be smooth (Brenan, 1959). The species tends to have a notably more complex trunk structure than *Vachellia tortilis*. According to the observations of the park rangers in THWS, elephants tend to browse on the species frequently. The preference is also mentioned by Legendijk et al. (2011).

2.4.2. TLS data acquisition

The TLS data were collected during the first dry season in January and February of 2020 in Taita Hills Wildlife Sanctuary. In total, 72 trees were scanned using a RIEGL VZ-400i TLS instrument (Fig. 2 and Fig. S6). The laser range of this instrument can reach up to 800 m with 5-mm accuracy. Data can be acquired with up to 500,000 measurements per second, while the laser pulse repetition rate can go up to 1.2 MHz. (RIEGL, 2019.)

The sampling areas were determined according to an elephant occurrence prediction raster, in addition to the local knowledge of the park rangers. It was concluded that the plains near the Taita Hills Lodge, the Salt Lick Lodge, and the river had the highest elephant activity, while areas further from the river had less elephant activity. The

Table 1
Tree architecture metrics analysed in this study.

Acronym	Description	Ecological relevance in relation to elephant density
<i>BRANCHVOL</i>	Branch volume. Volume of all the branches (L)	Elephants consuming the branches may decrease the branch volume.
<i>BRANCHAREA</i>	Branch area. Total branch surface area (m ²)	Elephants consuming the branches may reduce the surface area of the branches. If thinner branches are consumed, there may be a disproportional reduction in the branch surface area. (Used in normalizing other metrics.)
<i>DBH</i>	Diameter of the cylinder at 1.1–1.5 m (DBH)	
<i>AVGDIAM</i>	Average crown diameter (m)	Damage on the furthest branches may reduce the average crown diameter.
<i>MAXDIAM</i>	Maximum crown diameter (m)	Damage on the furthest branches may shorten the maximum crown diameter.
<i>CROWNAREA</i>	Crown area. Area of the alpha shape of the crown's planar projection (m ²)	Elephant damage on the branches may affect the shape of the tree crown, which may affect the crown area.
<i>CROWNratio</i>	Crown ratio. The ratio between the crown length and the tree length (%)	Elephants consuming the lowest branches may lead to shorter crowns.
<i>CROWNVOL</i>	Crown volume. Volume of the alpha shape of the crown (m ³)	Elephant damage on the branches may affect the shape of the tree crown, which may affect the crown volume.
<i>AVGORDER</i>	(Average) branching order	Elephants breaking the branches may lead to a lower average branching order.

elephants were known to be drawn to the water sources near the two lodges. An enclosed area within the park represented an area with no elephant activity. The electric enclosure had been established as a biodiversity recovery project in 2009. Hence, the samples were evenly distributed in areas with high and low elephant activity.

Each tree was scanned from three perspectives (scan positions). There were two measurements per position to ensure that the entire tree was fully measured: first with the scanner positioned vertically and then horizontally. The scanner was placed a few meters outwards from where the furthest branches ended. The trunk was marked with a reflective tape tied around it to make it easy to recognise the correct tree from the point cloud data.

2.4.3. Data processing

The raw data collected by the TLS were inspected and pre-processed using the RiSCANPro software. The six scans representing each tree were co-registered using RiSCANPro automatic registration algorithms, fixing the placements of the scan perspectives. In cases when the automatic registration could not register the project completely, manual multi-station adjustment was used to complete the registration. Once the co-registration of the six scans was successful, the tree was visually inspected and then manually separated from the surrounding area. This was done using RiSCANPro's Selection mode and Polyline selection. After the extraction of the tree, the point clouds were exported to LAS files.

Next, QSMs for each tree were created using the TreeQSM algorithm (Calders, et al., 2015; Raunonen et al., 2013). However, before the QSMs were calculated, the point clouds of each tree were filtered for removing ghost points and for removing leaves. Both filters had several adjustable parameters. Once the filtering procedures were completed, the QSMs for each tree were computed and the optimum model was selected. Each model was visually inspected and compared with the original point cloud. In cases where the resulted QSM did not provide a suitable representation of the tree (e.g., missing tree trunks), the script parameters were iteratively adjusted to enhance the modelling results.

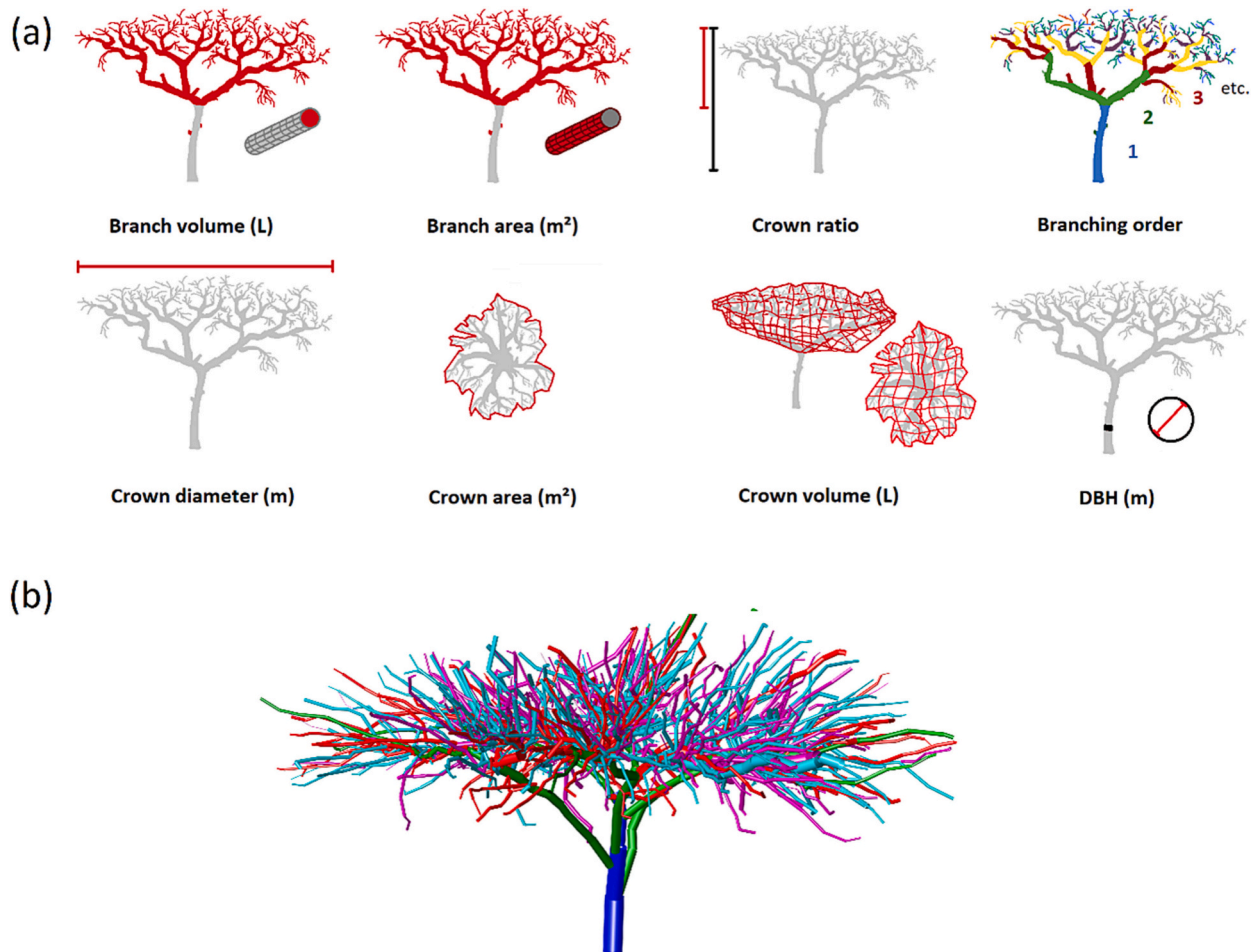


Fig. 3. (a) Sketches of the tree architecture metrics used in our study. (b) Example of Quantitative Structure Models of a *Vachellia tortilis* tree.

Since the *Newtonia hildebrandtii* trees have a rather complex tree structure and their leaves are blocking visibility, there were sometimes difficulties in creating intact models. Hence, from the total 63 trees that were successfully registered, only 53 resulted in good quality QSMs.

Finally, nine structural metrics were extracted from the QSMs (Table 1). Several other metrics were discarded due to the data of the furthest branches being unreliable because of the effect of wind to the shape of the tree. Sketches demonstrating the physical interpretation of the metrics are presented in Fig. 3 and a flowchart with the methodological steps undertaken during data processing are presented in Fig. S9 in the supplementary material.

The elephant track proximity, river proximity, and elephant density values at the location of each tree were extracted in QGIS, and a table was created to merge this information with the structural characteristics of each individual tree.

Most of the metrics were normalized for tree size variability using the DBH (except crown ratio and average branching order) and their relationships with elephant track and river proximity were estimated using linear mixed models. Lastly, the metrics that had the most statistically significant relationships with the elephant activity proxies were further explored to investigate how elephant activities could explain the changes in these key tree structural metrics.

2.5. Statistical analysis

First an exploratory analysis was conducted to evaluate the correlations between the tree densities and elephant track proximity, river proximity, and elephant density. The strength of the relationship

between the variables were assessed using Pearson's correlation index. Given the high number of points resulting from the rasters, the data were divided into classes and the distributions within each class was assessed using violin plots. The distribution of tree density as a function of different elephant activity proxies were then assessed using the violin plots displaying the median values and 95% confidence intervals of the distribution of tree density in relation to elephant density, track proximity, and river proximity. Next, multivariate models were trained to evaluate how the elephant activity proxies and proximity to river could explain the spatial patterns of tree density (Fig. S5, Supplementary material).

The correlation between the tree architecture metrics of the two tree species were assessed using Pearson's correlation, after which most of the metrics were normalized for tree size variability using the DBH (except crown ratio and average branching order). Lastly, the metrics that had the highest correlation (based on the Pearson correlation coefficient) with the elephant activity proxies were further explored by creating plots of predicted responses with 95% confidence intervals based on the linear models to investigate how elephant activities could explain the changes in these key tree structural metrics.

3. Results

3.1. Landscape vegetation structure inside and outside conservation areas

The tree density based on ALS shows significant differences between the wildlife reserves located in its extent and the areas outside (Figs. 4–5, Table 2). The tree density is lower within the reserves, especially when

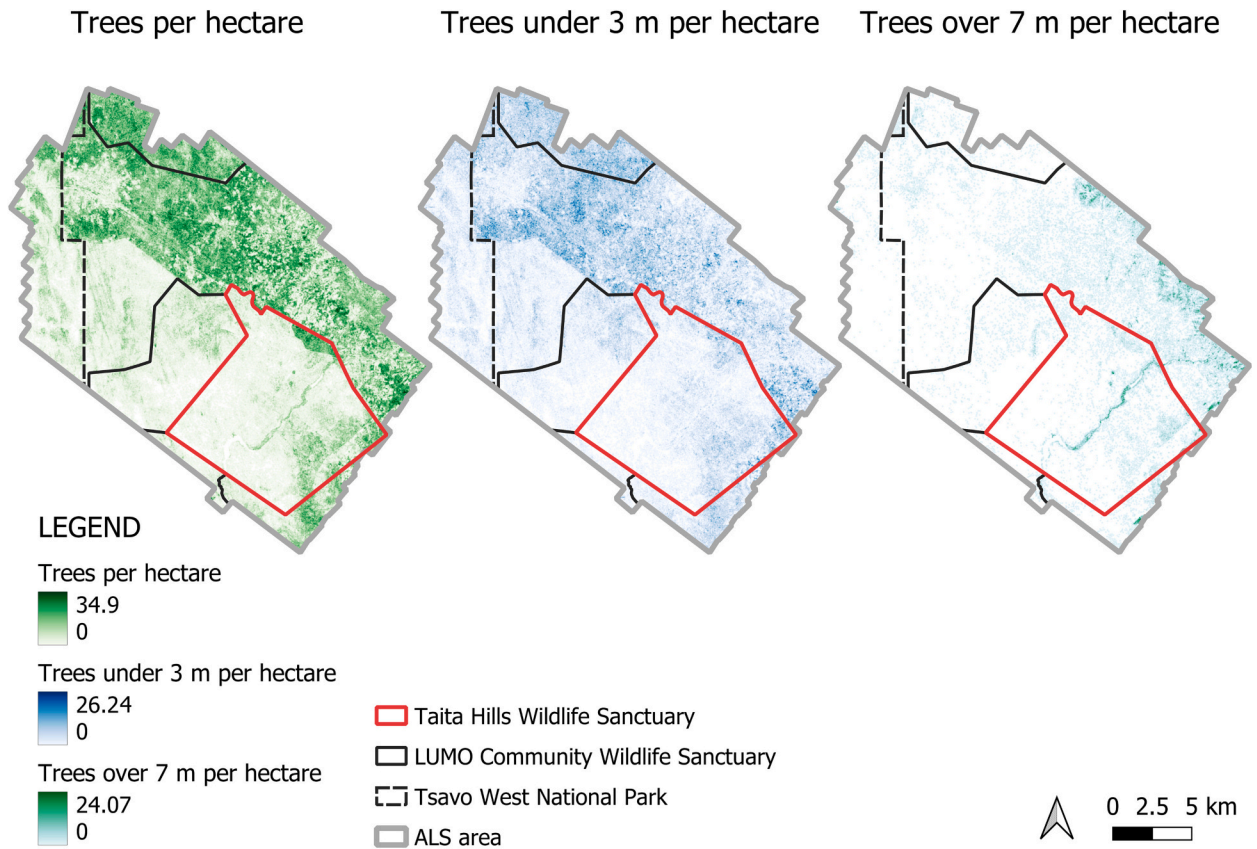


Fig. 4. Tree density in the area scanned with airborne laser scanning (ALS).

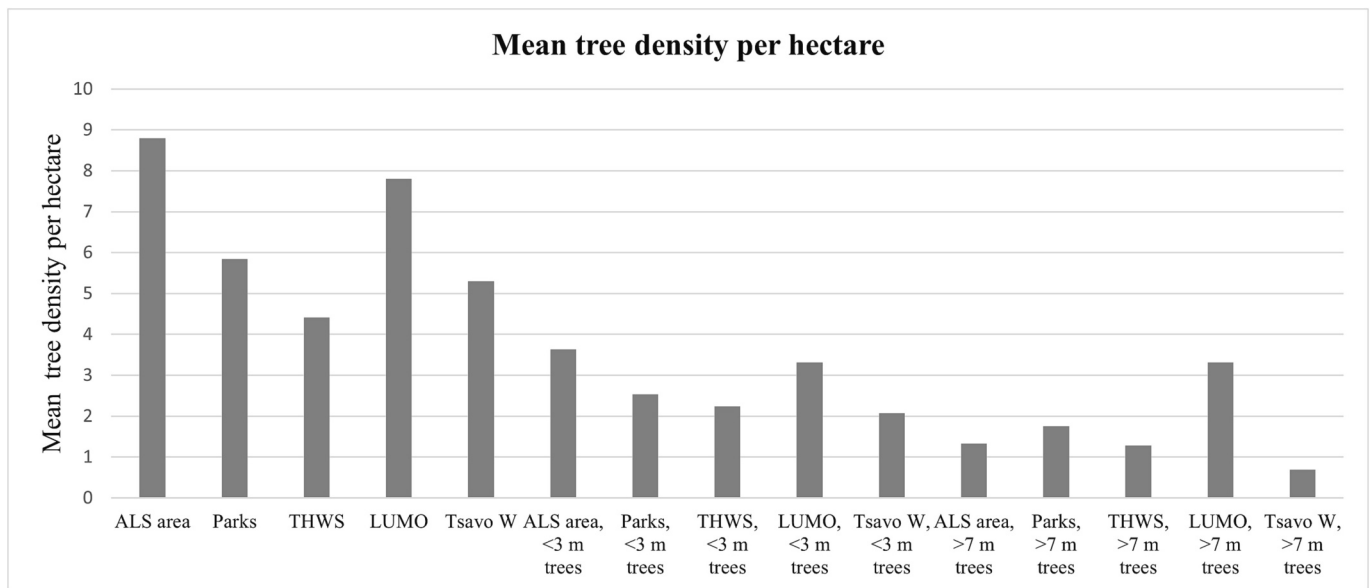


Fig. 5. Mean tree densities in the area scanned with ALS, the parts of the scanned area that belong to the wildlife reserves (Parks), Taita Hills Wildlife Sanctuary (THWS), LUMO Community Wildlife Sanctuary (parts within the ALS area), and Tsavo West National Park (parts within the ALS area).

considering all trees (−42.6%) and trees under three meters (−30%). The pattern is less pronounced with trees over seven meters, where areas of higher altitude in the northern part of the study area and the riverine forest in Taita Hills Wildlife Sanctuary are of the highest tree density. There is one exception in the northern part of LUMO Community Wildlife Sanctuary, where the tree densities of all trees and smaller trees are as high as in its surrounding areas. This area is used for livestock

management. There is also another cattle grazing area between LUMO and Tsavo West National Park that does not officially belong to the reserves but has a lower tree density.

When inspecting the same results within only THWS (Fig. 6), we observe that the northern enclosure (i.e., an area within THWS near its northern border where the entrance of wildlife is restricted from the south by fence, likely being one of the main causes for the high tree

Table 2
Mean tree densities outside and inside the protected areas.

Area	Mean tree density / ha
Areas outside the protected areas	10.17
Areas inside the protected areas	5.84
Areas outside the protected areas (2–3 m trees)	3.63
Wildlife parks (2–3 m trees)	2.54
Areas outside the protected areas (>7 m trees)	1.33
Areas inside the protected areas (> 7 m trees)	1.76

density) shows higher tree density than rest of the park, especially when trees of all sizes are considered. Lower tree density is often observed closer to the elephant tracks. The areas further from the Bura river, especially the south-eastern part of the park have denser tree cover than the areas closer to the river. The area with the least tree cover seems to align with the south-western cluster of elephant tracks.

Fig. 7 shows the tree density distribution over different ranges of elephant path proximity, river proximity, and elephant density. All proxies used to quantify the activity of elephants indicate that tree density decreases in areas with more elephants. This is the case with both elephant density and elephant track proximity. In the case of the median tree density per hectare of all trees and the smallest trees (i.e., 2–3 m height), with 0–1 elephants per 100 km² it is about 15 but only about 5 with 8–9 elephants per 100 km². The difference is smaller with the taller trees (i.e., >7 m height), where the median tree density with 0–1 elephants per 100 km² is around 15 trees per hectare and about 8 trees per hectare with 8–9 elephants per 100 km². The tree density has increased in areas with very low elephant density, but areas with >3 elephants per 100 km² are not much affected. This could mean that a

higher elephant density may not always lead to more impacts on trees.

In areas from 0 to 50 m from the elephant tracks, the median tree density of all trees and the smallest trees (2–3 m) is around 5 trees per hectare and about 18 trees per hectare in areas that are 500–600 m away from the tracks. The median taller tree density per hectare is around 8 in areas 0–50 m from the tracks and around 17 in areas that are 500–600 m away.

Tree density also increases further from the Bura river. The median tree density for all trees is around 9 trees/ha, for smaller trees around 8 trees/ha, and for taller trees around 10 trees/ha, where the proximity to the river is from 0 to 50 m. The median density of all trees and the smallest trees is about 18 trees/ha in areas from 500 to 550 m away from the river. The median density is around 16 trees/ha for taller trees in the same areas.

The results from the multiple regression analysis, presented in Table 3, show strong statistical significance of the relationship between tree density and the elephant proxies used in our study (*p*-values <0.01). Hence, it can be concluded that a higher elephant density and closer proximity to the elephant tracks lead to a lower tree density. The estimate is almost twice as high for the smallest trees compared to the larger trees. The result is twice as high for the taller trees compared to the smallest trees.

3.2. Tree scale analysis

The correlations between the tree architectural metrics, DBH, river proximity, and elephant track proximity, for the two species assessed in this study is presented in Figs. 8 and 9. The results between the two species differ from each other. Elephant track and river proximities correlate with each other with a strong statistical significance in the case

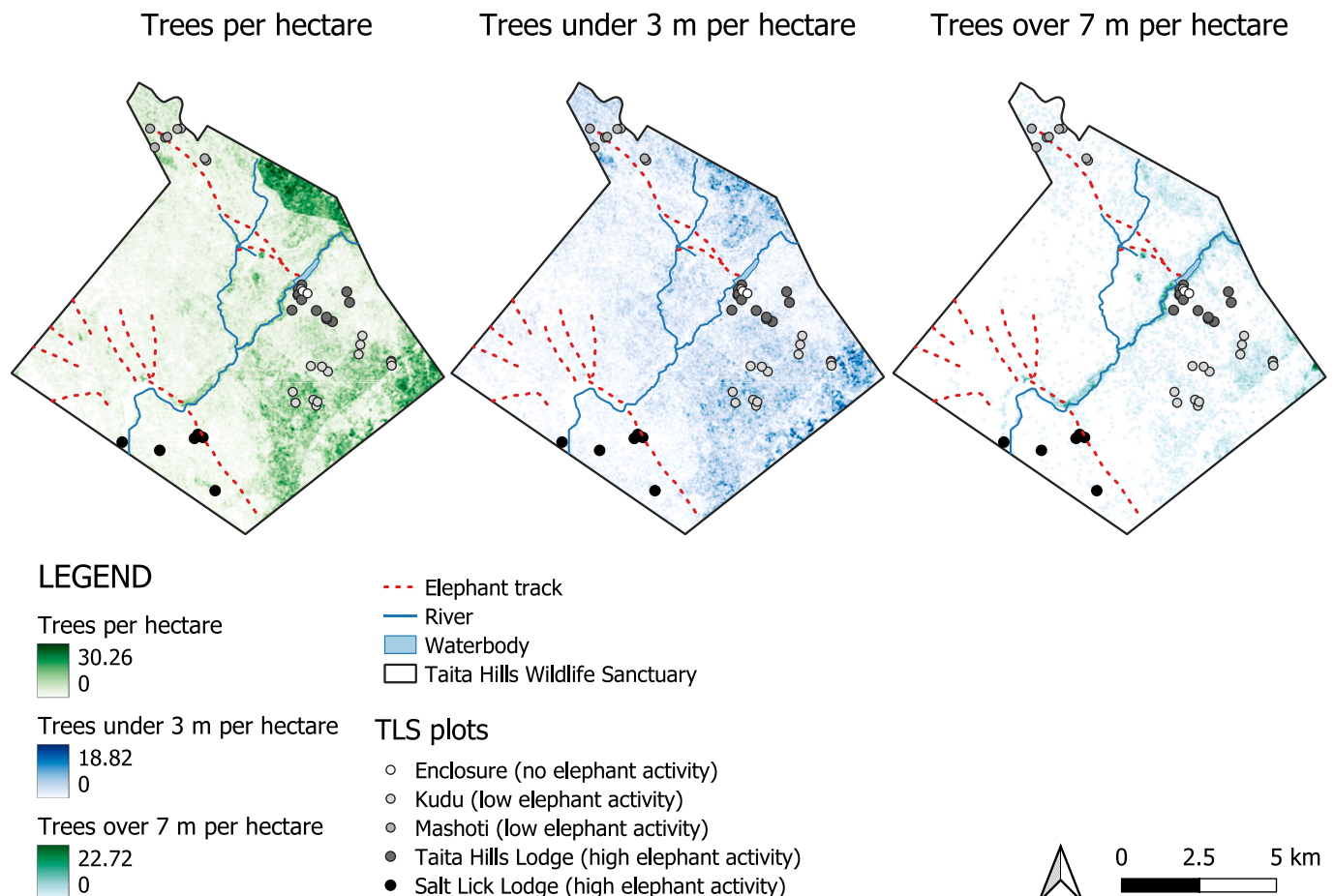


Fig. 6. Tree density in Taita Hills Wildlife Sanctuary.

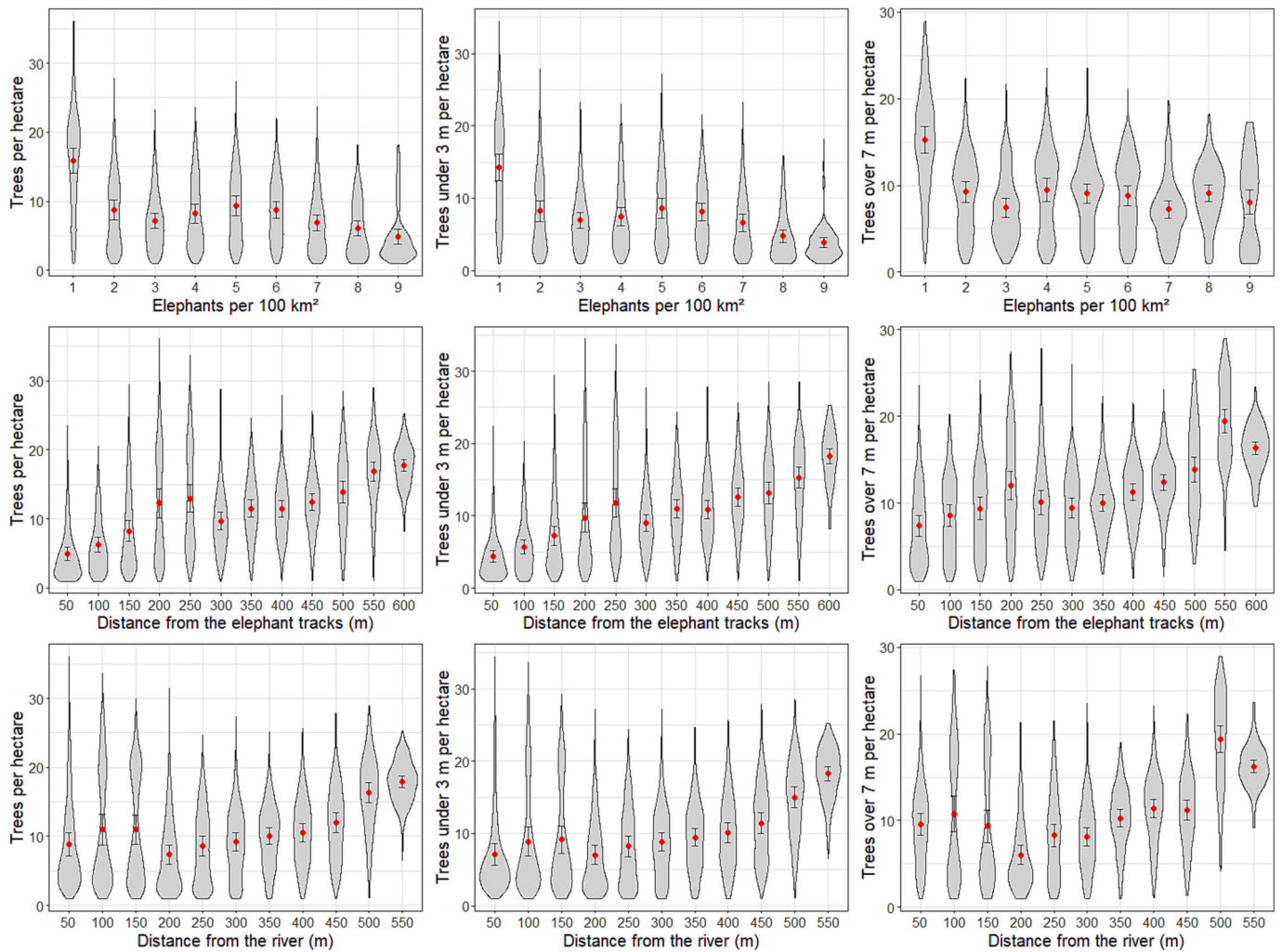


Fig. 7. The distribution of tree density in relation to elephant density, track proximity, and river proximity. The red dots show the median value of the distributions, while the black lines show the 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Multiple regression analysis of the relationship between tree density and different proxies for elephant activities (observed elephant density, proximity to elephant tracks and proximity to rivers). *** indicate p-value <0.001.

	Regression coefficient all trees	Regression coefficient 2–3 m trees	Regression coefficient >7 m trees
E. density ~ Trees/ha	−1.081 ***	−0.837 ***	−0.440 ***
Track prox. ~ Trees/ha	0.018 ***	0.017***	0.019 ***
River prox. ~ Trees/ha	−0.008 ***	−0.004 ***	−0.008 ***

of the *Vachellia tortilis* (Fig. 8) but not in the case of the *Newtonia hildebrandtii* (Fig. 9).

DBH correlates with several tree architectural metrics with both species, indicating that the metrics are size dependent. Some metrics, however, such as crown ratio and average branching order do not correlate with DBH in the case of both species. Also, branch volume lacks a strong statistical significance in the case of the Newtonias. Based on the above results, we normalized all the structural metrics, with the exceptions of crown ratio and average branching order, for tree age variability using the DBH.

Tables 4 and 5 show the results from the multiple linear regression analysis. The models were fitted using normalized tree architectural metrics, elephant density, elephant track proximity, and river proximity. Although there are similarities between the two tree species, some differences can be observed. In the case of both species, branch area ($p < 0.05$) and crown ratio ($p < 0.1$) have significant positive relationships with elephant track proximity. This means that the normalized branch areas and the crown ratios are larger further away from the tracks.

In the case of *Newtonia hildebrandtii*, crown ratio also has a significant positive relationship ($p < 0.1$) with elephant density, meaning that the relative lengths of the tree crowns would be larger where the elephant density is higher. The *Vachellia tortilis* trees also had a significant positive relationship with average branching order ($p < 0.1$), indicating that there would be smaller branches further from the trunk in areas with higher elephant density.

The results of the predictions of the best correlating metrics (crown ratio, branch area, and average branch diameter), based on the multiple linear regression model, show opposing patterns for the two species (Fig. 10). While the normalized branch areas of the *Vachellia tortilis* trees tend to decrease about 2% per each 100 m away from the tracks, the opposite occurs with the *Newtonia hildebrandtii* trees. The normalized branch areas are predicted to increase around 60% per each 100 m away from the tracks.

The crown ratio predictions for the two species also differ from each

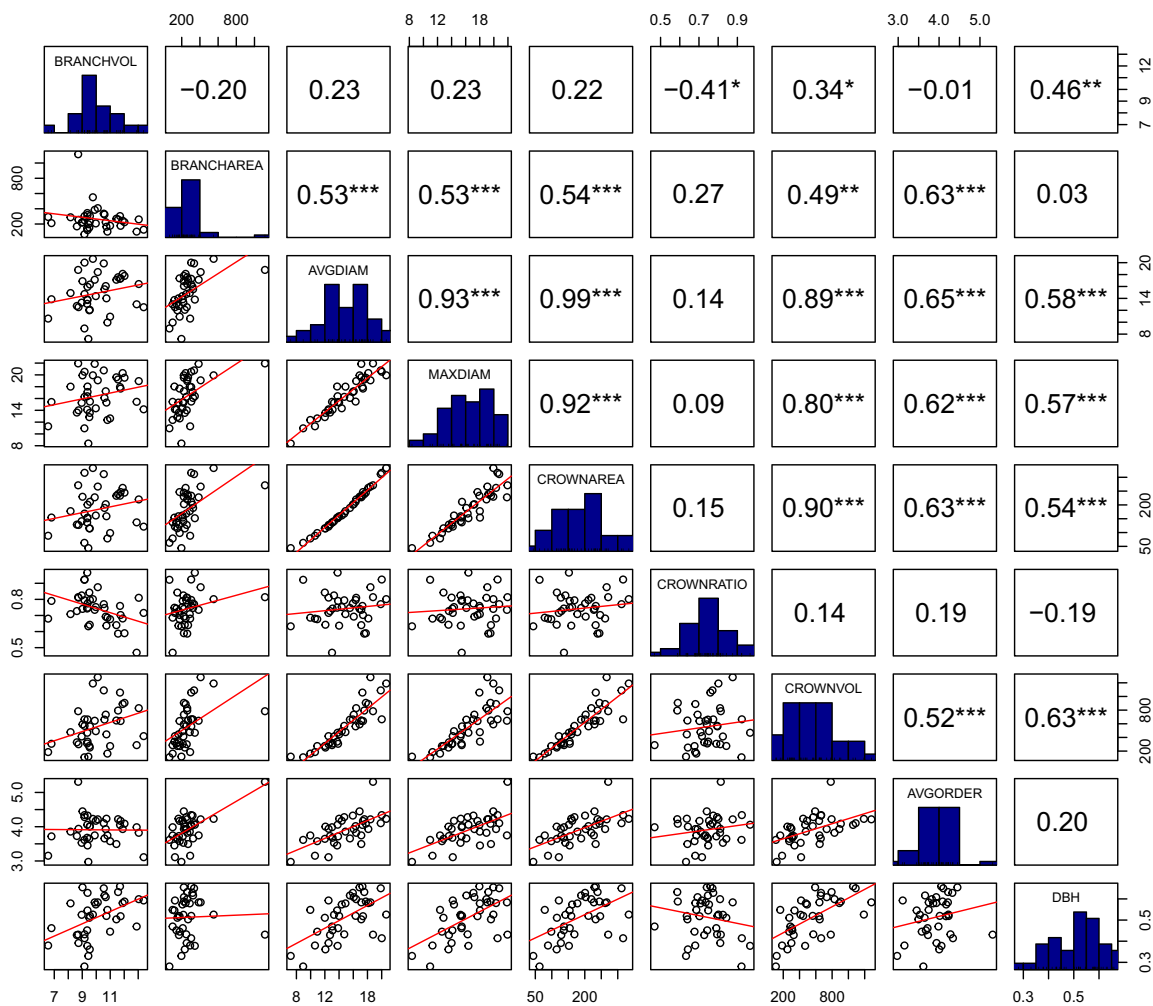


Fig. 8. Scatterplot matrix of the correlations between the tree architecture metrics of *Vachellia tortilis*. The regression coefficients are shown in the upper half of the matrix, and the stars indicate the statistical significances. The blue bars represent the metric distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

other (Fig. 11). While the relative lengths of the crowns of the *Vachellias* tend to decrease by about 5% per each 100 m further from the tracks, the crown ratios of the *Newtonias* are predicted to increase by about 8% per each 100 m further from the tracks.

Fig. 12 shows the modelled average branching order for the *Vachellia* trees with increasing elephant density, along with the modelled crown ratio for the *Newtonias*. The average branching order decreases with increasing elephant density (around 1.5% per elephant more per 100 km²). This indicates a lower number of smaller branches further away from the trunk in areas with high elephant densities. The crown ratio is predicted to decrease around 2% per elephant more per 100 km², meaning that the relative length of the tree crowns may be taller in areas with lower elephant densities.

4. Discussion

Our study applied multi-scale and multi-source remote sensing approaches to demonstrate a widespread impact of elephants on vegetation structure. At a regional scale, we identified individual trees from ALS data that was used to demonstrate how land management, through the creation of conservation areas, can strongly affect the landscape vegetation structure. Furthermore, landscape scale analysis showed strong evidence that elephant activity proxies, such as the tracks used by elephants in conservation areas, can effectively explain vegetation structural variability.

The analysis of high-resolution TLS data provided an unprecedented insight on the architectural characteristics of savanna trees. Our results thus showed that the impacts of elephants on vegetation structure can also be identified at tree level, through the modification of essential tree architectural metrics, such as crown ration and branch area.

While elephants seem to have a significant impact on woody vegetation, there are other herbivore species in savannas that can shape the architecture of the trees, such as giraffes and kudus. Nonetheless, it may not be realistic to untangle their effects from the elephant damage in scientific analysis.

4.1. Landscape scale analysis

The results derived from the ALS data show a general pattern of lower tree density within the wildlife reserves compared to the rest of the area scanned with ALS. The findings are in line with the study done by Amara et al. (2020) that highlighted the reduced biomass within the wildlife parks. Also, the role of African elephants as “ecosystem engineers” (Howard, 2017; Jones et al., 1994) and major agents of adult tree mortality (Asner and Levick, 2012; Guldmond and Van Aarde, 2008) could be argued to be present in the landscape-level patterns of vegetation structure, as evident from the conservation areas.

Our results suggest that higher elephant activity (higher elephant density and closer proximity to elephant tracks) lead to a lower tree density, indicating that the so-called “elephant problem” discussed in

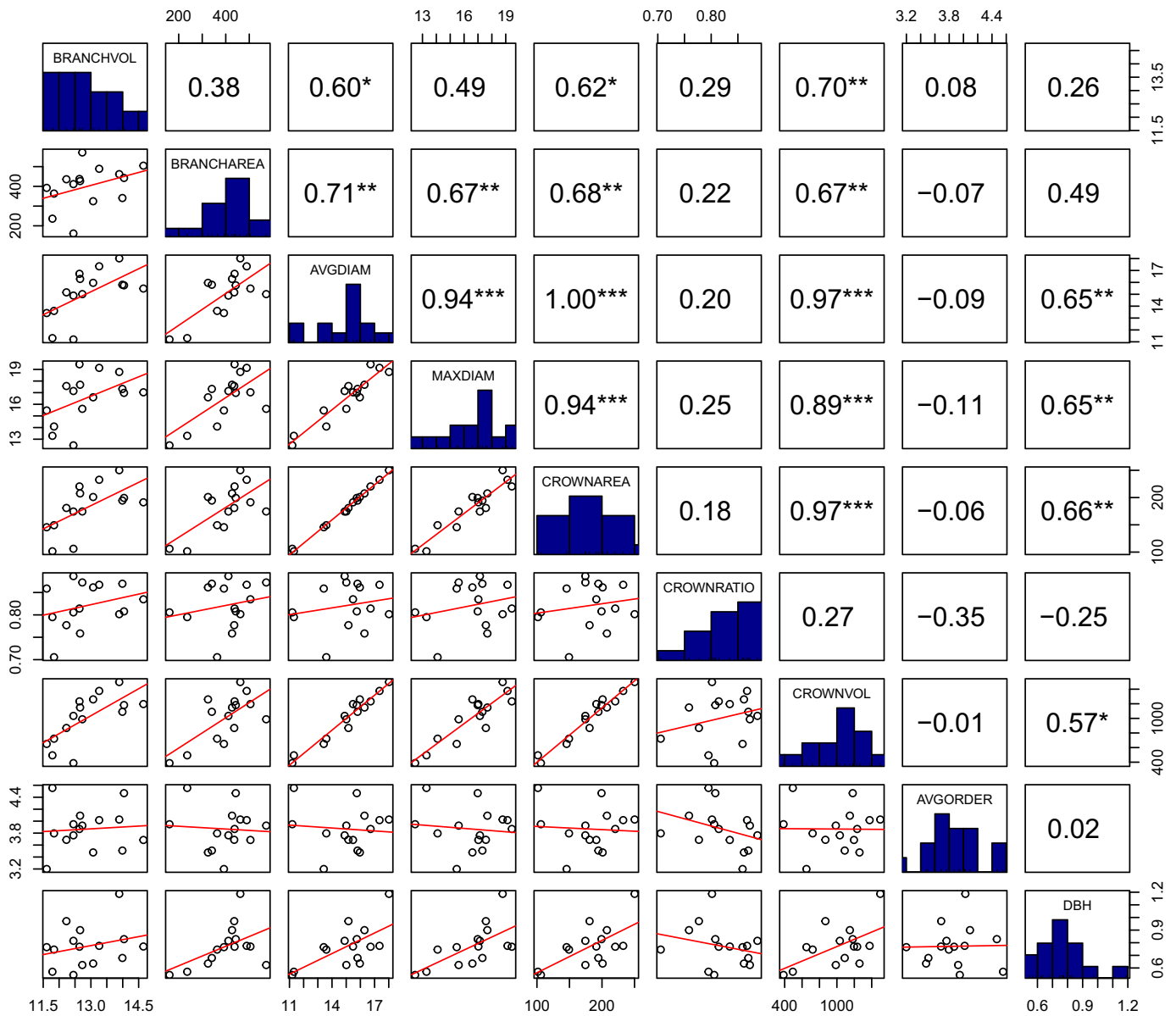


Fig. 9. Scatterplot matrix of the correlations between the tree architecture metrics of *Newtonia hildebrandtii*. The regression coefficients are shown in the upper half of the matrix, and the stars indicate the statistical significances. The blue bars represent the metric distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

scientific literature (Caughley, 1976; Glover, 1963) is still largely evident. Decreasing woody plant availability and tree recruitment continues to limit the foraging possibilities of elephants and other browsers, while also decreasing e.g., the soil nutrient concentrations, favourable microenvironments, wildlife habitats, forage quality, and grass productivity (Anderson et al., 2001; Belsky, 1994; Cruz et al., 1999; Ludwig et al., 2004; Ludwig et al., 2008; Scholes and Archer, 1997; Sebata, 2017). If the phenomenon leads to total tree cover loss, serious consequences to the survival of browsing herbivores along with the whole savanna ecosystem may follow.

Satellite images indicate that the tree cover was denser in 2001 than in 2020 (i.e., Figs. S1 & S2), showing evidence of disturbances leading to a decrease in woody vegetation. Although it is difficult to separate the effects of the elephants from the effects of other browser species, correlations between tree density, elephant density, elephant track proximity, and river proximity have high statistical significances.

The changes in tree density patterns observed in our results were more pronounced with considering only small trees. These results can be

explained by the fact that elephant activity during dry seasons is often more detrimental to smaller trees (Ihwagi et al., 2009). The extreme dry weather event occurred in the study area in 2013, causing losses in the tree cover, underlines the role of the dry season in affecting the tree cover of the wildlife reserve. The occurred phenomenon may have a connection with the intensified effect of elephants on the vegetation during the dry seasons, when the tree cover of their surrounding habitat is being consumed by large herds of elephants (Howes et al., 2020; Karvonen, 2018; Loarie et al., 2009; Owen-Smith et al., 2006).

Other factors could also have contributed for the reduced woody vegetation cover during the past years. It is known that some vegetation has also been damaged by wildfires. There is also a possibility that some trees have been cleared by humans around the safari lodges and roads in this area. Cutting trees near the roads or wildlife lodges is beneficial from the perspective of tourism, since the safari visitors can have a better visibility of wild animals, without the obstruction caused by vegetation. Hence, it is likely that current landscape pattern has emerged due to the contribution of many factors instead of only

Table 4
Results from the multiple linear regression for *Vachellia tortilis*. N = the metric has been normalized with DBH.

	Regression coefficient (Track proximity)	Regression coefficient (River proximity)	Regression coefficient (Elephant density)
Branch volume (N)	-0.001820	0.002665	-0.40912
Branch area (N)	-0.7151 *	0.2971	-29.1045
Avg crown diameter (N)	-0.011749	0.015897	-0.56172
Max crown diameter (N)	-0.01281	0.01734	-0.07828
Crown area (N)	-0.1111	0.2430	-3.6123
Crown ratio	-0.000302	0.0001335	-0.00257
Crown volume (N)	0.2310	-0.6654	-26.6231
Avg branching order	0.0005820	-0.00073	-0.06718.

Table 5
Results from the multiple linear regression for *Newtonia hildebrandtii*. N = the metric has been normalized with DBH.

	Regression coefficient (Track proximity)	Regression coefficient (River proximity)	Regression coefficient (Elephant density)
Branch volume (N)	-0.006442	-0.030990	-1.05528
Branch area (N)	2.916 *	-1.268	-16.788
Avg crown diameter (N)	0.01144	-0.04710	-0.73558
Max crown diameter (N)	0.01488	-0.05230	-1.00288
Crown area (N)	0.4398	-0.7829	-6.4799
Crown ratio	0.0008143 *	-0.0007779	-0.02441 **
Crown volume (N)	3.614	-5.378	-56.014
Avg branching order	-0.002861	0.003890	-0.01082

elephant damage.

The relationship between the river proximity and tree density seems to have conflicting results, most probably since there is a dense riverine forest around the river that affects the tree density results. Regardless, our results show tree density increasing further from the river, which can indicate that the plains next to the riverine forest have faced more disturbance than the areas closer to the borders of the park with less water available, since more vegetation could be expected in areas with more water availability. If this pattern of degraded vegetation is in fact caused by high elephant activity, the results would be in line with the observation by Glover (1963), who reported that elephants tend to destroy the vegetation near water sources in the area.

4.2. Tree scale analysis

Elephants tend to try to gain maximum energy output from a single source, hence trees with large foliage volumes are usually selected for consumption (Boundja and Midgley, 2010; Levick and Asner, 2013; Sali et al., 2012; Staub et al., 2013). The nature and severity of the impacts caused on the trees are often reflected in the tree structural characteristic (height, width, and DBH). Trees with large DBH are more likely to be debarked, while smaller trees are usually toppled by the elephants (Ihwagi et al., 2009). In some cases, trees will suffer from broken and torn branches. The preferred tree species have higher concentrations of nutrients and proteins (Holdo, 2003; Jachmann, 1989) and less tannin (Cooper and Owen-Smith, 1985). Therefore, tree architecture both determines the elephant impact and is further shaped by it.

Consequently, only some larger trees tend to remain standing in areas with intense elephant activity due to the uprooting of smaller trees. Younger trees not surviving lead to a reduction of canopy cover. In these extreme cases, entire areas can be changed from a savanna to a grassland. The lack of trees then limits the feeding possibilities of elephants and other species living in the reserve especially during the dry seasons when the woody plant availability is of importance. This could then be fatal to the fauna within the reserve.

In our results, we observed opposing differences between the two tree species, *Vachellia tortilis* and *Newtonia hildebrandtii*. For instance, the relationships between the elephant density and elephant track proximity were opposite to each other when comparing the results from the two species. While the branch areas and crown ratios of the *Vachellia tortilis* were larger in areas closer to elephant tracks, the case was the opposite with *Newtonia hildebrandtii*. Sometimes the conflicting results were within one species, where elephant density and elephant track proximity would differ from each other in their relationship to one variable, such

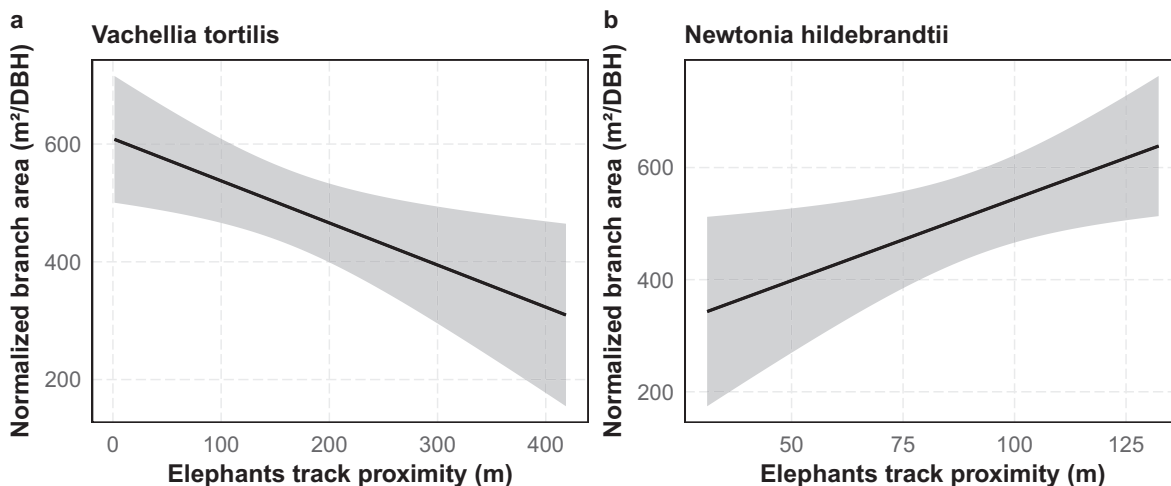


Fig. 10. Normalized branch area of (a) *Vachellia tortilis* and (b) *Newtonia hildebrandtii* with increasing elephant track proximity. The grey area shows the 95% confidence interval.

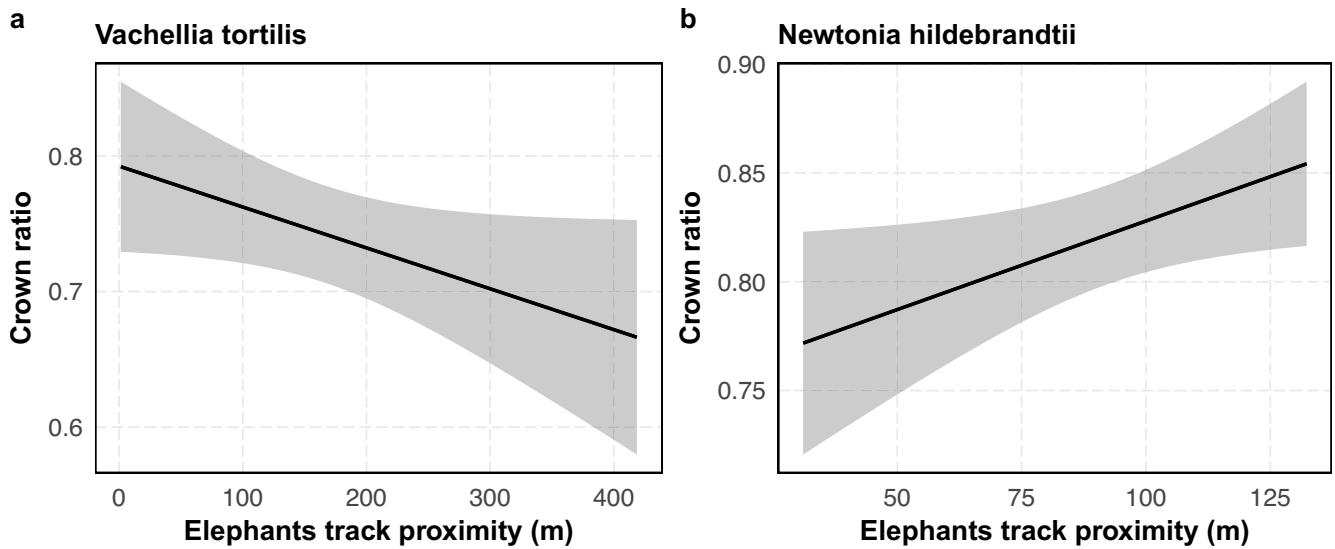


Fig. 11. a) Crown ratio of *Vachellia tortilis* with increasing elephant track proximity and b) crown ratio of *Newtonia hildebrandtii* with increasing elephant track proximity. The grey area shows the 95% confidence interval.

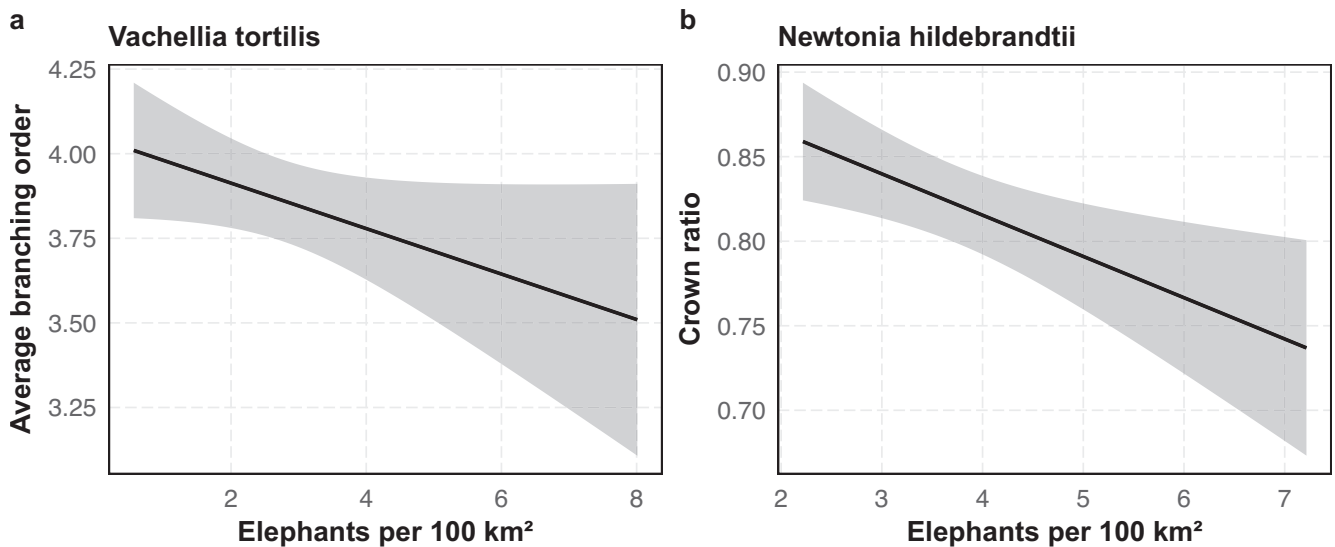


Fig. 12. a) Average branching order of *Vachellia tortilis* with increasing elephant density. b) Crown ratio of *Newtonia hildebrandtii* with increasing elephant density. The grey area shows the 95% confidence interval.

as in the relationship with the crown ratio of *Newtonia hildebrandtii*.

Some of the differences between the species may be caused by their differing structures and growing locations. *Newtonia hildebrandtii*, as a complex-structured riparian tree, seems to differ from the more simple-structured *Vachellia tortilis* that grows widely in the study area. Regardless, some tree structure metrics showed clear correlation with the elephant track proximity and elephant density. These metrics were surprisingly similar with each other between the tree species.

The metrics that had the most significant relationships with elephant density and elephant track proximity were crown ratio, branch area, and average branching order. The coefficients of the models were in some cases opposite to each other. It is possible that the difference between the two species in this analysis is caused by the unique morphological characteristics of each species. It could be argued that the different tree species have different relationships with the proximity to higher elephant activity in this wildlife reserve. The Newtonias are certainly shaped by being a riverine species in the area. Larger crown ratios associated with more intense elephant activity would have a

relationship that are in line with results presented by Ihwagi et al. (2019), who reported that elephants tend to destroy younger trees.

For both species, crown size increase as trees get older (Figs. 10 & 11), particularly *Vachellia tortilis*. Hence, although age contributes to growth in crown height and leads to high volume branches, wildlife consumption of the lowest branches is a possible cause for the changes in crown ratios when trees grow. As trees grow taller, more branches are growing further away from the reach of the large wildlife, making the crown relatively taller than younger trees.

The number of the measured and analysed trees was limited to 53, and they were all confined in a single wildlife reserve. Furthermore, the number of the analysed metrics was limited by the effect of the wind during the field work that distorted the furthest branches in the point cloud. This made it difficult to analyse metrics that were strongly connected to that part of the point cloud, reducing the architectural details that this study can cover reliably.

The number of trees in the analysis was reduced by about 31% from the original number that was meant to be analysed. Namely, 16 out of 69

trees were not included in the analysis due to difficulties in reconstructing proper QSM models of those trees. *Newtonia hildebrandtii* trees were particularly difficult to model with TreeQSM, since the method has been developed for deciduous temperate trees that tend to be structurally very different from the complexly formed Newtonias. Especially their stems can be quite complex. This means that the cross-sections are often not circular; in which case the cylinder may not well approximate the true diameter and volume. The leaves of the Newtonias also made it challenging to model. Also, wind affected the quality of the point cloud at the furthest branches of both tree species. Modelling the complex savanna tree architecture required a lot of adjustment of parameters, continuous experimentation, and testing, as described in previous studies (Muumbo et al., 2021).

5. Conclusions

This study investigated the impacts of elephants on the structural characteristics of vegetation in Eastern African Savannas. We made use of advanced geospatial technology, including airborne and terrestrial laser scanning, to unveil how elephants affect vegetation at multiple scales, ranging from general landscape to individual tree levels. Our results provide robust evidence that the impacts of elephants on vegetation permeates throughout different spatial scales, affecting landscape composition at a regional level and tree architecture at a local level.

We demonstrate an overall decrease in woody vegetation density in areas with high elephant activity. The observed patterns reinforce concerns that poorly planned conservation areas may lead to abrupt declines in the integrity of vegetation over savannas. Our results indicate that younger woody plants are less likely to survive in areas of wildlife reserves intensively visited by elephants.

The structural characteristics of individual trees were also affected. *Vachellia tortilis* trees tend to have larger canopies near areas with high elephant activity, while the case is generally the opposite for *Newtonia hildebrandtii*. Hence, our results demonstrate that the structure of different species may respond differently to interactions with elephants. Even though the cause for these differences could not be clarified in our study, the structural and locational differences between the two species could be considered as a possible explanation.

Changes in the structure of vegetation, at landscape or individual levels, have profound impacts on ecosystem processes, surface energy balance, and carbon storage. Therefore, the results of this study highlight the importance of accounting for vegetation-fauna interactions when planning and executing wildlife conservation areas in African savannas. Our study contributes to a better understanding of these interactions, offering new tools and methods for delineating strategies that can conciliate wildlife protection with the maintenance of basic ecosystem services provided by the vegetation.

CRedit authorship contribution statement

Hanna Elisabet Sorokina: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft. **Matheus Henrique Nunes:** Data curation, Writing – review & editing. **Janne Heiskanen:** Data curation, Writing – review & editing. **Martha Munyao:** Data curation, Writing – review & editing. **James Mwang'ombe:** Resources, Writing – review & editing. **Petri Pellikka:** Writing – review & editing. **Pasi Raunonen:** Methodology, Writing – review & editing. **Eduardo Eiji Maeda:** Conceptualization, Data curation, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

Data availability

Data will be made available on request.

Acknowledgements

This study was funded by the Academy of Finland (decision numbers 318252, 319905 and 340175). The authors would like to thank research assistant Darius Kimuzi of the Taita Research Station and Park Ranger Paul of THWS their great contribution in the field. Field Master of the Taita Research Station of the University of Helsinki Mwadime Mjomba for his advice on selecting suitable tree species for the study, and the hospitality and support given by the staff of Taita Research Station. PP was funded by Academy of Finland decision number: 318645. Research permit P/18/97336/26355 from National Council for Science and Technology of Kenya is greatly acknowledged.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2023.102435>.

References

- Åkerblom, M., Raunonen, P., Mäkipää, R., Kaasalainen, M., 2017. Automatic tree species recognition with quantitative structure models. *Remote Sens. Environ.* 191, 1–12. <https://doi.org/10.1016/j.rse.2016.12.002>.
- Amara, E., Adhikari, H., Heiskanen, J., Siljander, M., Munyao, M., Omondi, P., Pellikka, P., 2020. Aboveground biomass distribution in a multi-use Savanna landscape in southeastern Kenya: impact of land use and fences. *Land* 9 (10), 381. <https://doi.org/10.3390/land9100381>.
- Amara, E., Adhikari, H., Mwamodenyi, J.M., Pellikka, P.K.E., Heiskanen, J., 2023. Contribution of tree size and species on aboveground biomass across land cover types in the Taita Hills, southern Kenya. *Forests* 14 (3), 642. <https://doi.org/10.3390/f14030642>.
- Anderson, G.D., Walker, B.H., 1974. Vegetation composition and elephant damage in the Sengwa wildlife research area, Rhodesia. *S. Afr. J. Wildl. Res.* 4, 1–14. https://hdl.handle.net/10520/AJA03794369_3310.
- Anderson, L.J., Brumbaugh, M.S., Jackson, R.B., 2001. Water and tree-understorey interactions: a natural experiment in a savanna with oak wilt. *Ecology* 82, 33–49. [https://doi.org/10.1890/0012-9658\(2001\)082\[0033:WATUIAJ\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0033:WATUIAJ]2.0.CO;2).
- Asner, G.P., Levick, S.R., 2012. Landscape-scale effects of herbivores on treefall in African savannas. *Ecol. Lett.* 15, 1211–1217. <https://doi.org/10.1111/j.1461-0248.2012.01842.x>.
- Barnes, R.F.W., 1982. Elephant feeding behaviour in Ruaha National Park, Tanzania. *Afr. J. Ecol.* 20, 123–136. <https://doi.org/10.1111/j.1365-2028.1982.tb00282.x>.
- Beetje, H.J., 1998. *J. M. Hildebrandt (1847-1881): notes on his travels and plant collections.* *Kew Bull.* 53 (4), 835–856.
- Beland, M., Parker, G., Sparrow, B., Harding, D., Chasmer, L., Phinn, S., Antonarakis, A., Strahler, A., 2019. On promoting the use of lidar systems in forest ecosystem research. *For. Ecol. Manag.* 450, 450. <https://doi.org/10.1016/j.foreco.2019.117484>.
- Belsky, A.J., 1994. Influences of trees on savanna productivity: test of shade, nutrients, and tree-grass competition. *Ecology* 75, 922–932. <https://doi.org/10.2307/1939416>.
- Berzagli, F., Longo, M., Ciais, P., Blake, S., Bretagnolle, F., Vieira, S., Scaranello, M., Scarascia-Mugnozza, G., Doughty, C.E., 2019. Carbon stocks in central African forests enhanced by elephant disturbance. *Nat. Geosci.* 12, 725–729. <https://doi.org/10.1038/s41561-019-0395-6>.
- Berzagli, F., Bretagnolle, F., Durand-Bessart, C., Blake, S., 2023. Megaherbivores modify forest structure and increase carbon stocks through multiple pathways. *Proc. Natl. Acad. Sci.* 120 (5), e2201832120 <https://doi.org/10.1073/pnas.2201832120>.
- Bingham, B.T., Ballings, P., Hyde, M.A., 2020. Flora of Zambia: species information: *Newtonia hildebrandtii* var. *hildebrandtii*. Flora of Zambia. Retrieved 24.11.2020 from. https://www.zambiaflora.com/speciesdata/species.php?species_id=126410.
- Blake, S., Deem, S.L., Mossimbo, E., Maisels, E., Walsh, P., 2009. Forest elephants: tree planters of the Congo. *Biotropica* 41 (4). <https://doi.org/10.1111/j.1744-7429.2009.00512.x>.
- Blanc, J., Brnes, R., Craig, G., Dublin, H., Thouless, C., Douglas Hamilton, I., 2007. African Elephant Status Report 2007: An Update from the African Elephant Database. IUCN, Gland, Switzerland. ISBN: 9782831709703.
- Boström, M., 2015. Taita Hills & LUMO Wildlife Sanctuaries. [Map]. University of Helsinki.
- Boundja, R., Midgley, J., 2010. Patterns of elephant impact on woody plants in the Hluhluwe Imfolozi park, Kwazulu Natal, South Africa. *Afr. J. Ecol.* 48, 206–214. <https://doi.org/10.1111/j.1365-2028.2009.01104.x>.
- Brenan, J.P.M., 1959. *Flora of Tropical East Africa.* Kew Publishing, England, UK, p. 1. ISBN 9781842462768.
- Bunney, K., Bond, W.J., Henley, M., 2017. Seed dispersal kernel of the largest surviving megaherbivore—the African savanna elephant. *Biotropica* 49 (3), 395–401. <https://doi.org/10.1111/btp.12423>.
- Calders, et al., 2015. Nondestructive estimates of above-ground biomass using terrestrial laser scanning. *Methods Ecol. Evol.* 6, 198–208. <https://doi.org/10.1111/2041-210X.12301>.

- Campos-Arceiz, A., Blake, S., 2011. Megagardeners of the forest – the role of elephants in seed dispersal. *Acta Oecol.* 37 (6), 542–553. <https://doi.org/10.1016/j.actao.2011.01.014>.
- Caughley, G., 1976. The elephant problem – an alternative hypothesis. *East Afr. Wildl. J.* 14, 265–283. <https://doi.org/10.1111/j.1365-2028.1976.tb00242.x>.
- Chase, M.J., et al., 2016. Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ* 4, e2354. <https://doi.org/10.7717/peerj.2354>.
- Cochrane, E.P., 2003. The need to be eaten: *Balanites wilsoniana* with and without elephant seed dispersal. *J. Trop. Ecol.* 19 (5), 579–589. <https://doi.org/10.1017/S0266467403003638>.
- Cooper, S., Owen-Smith, N., 1985. Condensed tannins deter feeding by browsing ruminants in south African savanna. *Oecologia* 67, 142–146. <https://doi.org/10.1007/bf00378466>.
- Croze, H., 1974. Seronera bull problem. I. The elephants. *East Afr. Wildl. J.* 12, 1–27. <https://doi.org/10.1111/j.1365-2028.1974.tb00104.x>.
- Cruz, P., Sierra, J., Wilson, J.R., Dulorme, M., Tournebize, R., 1999. Effects of shade on the growth and mineral nutrition of tropical grasses in silvopastoral systems. *Ann. Arid Zone* 38, 335–361. <https://hal.inrae.fr/hal-02696431/document>.
- Davies, A.B., Asner, G.P., 2019. Elephants limit aboveground carbon gains in African savannas. *Glob. Chang. Biol.* 25 (4), 1368–1382. <https://doi.org/10.1111/gcb.14585>.
- Dublin, H. T., Sinclair, A. R. E & Mcglade, J. (1990). Elephant and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J. Anim. Ecol.*, 59, 1147–1164. doi:<https://doi.org/10.2307/5037>.
- Enquist, J.B., West, B.G., Brown, H.J., 2009. Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proc. Natl. Acad. Sci. USA* 106, 7040–7051. <https://doi.org/10.1073/pnas.0812303106>.
- FAO, 1983. Manual on taxonomy of Acacia species. FAO. Retrieved 23.11.2020 from <http://www.fao.org/3/Q2934E/Q2934E00.htm#TOC>.
- Fontes, C.G., Chambers, J.Q., Higuchi, N., 2018. Revealing the causes and temporal distribution of tree mortality in Central Amazonia. *For. Ecol. Manag.* 424, 177–183. <https://doi.org/10.1016/j.foreco.2018.05.002>.
- Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The importance of land-use legacies to ecology and conservation. *BioScience* 53 (1), 77–88. [https://doi.org/10.1641/0006-3568\(2003\)053\[0077:TLOLUL\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0077:TLOLUL]2.0.CO;2).
- Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. *Bioscience* 37, 550–556. <https://doi.org/10.2307/1310665>.
- Gandiwa, E., Magwati, T., Zisadza, P., Chinuwa, T., Tafangenyasha, C., 2011. The impact of African elephants on Acacia tortilis woodland in northern Gonarezhou National Park, Zimbabwe. *J. Arid Environ.* 75 (9), 809–814. <https://doi.org/10.1016/j.jaridenv.2011.04.017>.
- Gaugris, J., Van Rooyen, M., 2010. Effects of water dependence on the utilization pattern of woody vegetation by elephants in the Tembe Elephant Park, Maputaland, South Africa. *Afr. J. Ecol.* 48, 126–134. <https://doi.org/10.1111/j.1365-2028.2009.01095.x>.
- Glover, J., 1963. The elephant problem at Tsavo. *Afr. J. Ecol.* 1 (1), 30–39. <https://doi.org/10.1111/j.1365-2028.1963.tb00176.x>.
- Goldbergs, G., Maier, S.W., Levick, S.R., Edwards, A., 2018. Efficiency of individual tree detection approaches based on light-weight and low-cost UAS imagery in Australian savannas. *Remote Sens.* 10 (2), 161. <https://doi.org/10.3390/rs10020161>.
- Grant, C.C., Scholes, M.C., 2006. The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biol. Conserv.* 130, 436–437. <https://doi.org/10.1016/j.biocon.2006.01.004>.
- Grobler, D., Van Altena, J., Malan, J., Mackey, R., 2001. The African elephant (*Loxodonta africana*) as a game ranch animal. In: Scholes, R., Mennell, K. (Eds.), *Elephant management: A scientific assessment for South Africa*. Wits University Press, Johannesburg, pp. 241–256.
- Guldemon, R., Van Aarde, R., 2008. A meta-analysis of the impact of African elephants on savanna vegetation. *J. Wildl. Manag.* 72, 892–899. <https://doi.org/10.2193/2007-072>.
- Holdo, R., 2003. Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. *J. Trop. Ecol.* 19, 189–196. <https://doi.org/10.1017/S0266467403003213>.
- Hollender, C.A., Dardick, C., 2014. Molecular basis of angiosperm tree architecture. *New Phytol.* 206 (2), 541–556. <https://doi.org/10.1111/nph.13204>.
- Howard, M., 2017. *Loxodonta africana*. Animal Diversity Web. Retrieved 3.8.2020 from https://animaldiversity.org/accounts/Loxodonta_africana/.
- Howes, B., Doughty, L.S., Thompson, S., 2020. African elephant feeding preferences in a small south African fenced game reserve. *J. Nat. Conserv.* 53, 125700. <https://doi.org/10.1016/j.jnc.2019.03.001>.
- Ihwagi, F., Vollrath, F., Chira, R., Douglas Hamilton, I., Kironchi, G., 2009. The impact of elephants, *Loxodonta africana*, on woody vegetation through selective debarking in Samburu and Buffalo Springs National Reserves, Kenya. *Afr. J. Ecol.* 48 (1), 87–95. <https://doi.org/10.1111/j.1365-2028.2009.01089.x>.
- Jachmann, H., 1989. Food selection by elephants in the 'Miombo' biome, in Rela on to leaf chemistry. *Biochem. Syst. Ecol.* 17 (1), 15–24. [https://doi.org/10.1016/0305-1978\(89\)90037-9](https://doi.org/10.1016/0305-1978(89)90037-9).
- Johnson, J.E., Ebersole, J.J., 2017. Response of Acacia tortilis to elephant browsing in Tarangire National Park, Tanzania: possible above-ground compensation? *J. Young Investig.* 32 (1) <https://doi.org/10.22186/jyi.32.1.1-6>.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69 (3), 373–386. <https://doi.org/10.2307/3545850>.
- Karvonen, V., 2018. Elephants in Taita Taveta County Kenya: Analysing and Predicting the Distribution. University of Helsinki.
- Kristensen, J.A., Svenning, J.-A., Georgiou, K., Malhi, Y., 2022. Can large herbivores enhance ecosystem carbon persistence? *Trends Ecol. Evol.* 37 (2), 117–128. <https://doi.org/10.1016/j.tree.2021.09.006>.
- Lagendijk, D.D.G., Mackey, R.L., Page, B.R., Slotow, R., 2011. The effects of herbivory by a mega- and Mesoherbivore on tree recruitment in sand Forest, South Africa. *PLoS One* 6 (3) e17983.
- Lau, A., Martius, C., Bartholomeus, H., Shenkin, A., Jackson, T., Malhi, Y., Herold, M., Bentley, L.P., 2019. Estimating architecture-based metabolic scaling exponents of tropical trees using terrestrial LiDAR and 3D modelling. *For. Ecol. Manag.* 439, 132–145. <https://doi.org/10.1016/j.foreco.2019.02.019>.
- Laws, R.M., 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21 (1), 1–15. <https://doi.org/10.2307/3543832>.
- Lemieux, A., Clarke, R., 2009. The international ban on ivory sales and its effects on elephant poaching in Africa. *Br. J. Criminol.* 49, 451–471. <https://doi.org/10.1093/bjc/azp030>.
- Levick, S., Asner, G., 2013. The rate and spatial pattern of treefall in a savanna landscape. *Biol. Conserv.* 157, 121–127. <https://doi.org/10.1016/j.biocon.2012.07.009>.
- Loarie, S., van Aarde, R., Pimm, S.L., 2009. Elephant seasonal vegetation preferences across dry and wet savannas. *Biol. Conserv.* 142 (12), 3099–3107. <https://doi.org/10.1016/j.biocon.2009.08.021>.
- Ludwig, F., De Kroon, H., Berendse, F., Prins, H.H.T., 2004. The influence of savanna trees on nutrient, water and light availability and the understory vegetation. *Plant Ecol.* 170 (1), 93–105. <https://doi.org/10.1023/B:VEGE.0000019023.29636.92>.
- Ludwig, F., De Kroon, H., Prins, H.H.T., 2008. Impacts of savanna trees on forage quality for a large African herbivore. *Oecologia* 155 (3), 487–496.
- MacGregor, S.D., O'Connor, T.G., 2004. Response of Acacia tortilis to utilization by elephants in a semi-arid African savanna. *S. Afr. J. Wildl. Res.* 34 (1), 55–66. <https://journals.co.za/doi/pdf/10.10520/EJC117183>.
- Mackey, R., Page, B., Duffy, K., Slotow, R., 2006. Modelling elephant population growth in small, fenced, south African reserves. *Afr. J. Wildl. Res.* 36, 33–43.
- Maeda, E., Nunes, M.H., Calders, K., Mendes de Moura, Y., Raunonen, P., Tuomisto, H., Verley, P., Vincent, G., Zuquim, G., Camargo, J.L., 2022. Shifts in structural diversity of Amazonian forest edges detected using terrestrial laser scanning. *Remote Sens. Environ.* 271, 112895. <https://doi.org/10.1016/j.rse.2022.112895>.
- Malhi, Y., Jackson, T., Bentley, L.P., Lau, A., Shenkin, A., Herold, M., Calders, K., Bartholomeus, H., Disney, M.I., 2018. New perspectives on the ecology of tree structure and tree communities through terrestrial laser scanning. *Interf. Focus* 8, 200170052. <https://doi.org/10.1098/rsfs.2017.0052>.
- Martin-Ducup, O., Mofack, G., Wang, D., Raunonen, P., Ploton, P., Sonké, B., Barbier, N., Couteron, P., Pellissier, R., 2021. *Ann. Bot.* 128 (6), 753–766. <https://doi.org/10.1093/aob/mcab051>.
- Muteti, D., Maloba, M., 2013. Taita Hills Wildlife Sanctuary: Dry Season Total Ground Wildlife Census. Unpublished data.
- Muumbe, T.P., Baade, J., Singh, J., Schullius, C., Thau, C., 2021. Terrestrial laser scanning for vegetation analyses with a special focus on savannas. *Remote Sens.* 13 (3), 507. <https://doi.org/10.3390/rs13030507>.
- Newnham, G.J., Armstrong, J.D., Calders, K., Disney, M.I., Lovell, J.L., Schaaf, C.B., Strahler, A.H., Markanson, F., 2015. Terrestrial laser scanning for plot-scale forest measurement. *Curr. Forest. Rep.* 1, 239–251. <https://link.springer.com/article/10.1007/s40725-015-0025-5>.
- Ngene, S., Njumbi, S., Nzisa, M., Kimitei, K., Mukeka, J., Muya, S., Ihwagi, F., Omondi, P., 2013. Status and trends of the elephant population in the Tsavo-G-Mkomazi ecosystem. *Pachyderm* 53, 38–50.
- Ngene, S., Lala, F., Nzisa, M., Kimitei, K., Mukeka, J., Kiambi, S., Davidson, Z., Bakari, S., Lyimo, E., Khayala, C., Ihwagi, F.W., Douglas-Hamilton, I., 2017. Aerial Total Count of Elephants, Buffalo and Giraffe in the Tsavo-Mkomazi Ecosystem* (February 2017). Kenya Wildlife Service, Arusha, Tanzania. ISBN 978-9966-117-16-8.
- Ogutu, J.O., Piepho, H.P., Said, M.Y., Ojwang, G.O., Nijno, L.W., Kifugo, S.C., Wargute, P.W., 2016. Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: what are the causes? *PLoS One* 11, 1–46. <https://doi.org/10.1371/journal.pone.0163249>.
- Owen-Smith, N., 1988. Megaherbivores. The Influence of Very Large Body Size on Ecology. Cambridge University Press, Cambridge.
- Owen-Smith, N., Kerley, G., Page, B., Slotow, R., Van Aarde, H., 2006. A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *S. Afr. J. Sci.* 102, 389–394.
- Pellew, R.A.P., 1983. The impacts of elephant, giraffe and fire upon the Acacia tortilis woodlands of the Serengeti. *Afr. J. Ecol.* 21 (1), 41–74. <https://doi.org/10.1111/j.1365-2028.1983.tb00311.x>.
- Pellikka, P.K.E., Clark, B.J.F., Gosa, A.G., Himberg, N., Hurskainen, P., Maeda, E., Mwangombe, J., Omoro, L.M.A., Siljander, M., 2013. Chapter 13—Agricultural expansion and its consequences in the Taita Hills, Kenya. In: Paolo Paron, D.O.O., Christian Thine, O. (Eds.), *Developments in Earth Surface Processes*. Elsevier, Amsterdam, The Netherlands. <https://doi.org/10.1016/B978-0-444-59559-1.00013-X>.
- Pellikka, P.K.E., Heikinheimo, V., Hietanen, J., Schäfer, E., Siljander, M., Heiskanen, J., 2018. Impact of land cover change on aboveground carbon stocks in Afromontane landscape in Kenya. *Appl. Geogr.* 94, 178–189. <https://doi.org/10.1016/j.apgeog.2018.03.017>.
- Peters, E.B., Wythers, K.R., Bradford, J.B., Reich, P.B., 2013. Influence of disturbance on temperate forest productivity. *Ecosystems* 16, 95–110. <https://doi.org/10.1007/s10021-012-9599-y>.
- Potapov, I., Järvenpää, M., Åkerblom, M., Raunonen, P., Kaasalainen, M., 2017. Bayes Forest: a data-intensive generator of morphological tree clones. *GigaScience* 6 (10). <https://doi.org/10.1093/gigascience/gix079>.

- QGIS Development Team, 2023. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>.
- Raunonen, P., Kaasalainen, M., Åkerblom, M., Kaasalainen, S., Kaartinen, H., Vastaranta, M., Holopainen, M., Disney, M., Lewis, P., 2013. Fast automatic precision tree models from terrestrial laser scanner data. *Remote Sens.* 5 (2), 491–520. <https://doi.org/10.3390/rs5020491>.
- Raunonen, P., Casella, E., Calders, K., Murphy, S., Åkerblom, M., Kaasalainen, M., 2015. Massive-scale tree modelling from TLS data. In: *ISPRS Annals of the Photogrammetry Volume II-3/W4 PIA15+HRIG15*. Joint ISPRS Conference 2015, 25–27 March 2015, Munich, Germany. <https://doi.org/10.5194/isprsannals-II-3-W4-189-2015>.
- Reckziegel, R.B., Mbongo, W., Kunneke, A., Morhart, C., Sheppard, J.P., Chirwa, P., du Toit, B., Kahle, H.-P., 2022. Exploring the branch wood supply potential of an agroforestry system with strategically designed harvesting interventions based on terrestrial LiDAR data. *Forests* 13 (5), 650. <https://doi.org/10.3390/f13050650>.
- Reyer, C.P.O., Bathgate, S., Blennow, K., Borges, J.G., Bugmann, H., Delzon, S., Faias, S. P., Garcia-Gonzalo, J., Gardiner, B., Gonzalez-Olabarria, J.R., 2017. Are forest disturbances amplifying or cancelling out climate change-induced productivity changes in European forests? *Environ. Res. Lett.* 12, 034027 <https://doi.org/10.1088/1748-9326/aa5ef1>.
- RIEGL, 2019. RIEGL VZ @-400i. RIEGL. Referenced: 28.2.2020. available: http://www.riegl.com/uploads/tx_pxriegl/downloads/RIEGL_VZ-400i_Datasheet_2019-11-22.pdf.
- Roussel, J.-R., Auty, D., Coops, N.C., Tompalski, P., Goodbody, T.R.H., Sánchez Meador, A., Bourdon, J.-F., de Boissieu, F., Achim, A., 2020. lidR: an R package for analysis of airborne laser scanning (ALS) data. *Remote Sens. Environ.* 251, 112061. <https://doi.org/10.1016/j.rse.2020.112061>.
- Scholes, R.J., Archer, S.R., 1997. Tree–grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28, 517–544. <https://www.jstor.org/stable/2952503>.
- Sebata, A., 2017. Ecology of Woody plants in African savanna ecosystems. *Plant Ecol.* <https://doi.org/10.5772/intechopen.69865>.
- Smith, R.J., Kasiki, S.M., 2000. A Spatial Analysis of Human-Elephant Conflict in the Tsavo Ecosystem, Kenya. African Elephant Specialist Group, Human-Elephant Conflict Task Force of IUCN, Gland, Switzerland.
- Ssali, F., Sheil, D., Nkurunungi, J., 2012. How selective are elephants as agents of forest tree damage in Bwindi impenetrable National Park, Uganda? *Afr. J. Ecol.* 51, 55–65. <https://doi.org/10.1111/aje.12006>.
- Staub, C., Binford, M., Stevens, F., 2013. Elephant herbivory in Majete wildlife reserve, Malawi. *Afr. J. Ecol.* 51, 536–543. <https://doi.org/10.1111/aje.12064>.
- Thouless, C., et al., 2016. African Elephant Status Report 2016: An Update from the African Elephant Database. IUCN, Gland, Switzerland. ISBN: 9782831718132.
- Tomlinson, P.B., 1983. Tree architecture: new approaches help to define the elusive biological property of tree form. *Am. Sci.* 71, 141–149. <https://www.jstor.org/stable/27851897>.
- Valladares, F., Niinemets, U., 2007. The architecture of plant crowns: From design rules to light capture and performance. In: Pugnnaire, F., Valladares, F. (Eds.), *Functional Plant Ecology*. Taylor and Francis, New York, NY. <https://doi.org/10.1201/9781420007626>.
- Viergever, K.M., Woodhouse, I.H., Stuart, N., 2008. Monitoring the world's savanna biomass by earth observation. *Scott. Geogr. J.* 124, 218–225. <https://doi.org/10.1080/14702540802425279>.
- van Wijngaarden, W., 1985. Elephants, Trees, Grass, Grazers : Relationships between Climate Soils, Vegetation and Large Herbivores in a Semi-Arid Savanna Ecosystem (Tsavo, Kenya). ITC, Enschede, Netherlands. ISBN 9789061640486. <https://research.wur.nl/en/publications/elephants-trees-grass-grazers-relationships-between-climate-soils>.
- Wu, J., Van Aardt, J.A.N., Asner, G.P., Kennedy-Bowdoin, T., Knapp, D., Erasmus, B.F.N., Mathieu, R., Wessels, K., Smit, I.P.J., 2009. LiDAR waveform-based woody and foliar biomass estimation in savanna environments. In: *Silvilaser 2009*, October 14–16, 2009. College Station, Texas, USA.
- Zimbres, B., Shimbo, J., Bustamante, M., Levick, S., Miranda, S., Roitman, I., Silvério, D., Gomes, L., Fagg, C., Alencar, A., 2020. Savanna vegetation structure in the Brazilian Cerrado allows for the accurate estimation of aboveground biomass using terrestrial laser scanning. *For. Ecol. Manag.* 458, 117798. <https://doi.org/10.1016/j.foreco.2019.117798>.