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ARTICLE

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# Investigating the patterns of tree cover and density in relation to abiotic and biotic factors in Kruger National Park

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**Abstract**

Across savanna ecosystems worldwide, the decline of large trees and the rapid expansion of shrubs present major conservation challenges. These trends are especially pronounced in South Africa's Kruger National Park (KNP), the country's largest protected area. To quantify their extent and identify their drivers, we conducted a spatial assessment of tree cover and density across KNP from 2011 until 2022. We then evaluated how these response variables are influenced by abiotic factors, including fire, climate, soil, and geology, and by biotic factors, such as the densities of African elephant adult male bulls and herds, including females and calves. We defined trees as land-cover elements that cast a distinct shadow and stand taller than 5 m. Using Collect Earth, an open-source software for augmented visual interpretation of high-resolution satellite imagery, we assessed tree cover and density on 4258 plots of 0.5 ha each. We recorded 27,918 trees, equivalent to an average density of 13 trees/ha. Counts in each plot were truncated to a maximum of 30 individuals. We validated our estimates of tree cover and height against independent, high-resolution airborne LiDAR measurements, which yielded an RMSE of 8.89% for trees taller than 3 m. The relative influence of selected predictors on tree cover and density was analyzed through logistic and survival regressions. Geology had the greatest influence on tree distribution, where both tree cover and density were higher on nutrient-poor granitic substrates than on nutrient-rich basalts. Tree cover and density were higher in areas with low fire frequency, close to main rivers, and with higher sand content in the soil. The mean annual rainfall showed a positive correlation with tree cover, while it had a negative correlation with the number of trees. Elephant bulls were found to be negatively correlated with both tree cover and density. In contrast, elephant herds exhibited a positive correlation with tree cover and density. This study highlights the importance of understanding the effects of multiple factors on tree distribution and aims to provide a baseline for assessing tree cover and density across KNP to support ongoing tree management strategies and contribute to future conservation priorities.

**KEYWORDS**
African elephant, Collect Earth, drylands, Kruger National Park, protected areas, savanna ecosystem, South Africa

# INTRODUCTION

Kruger National Park (KNP), established in 1926, is the largest protected area in South Africa, providing valuable insight into the savanna ecosystem and the intricate relationship between humans and nature. Savanna ecosystems are maintained and shaped by multiple environmental factors such as abundant megaherbivores, evolving fire management regimes, fluctuating wet-dry cycles, varied geological substrates, and complex soil compositions, as well as global changes in $CO_2$ levels and rainfall patterns (Buisson et al., 2019; Sankaran et al., 2005; Staver et al., 2011).

During the past few decades, shifts in these environmental factors have led to two major and interconnected concerns in savannas worldwide (Honda & Durigan, 2016; Rosan et al., 2019; Stevens et al., 2017) and in KNP specifically (Case & Staver, 2017; Kellner et al., 2022; Strydom et al., 2023; Venter et al., 2018). These concerns are the loss of large trees and the progressive encroachment of woody vegetation (i.e., shrubs and small trees) that gradually transform grasslands into more densely wooded areas. In savannas, and more specifically in KNP, large trees are typically defined as woody individuals at least 5 m tall, whereas taller shrubs and small trees fall between 3 and 5 m (Coetsee, Botha, et al., 2023; Henley & Cook, 2019; Shannon et al., 2008).

These woody plants provide vital habitats and sources of food and shade for wildlife, while also protecting against erosion, enhancing soil fertility, and strengthening landscape resilience (Shannon et al., 2008). In savanna and grassland ecosystems, sparse tree cover is not inherently a sign of degradation or deforestation; in fact, overly dense tree cover can compromise the integrity of these naturally open landscapes. That is, dense tree and woody cover can severely limit the richness and productivity of light-demanding herbaceous plants (Wieczorkowski & Lehmann, 2022), and it can reduce available habitat for native animals adapted to open environments (Parr et al., 2012). They may also alter nutrient cycles, as trees typically require more water and soil nutrients (Berthrong et al., 2012), and impair other critical ecosystem services (Veldman et al., 2015).

Megaherbivores are a key biotic driver of vegetation structure in KNP. African elephants (*Loxodonta africana*), in particular, act as ecosystem engineers by physically altering and creating habitats while selectively feeding on plant resources (Ripple et al., 2015). The conservation status and the perception of the importance of African elephants vary; while some countries are struggling to conserve elephant numbers due to illegal poaching and an increase in human–wildlife conflict (Goswami et al., 2015; Shaffer et al., 2019), elephant numbers within KNP have risen steadily since the early 1900s (Ferreira et al., 2017). Movement patterns of elephants change based on forage quality and quantity (Shrader et al., 2012) and accessibility to surface water (Chamaillé-Jammes et al., 2007; Smit & Ferreira, 2010). Elephants responding to these factors can influence trees and biodiversity in savannas because of their ability to tear off leaves and branches, stripping down the bark or uprooting trees completely (Henley & Cook, 2019).

In addition to herbivory, fire is a central ecological driver in savannas, influencing both vegetation structure and landscape heterogeneity (van Wilgen et al., 2003). Fire management policies in KNP have evolved over time from occasional prescribed burning to fire suppression to the more adaptive and integrated management system applied today (van Wilgen et al., 2022). These strategies have recognized the combined effect of fire with both abiotic factors such as geology, soil, climate, and biotic factors like herbivory in maintaining biodiversity, landscape heterogeneity, preventing woody encroachment, and the loss of large trees (MacFadyen et al., 2016; Staver et al., 2017; van Wilgen et al., 2022).

Given the increasing urgency of addressing large tree loss and woody vegetation encroachment in savannas, there is a critical need for systematic, easy-to-use, and accessible monitoring tools to support science-based, adaptive landscape management strategies. We conducted a large-scale spatial assessment of tree cover and density across KNP using the open-source tool Collect Earth (Bey et al., 2016). We then examined how these response variables correlate with key abiotic and biotic drivers. Through this, we support ongoing tree management strategies and contribute to future conservation priorities.

# METHODS

## Study area

KNP is the largest protected area in South Africa, covering approximately 2 million ha, and is located in the northeastern region of the country sharing its eastern border with Mozambique and northern border with Zimbabwe (Figure 1). KNP is described as a deciduous savanna with diverse vegetation types (Gertenbach, 1983) and is crossed by eight major rivers flowing from the higher escarpments in the west toward Mozambique. A narrow north–south geological gradient underlies KNP, with granite rocks covering the west and basalt rock running down the eastern side. In the southern part of the park, a thin strip of Ecca shales, which is part of the Karoo geological Supergroup, runs between these dominant substrates (Venter et al., 2003). In addition to the dominant basalt and granite substrates, KNP also features smaller, patchy occurrences of gabbro, gneiss, schist, and alluvial deposits, which contribute to the park's geological and ecological diversity (Venter et al., 2003). KNP receives the majority of its annual rainfall during summer (October–April) with a decreasing rainfall gradient from south to north (Zambatis, 2003). Rainfall, geology, and soils establish KNP's abiotic template (MacFadyen et al., 2016). Biotic forces ranging from termites to African elephants, together with fire management practices, then reshape vegetation and maintain ecosystem heterogeneity (Abraham et al., 2021; Smit et al., 2013).

## Datasets

### Collect Earth

Collect Earth is a free, open-source software developed by the Food and Agriculture Organization of the United Nations (FAO) that combines satellite imagery with augmented visual interpretation for land monitoring assessments at a regional to global scale (Bey et al., 2016). The software is built on Google Earth and Google Earth Engine (GEE) technologies, allowing users to access a wide range of imagery sources. For this study, we primarily used very high-resolution imagery from Google Earth and Microsoft Bing Maps, with the acquisition date of the images spanning from 2011 to 2022 (only two plots used older imagery from 2003 and 2004) and a spatial resolution of less than 2 m. In addition, Collect Earth provides access to long-term normalized difference vegetation index (NDVI) time series from Landsat (30 m, since the 1980s), MODIS (250–500 m, since 2000), and Sentinel-2 (10–20 m, since 2015) via GEE. During the data collection, we used NDVI time series to contextualize vegetation dynamics and distinguish stable woody cover from seasonally variable herbaceous growth (Bey et al., 2016).

Prior to the data collection, the user develops a customized questionnaire which may include questions about land-cover type (e.g., trees, shrubs, crops), land-cover density, land use (e.g., forests, shrubland, grassland, wetland), and land-use changes based on the project's main objectives. The definitions of land use and land cover are specific to each project and are established at the beginning of the study. The user then creates a grid of sample plots across a study area, representing the locations where data will be collected. The plots are then imported into Collect Earth, and when a user clicks on a sample plot, the questionnaire appears alongside the plot, and the user visually interprets the plots using access to multiple satellite imagery and the NDVI long-term time series. To further help the user with the data collection, each plot is subdivided into 49 sample points, each representing approximately 2% of the plot area. The subdivision helps assess the percentage of cover of different land-cover elements inside the plot. Each land element (e.g., trees, shrubs) that falls under one of the sample points is counted as 2% cover of that element type. Once all plots have been assessed, the data can be exported in CSV or KML format and used for further environmental and statistical analysis. For further information, refer to Bey et al. (2016).

### Data collection

For this assessment, 4258 sample plots were systematically distributed across KNP with a 2 km distance

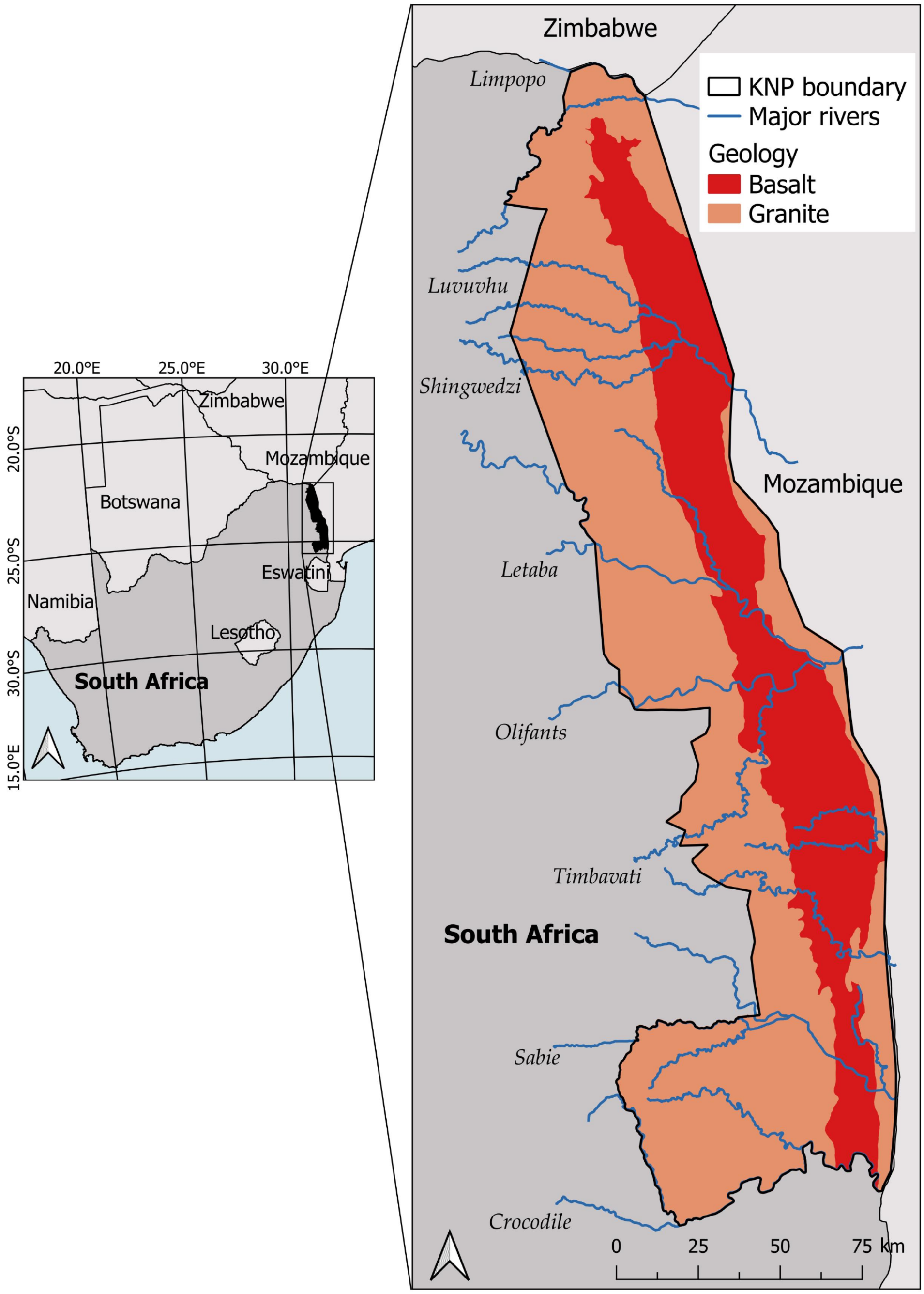


**FIGURE 1** Study area with a close-up of Kruger National Park (KNP) showing the park boundary, major rivers, and the two main geological substrates, basalt and granite (simplified geology).

between the centers of each plot. The plot size of 0.5 ha (70 m × 70 m) was chosen based on previous studies (Bey et al., 2016; Riccardi et al., 2020). Between October 2021 and January 2022, seven operators classified each image subset (plot) into distinct land-use and land-cover categories. In this study, land-cover elements that cast a distinct shadow, resulting from their height and structure (Bey et al., 2016), were classified as trees. Smaller vegetation that does not cast a shadow was classified as shrubs. Only observations classified as trees were retained for analysis. Tree cover was estimated in discrete classes: 0%, 2%, 4%, 6%, 8%, 10%–19%, 20%–29%, and subsequent 10% intervals up to 100%. Tree counts were truncated at 30 per plot; thus, a recorded value of 30 indicates 30 or more trees. Examples of three classified plots are shown in Appendix S1: Figures S1–S3.

## Data validation: LiDAR imagery

To assess the accuracy of the tree cover data collected through Collect Earth and to validate the height of the land elements classified as trees, we used LiDAR imagery collected in KNP by the Harvard Animal Landscape Observatory (HALO) across 48 sites in January 2021. HALO integrates a high-resolution LiDAR sensor (Riegl VUX-1LR), a thermal camera, and an RGB imaging camera mounted on a UAV (Boucher et al., 2023), which for this study was either a DJI M600 or a Freefly Alta-X. The UAV flights were conducted at 100 m above ground level with a flight speed of 8 m s$^{-1}$. Surveys were conducted in January, February, October, and November 2020; June 2021; and September 2022. LiDAR data were acquired at a 600 kHz laser pulse repetition rate with flight lines spaced 114 m apart to yield 60% side overlap with a 110-degree field of view. All UAV flights were conducted in accordance with South African Civil Aviation Authority (SACAA) requirements under a Registered Operating Certificate belonging to Integrated Aerial Systems. A SACAA-certified pilot performed all flights, and permission to operate in KNP was obtained from South African National Parks (permit number DAVAB1630) prior to the surveys.

LiDAR images offer highly detailed, three-dimensional information on vegetation structure and are widely considered a reliable source for validating remote sensing data (Boucher et al., 2023). LiDAR data have already been used to quantify canopy height and cover (Asner et al., 2016; Boucher et al., 2023; Strydom et al., 2023), but never to validate Collect Earth estimates. Initially, fewer than 30 plots of the Collect Earth dataset overlapped with the available LiDAR coverage; therefore, 206 new validation sample plots were systematically generated inside the LiDAR coverage areas, with 1 km spacing between the centers of each plot. The new validation sample plots were uploaded to Collect Earth, and tree cover was assessed using the same questionnaire. To minimize bias, one operator independently assessed tree cover using Collect Earth, while a second operator conducted a separate evaluation using LiDAR imagery.

An initial spatial assessment was conducted on the 206 systematically generated plots to ensure data quality by verifying that no plots were located too close to the boundaries of the LiDAR coverage area. Following this assessment, 144 plots were confirmed to be fully contained within the LiDAR extent. For each of these, a masked canopy height model (CHM) was extracted using the *raster* package in R version 4.2.3 (R Core Team, 2025). Pixels in the CHM were then reclassified as 0 if they were $\leq 3$ m $= 0$ and 1 if they were $>3$ m. After controlling for missing values (i.e., NAs), the percentage of woody cover per plot was calculated using an off-the-shelf coverage mean function for precision and run through the *exactextractr* package in R:

$$\bar{x}_w = \frac{\sum_{i \in P_{\mathrm{CE}}} \mathrm{pixel}_i \times \mathrm{coverage}_i}{\sum_{i \in P_{\mathrm{CE}}} \mathrm{coverage}_i}, \tag{1}$$

where $P_{\mathrm{CE}}$ is the CHM pixel set intersecting with the CE plot, $\bar{x}_w$ is the weighted percentage woody cover value, pixel$_i$ is the binary pixel classified value, and coverage$_i$ is the coverage fraction of the pixel that intersects with the CE plot. This provided an accurate plot-scale determination for the percentage of woody cover above 3 m.

## Environmental variables

Six abiotic factors and two biotic factors that are believed to influence tree distribution in KNP were chosen (MacFadyen et al., 2019; Scholtz et al., 2014; Smit et al., 2010; Staver et al., 2017) (Table 1).

### Abiotic factors

Datasets related to geology, main rivers, monthly rainfall, and fire frequency were provided by SANParks (Scientific Services Data Repository). The geology predictor is shown in Figure 1 and the other four abiotic factors in Figure 2.

Only two geological substrates, basalt and granite, were considered in this study; other geological substrates with limited spatial extent and fragmented distribution within the park were incorporated into these two dominant classes. To calculate the distance to the nearest river, we used the main rivers map and calculated the Euclidean distance within the park boundaries using QGIS Development Team (2023) version 3.22. R Core Team (2025) version 4.3.1 was used to obtain the mean annual rainfall and mean fire-return interval. The mean

**TABLE 1** Variables used in the study.

| Variable | Type | Range/ levels |
|---|---|---|
| Response variables | | |
| Tree cover (%) | Ordinal | 0–100 |
| Tree density (no.) | Ordinal | 0–30+ |
| Environmental variables | | |
| Geology | Factor | Granite/ basalt |
| Distance to nearest river (m) | Continuous | 0–12,420 |
| Sand content (g/kg) | Continuous | 354–733 |
| Mean annual rainfall (mm) | Continuous | 313–840 |
| Mean fire-return interval (years) | Continuous | 3–40 |
| Bulls (smoothed/100 m$^2$) | Continuous | 0.0068–0.0269 |
| Herds (smoothed/100 m$^2$) | Continuous | 0.0423–0.1622 |

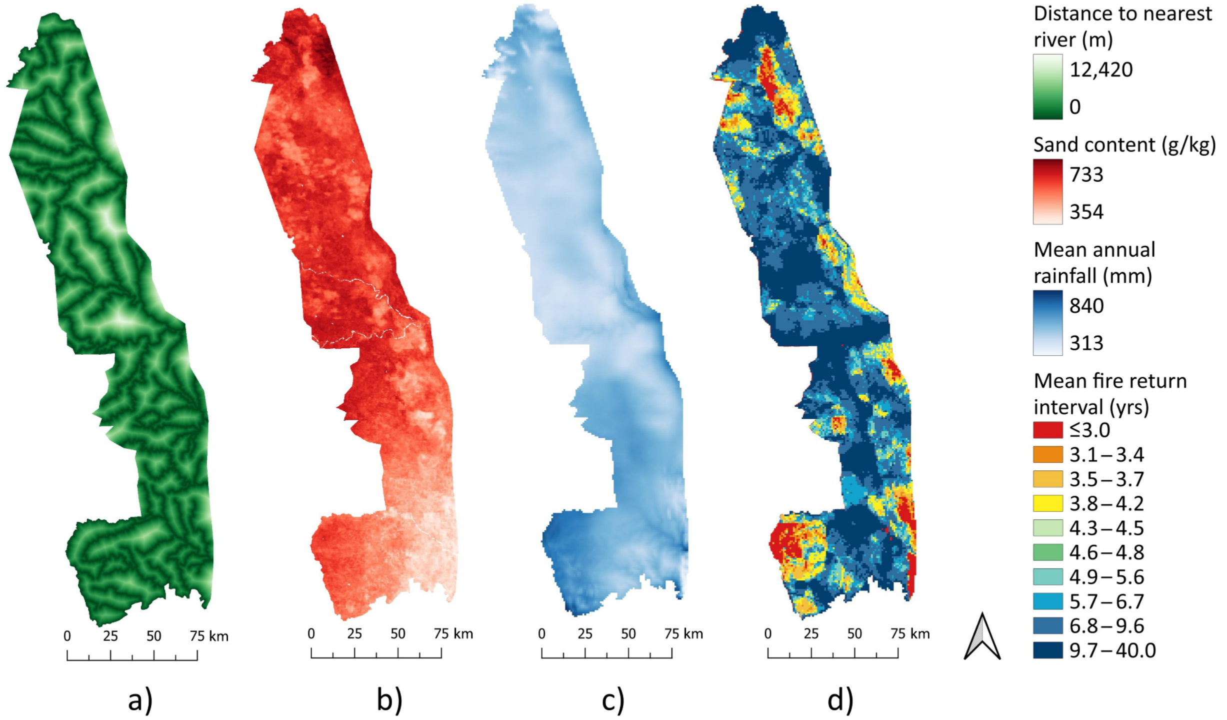


**FIGURE 2** Environmental variables considered as predictors in this study: (a) distance to nearest river, (b) sand content, (c) mean annual rainfall, (d) mean fire-return interval.

annual rainfall was calculated using the monthly rainfall dataset (1979–2018), and the mean fire-return interval was determined using the fire frequency dataset (1981–2021). The mean fire-return interval is defined as the average of the sum of years between consecutive fires. To calculate this variable, we first transformed the fire areas from vectors into binary rasters, 1 for burned areas and 0 for areas not burnt. We then stacked all rasters using the *raster* package and counted the years between consecutive fires and returned the average for every pixel (Smit et al., 2013). The sand content (in grams per kilogram) was downloaded from the SoilGrids database with depth 0–5 and 250 m spatial resolution (Hengl et al., 2014, 2017). The mean annual temperature was downloaded from CHELSA (Brun et al., 2022; Karger et al., 2017).

## Biotic factors

We considered the density of adult male elephants ("bulls" from now on) and the density of mixed adult females, calves, and occasional adult males ("herds" from now on) as our two biotic factors (Figure 3).

The group has a biological significance, as breeding herds exhibit different habitat preferences, live in sexually segregated social groups for the majority of the year, and exhibit very different foraging behavior compared to solitary or bull-only groups (Smit et al., 2007; Stokke & Du Toit, 2002; Wittemyer et al., 2005). The density was derived from aerial census data spanning a period of 10 years (2003–2012), selected as it followed the cessation

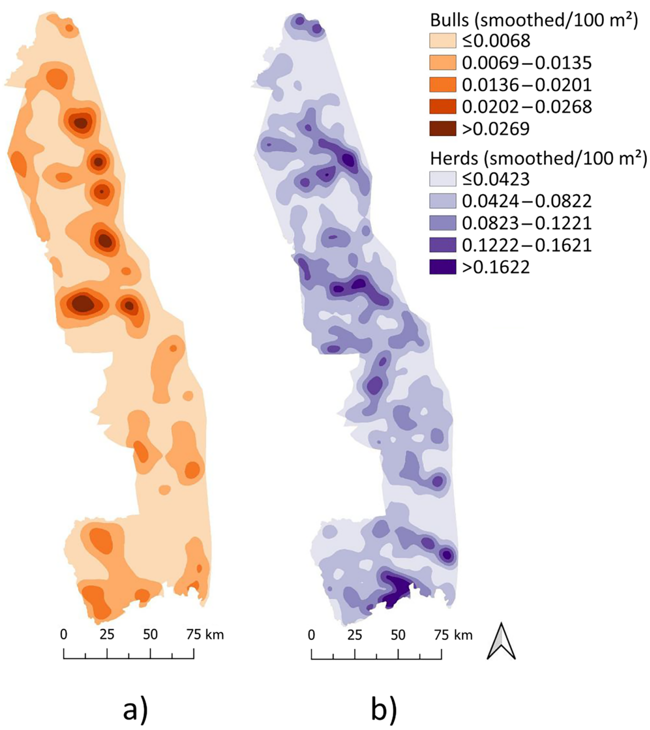


**FIGURE 3** Elephant density considered as predictors in this study: (a) bulls and (b) herds.

of systematic annual culling to reduce elephant numbers (van Aarde et al., 1999). Data from aerial censuses included: number of elephants counted, GPS coordinates, and the group composition (bulls/herds). Aerial censuses of elephants are conducted once a year in August—the peak of the dry season in KNP.

Since elephants increasingly feed on woody plants as the dry season progresses (Kos et al., 2012; Pretorius et al., 2012), we considered their distribution and local abundance in August to represent a good approximation of foraging pressure on tree cover and density. To estimate spatial density, we used a Kernel density approach rather than a modeling approach using ecological covariates as predictors of elephant local densities. This is due to the fact that multivariate models would necessarily include covariates that would have been used to predict tree cover and density, thus violating observation independence required by regression analyses.

We used QGIS Development Team (2023) v 3.22 to apply the Kernel Density Estimation to the georeferenced elephant census data, weighted for the number of elephants observed at each data point. We first calculated the mean center of all elephant GPS locations and the standard distance of the locations (σ, a measure of spatial point dispersion around the mean center), using the Spatial Point Patterns Analysis tool. We then calculated the optimal Kernel Density bandwidth using the formula: $\mathrm{Hopt} = \sigma\left(\frac{2}{3}n\right)^{1/4}$, where $n$ is the sample size (i.e., total number of GPS locations; Fotheringham et al., 2000). The calculated standard distance values were 97,973 for herds and 100,290 for bulls, while the optimal bandwidths were 9547 and 9432, respectively.

Using the Heatmap Plugin, two different Kernel Density rasters (with a quartic biweight Kernel shape) were generated: bulls and herds. The obtained Kernel densities were thus not an estimate of elephant densities but rather reflected an index of intensity of use (i.e., number of elephant sightings weighted by group size in a specific area over time). Therefore, for brevity, we liberally use the terms bulls and herds to refer to the Kernel Density estimates. The Kernel Density raster values range in Figure 3 represent the smoothed weighted number of bulls and herds per square kilometer (elephants per square kilometer). These values are fractional due to the smoothing effect of the Kernel function and reflect the relative intensity of area use rather than absolute counts. Each pixel corresponds to a 1 km × 1 km area, so the density values express the intensity of elephant presence averaged over this spatial scale.

## Data analyses

All spatial analysis on tree cover and density was carried out using QGIS Development Team (2023) v 3.22 and all statistical analysis was performed using R Core Team (2025) v 4.3.1. Firstly, a Pearson correlation analysis was performed on the environmental variables (excluding the categorical geology variable) to check for multicollinearity, and the mean annual temperature was removed due to a moderate correlation with mean annual rainfall.

Both tree cover and density were recorded according to interval classes; however, we merged low proportion classes to obtain more evenly distributed ranges: 0%, 2%–6%, 8%–29%, ≥30% for tree cover and 0, 1–4, 5–14, ≥15 for tree density. To account for differences in units of measurement and to facilitate comparison among predictors, all continuous abiotic and biotic variables (except the categorical geology variable) were standardized to have a mean of zero and a SD of one. We then performed two Wilcoxon tests, one to look for differences between the tree cover and density classes and geology, and another to look for differences between bulls and herds on the two geological substrates. Furthermore, we also performed a chi-squared test to check for significant differences between the two geologies and the four interval classes for both tree cover and density.

To analyze the distribution of tree cover we applied the Proportional Odds Logistic Regression (POLR), also referred to as cumulative link model. The model belongs to a class of generalized linear models used for modeling the dependence of an ordinal response on discrete or continuous covariates (Agresti, 2002). We report the odds ratio (OR) for increments from each lower to each higher category. To analyze tree density, we used the parametric survival regression formula (Kalbfleisch & Prentice, 2002), taking into consideration the truncated and categorical nature of the variable. A survival analysis examines the relationship of the survival variable (generally survival time, in our case, the tree density truncated at 30 trees) and the predictor variables (covariates), however, considering the censoring issue of the response variable. For further details on the model, we refer to Kalbfleisch and Prentice (2002) and Schober and Vetter (2018). When predicting a categorical variable, the interpretation is slightly different: we did not predict tree cover directly, but the probability of falling in a higher tree cover or tree density class. For both the POLR and the survival regression, every unit increases in a predictor variable, the probability of falling in a higher class changes (in percentage) in relation to the ordinal regression coefficient: $\Delta P = (\mathrm{OR} - 1) \times 100$. The association between tree cover and the predictor is positive when OR $> 1$ and negative in the opposite case.

After performing the POLR model, we analyzed the variance inflation factor (VIF) (Naimi et al., 2014). The VIFs were then calculated separately for the tree cover and tree density models; all VIFs were below 1.48, indicating low multicollinearity in both cases (Appendix S1: Tables S1 and S2). To measure the goodness of fit, considering the ordinal nature of the variables, we calculated the residuals for each explanatory variable using the surrogate approach (Liu & Zhang, 2018). For further details on residuals for ordinal regression models, we refer to Liu and Zhang (2018). The *sure* package was used to calculate the surrogate residuals for tree cover POLR, where the fitted values and reference distribution (used in Q-Q plots) are automatically extracted (Appendix S1: Figure S6). To obtain the residuals for the tree density response variable, which is ordinal and truncated, we used the *residuals* package coupled with a smoothing function (Appendix S1: Figure S7).

Finally, to better understand which of the variables in the regression were most contributing to the model, we used the *party* package and ran a random forest variable ranking analysis for tree cover and density. Ranked probability score (RPS) has been shown to be particularly appropriate for the evaluation of probability forecasts of ordinal variables (Janitza et al., 2016).

# RESULTS

## Sampling scope and imagery sources

Data were collected in all 4258 plots, of which 4168 were retained after intersecting with the chosen abiotic and biotic layers for the statistical analysis. Eighty-four percent of plots were interpreted from Google Earth imagery (2017–2022) and Bing Maps imagery (2019–2022).

## Tree cover, density, and LiDAR validation

The percentage of cover and density reflects the data collected in each plot, considering the regrouping intervals used for the statistical analysis (Figure 4). In total, across all 4258 plots, 27,918 trees were counted, giving an average of 7 trees/plot or 13 trees/ha, based on which we estimated that the total area of KNP (19,485 km$^2$) contains more than 25 million trees. In the assessment, 16% of the

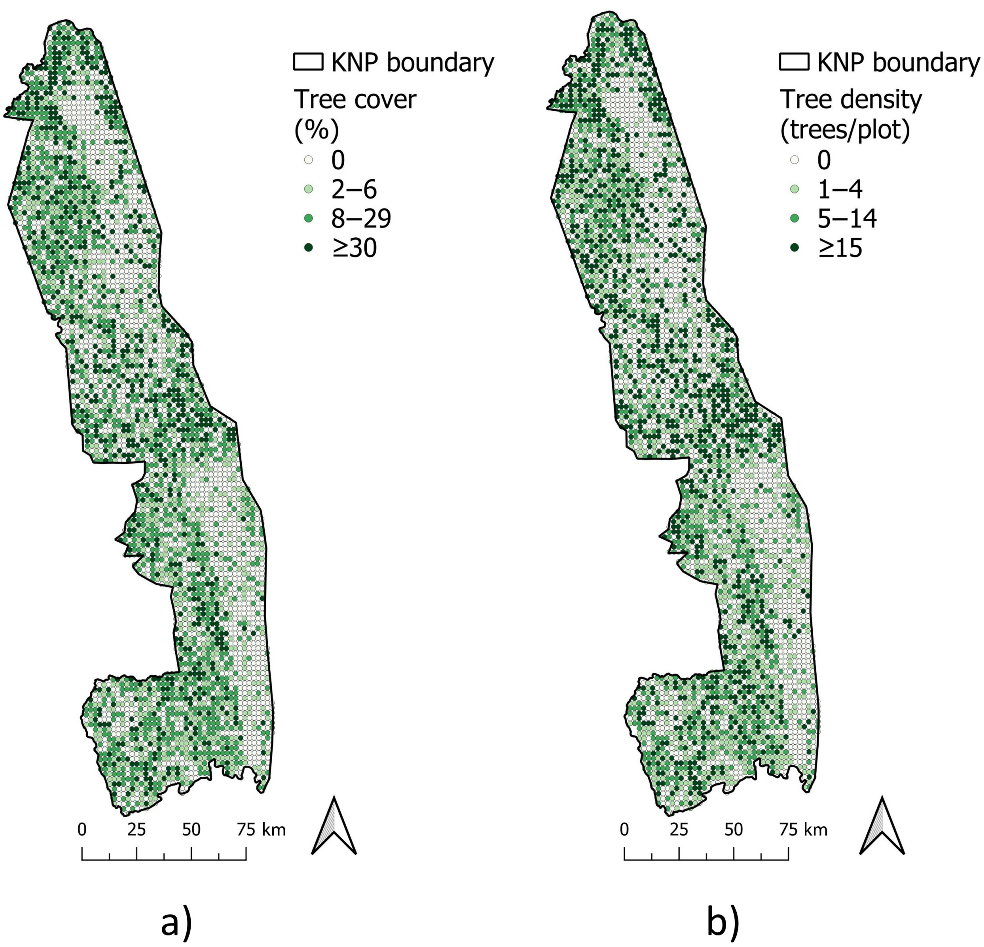


**FIGURE 4** (a) Tree cover and (b) tree density recorded for each plot, mapped using color classes corresponding to four percentage ranges defined for data analysis. KNP, Kruger National Park.

plots had a tree cover higher than 30%, 26% had a cover of 8%–29%, 21% of the plots had a tree cover of 2%–6%, while 37% of the plots had no tree cover.

Collect Earth estimates of tree cover agreed well with LiDAR-derived tree cover. We calculated the root mean square error (RMSE) using the midpoints of the interval classes and obtained a value of 8.89% for the percentage of woody cover above 3 m. A Wilcoxon paired test ($p > 0.05$) indicated no significant difference between the two datasets (Appendix S1: Figures S4 and S5).

## Tree patterns and abiotic-biotic variables

Tree cover and density were consistently higher on granitic than on basaltic substrates (Figure 5). A stacked plot was used to compare tree cover and tree density between basalt ($n = 1432$) and granite ($n = 2736$) plots, accounting for the differing number of plots within each geology. Nineteen percent of granite plots had ≥30% cover versus 10% on basalt, while 54% of basalt plots lacked trees compared with 28% on granite (Figure 5a). Similarly, tree density showed a comparable trend (Figure 5b). Twenty-five percent of granite plots had ≥15 trees per plot, compared to 15% of plots on basalt. The percentage of plots with no trees was substantially greater on basalt, 54%, than on granite, 28%. Wilcoxon rank sum tests confirmed significant differences for both tree cover ($W = 2{,}570{,}841$, $p < 0.001$; Figure 5a) and tree density ($W = 2{,}525{,}182$, $p < 0.001$; Figure 5b) between granite and basalt substrates.

Bull elephants showed a pronounced preference for basalt ($W = 1{,}338{,}701$, $p < 0.001$; Figure 6a), whereas herds exhibited no strong geological bias ($W = 2{,}018{,}136$, $p = 0.109$; Figure 6b).

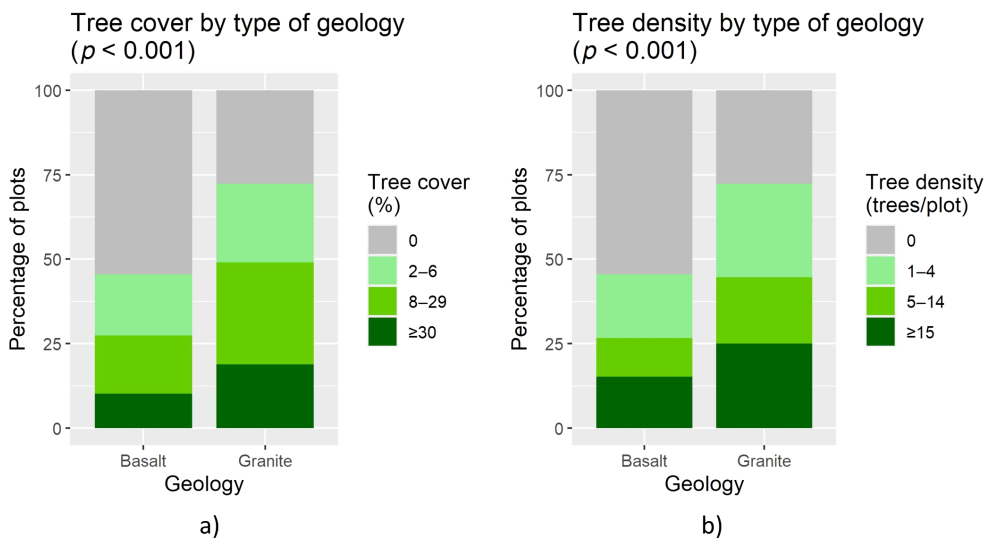


**FIGURE 5** Percentage of plots in each geology, classified according to (a) tree cover and (b) tree density.

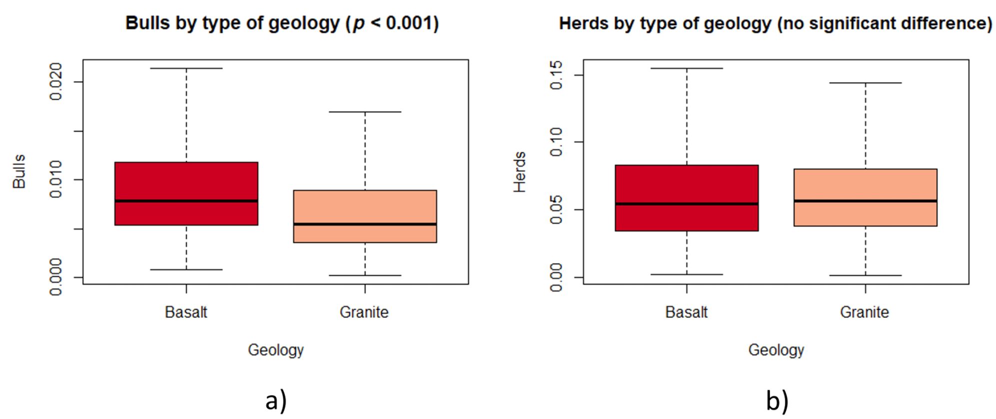


**FIGURE 6** Boxplots showing (a) bulls by geology and (b) herds by geology. The midline represents the median, the box limits indicate the first and third quartiles (interquartile range), the whiskers extend to the minimum and maximum values within 1.5× the interquartile range, and points beyond the whiskers represent outliers.

## Multivariate models and relative importance

The ordered logistic and survival regressions (Tables 2 and 3) identified geology, sand content, rainfall, distance to rivers, fire-return interval, and elephant densities as significant predictors ($p < 0.05$). Tree cover increased with higher rainfall, higher sand content, closer to main rivers, and longer fire-return intervals and lower bull densities, whereas it decreased with higher herd density. Tree density showed similar results to tree cover; however, it decreased with higher rainfall.

Variable-importance analysis highlighted geology and mean fire-return interval as the strongest determinants of both tree cover and density, followed by sand content, rainfall, distance to rivers, and elephant metrics (Figure 7).

**TABLE 2** Ordered logistic regression model coefficients, odds ratio (OR), 95% CIs, and *p* value for tree cover.

| Environmental variables | OR | CI | *p* |
|---|---|---|---|
| Geology–granite | 2.35 | 2.07–2.67 | <0.001 |
| Distance to nearest river | 0.87 | 0.82–0.93 | <0.001 |
| Sand | 1.22 | 1.14–1.30 | <0.001 |
| Mean annual rainfall | 1.10 | 1.04–1.17 | <0.001 |
| Mean fire-return interval | 1.28 | 1.21–1.36 | <0.001 |
| Bulls | 0.85 | 0.80–0.91 | <0.001 |
| Herds | 1.07 | 1.01–1.14 | 0.03 |

**TABLE 3** Ordered logistic regression model coefficients, odds ratio (OR), 95% CIs, and *p* value for tree density.

| Environmental variables | OR | CI | *p* |
|---|---|---|---|
| Geology–granite | 1.53 | 1.40–1.67 | <0.001 |
| Distance to nearest river | 0.96 | 0.92–0.99 | 0.03 |
| Sand | 1.18 | 1.14–1.22 | <0.001 |
| Mean annual rainfall | 0.95 | 0.91–0.99 | 0.02 |
| Mean fire-return interval | 1.17 | 1.12–1.22 | <0.001 |
| Bulls | 0.94 | 0.90–0.98 | 0.004 |
| Herds | 1.05 | 1.01–1.10 | 0.02 |

# DISCUSSION

## Overview of tree cover and density patterns in KNP

In the savanna ecosystem, it is crucial to consider multiple environmental factors together with African elephant pressure to better understand vegetation patterns (Smit et al., 2013; Staver et al., 2017). This study provides a comprehensive assessment of tree cover and density across more than 4000 plots of 0.5 ha in KNP (Figure 4), validated through LiDAR, and highlights what the main factors are that correlate with their distribution. Overall, we found that geology and fire-return interval were the most influential factors, but rainfall, sand content, proximity to rivers, and the difference between elephant male bulls and females and calves also played important roles (Figure 7).

The results of the assessment of tree cover and density with Collect Earth highlighted the heterogeneous distribution of tree cover across KNP. An average tree density of 13 trees/ha across KNP is low compared to other studies (Wigley et al., 2014). However, this estimate does not take into consideration the difference in landscape heterogeneity and the truncated nature of the variable,

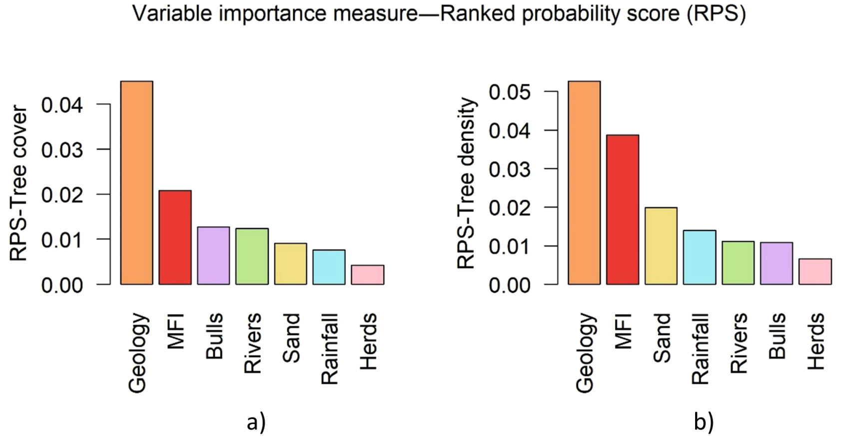


**FIGURE 7** Variable importance for (a) tree cover and (b) tree density, based on ranked probability scores (RPS). The model includes abiotic variables, such as distance to nearest river, geology, mean fire-return interval (MFI), sand content, and mean annual rainfall, and biotic variables, such as elephant bull and herd densities.

where a maximum of 30 trees per plot was recorded. Therefore, it is important to interpret the findings based on the statistical analysis, which highlights how tree density is influenced by all abiotic and biotic variables.

## Geology as the primary template

Geology was the strongest predictor of tree cover and density, highlighting its fundamental role in shaping savanna vegetation (Venter et al., 2003). Our results corroborate previous findings that granites, characterized by deeper soils and higher water infiltration, can support a higher tree cover than basalts (Tables 2 and 3) (Urban et al., 2020). On the other hand, basalts, despite their fertile clay substrates, promote grass productivity and higher fire intensities to the detriment of trees and other woody plants (Scholes et al., 2003; Staver et al., 2017).

In addition to geology, sand content was also positively correlated with both tree cover and tree density (Tables 2 and 3), reinforcing the idea that porous, coarse-grained sandy soils with high water infiltration potential promote the accumulation of deep-rooted trees (Staver et al., 2017). Clay soils with lower water infiltration and conductivity rates cause water stress under dry conditions and thus prevent the increase of large trees in savanna landscapes and instead favor the growth of the grassy layer (Colgan et al., 2012; Fensham et al., 2015).

## Hydrological gradients and riparian zones

Tree cover and density rose sharply near major rivers. Proximity to rivers was positively correlated with both tree cover and density (Tables 2 and 3), consistent with the presence of riparian vegetation/riverine forests along major rivers (van Coller et al., 1997). Successive flood events have most likely led to the formation of deeper soils, which are more favorable to the development of forests with high tree cover and density, as observed by O'Connor (2010) in the Mapungubwe National Park, Limpopo Province. Furthermore, in these areas, trees have better access to water for longer periods during the dry season as opposed to trees further away from rivers. Riparian zones experience less fire (Figure 2) due to the cooler, moister microclimate created by the dense tree canopy, which inhibits fire spread and suppresses the growth of flammable grasses through shading (van Wilgen et al., 2003). These areas are also attractive to elephants, providing year-round access to water. However, the combined effect of fire and elephants in these areas remains complex to disentangle (Smit & Archibald, 2019).

## Rainfall and grass competition

Unexpectedly, rainfall was positively associated with tree cover (Table 2) but negatively associated with tree density (Table 3). While, on average, tree cover in savannas increases with precipitation (Sankaran et al., 2005; Staver et al., 2017), the observed decline in tree density in wetter areas may reflect stronger competition from grasses, which thrive in high-rainfall zones and suppress tree recruitment and limit tree growth (February et al., 2013). In contrast, large trees with a broad canopy cover and deeper roots are favored by increased rainfall, while not being limited by competition with grasses. Nevertheless, this result needs to be further investigated to fully understand the interaction between abiotic and biotic factors and drivers of vegetation change at the park level.

## Role of fire in shaping tree patterns

Fire is a key top-down driver of savanna vegetation (van Wilgen et al., 2003), and our analysis showed that areas with longer periods between successive fires (i.e., greater mean fire-return interval) had a higher tree cover and density (Tables 2 and 3). These results align with long-term fire experiments in KNP (Smit et al., 2010) and park-wide studies showing that frequent fires reduce tree (Strydom et al., 2023) and woody vegetation (Case & Staver, 2017; Smit et al., 2010). While this suggests that a reduction in fire frequency would limit the loss of large trees, this, in turn, could lead to an increase in woody encroachment and the possibility of higher intensity fires breaking out due to high above-grass biomass (van Wilgen et al., 2022). Therefore, effective fire management in KNP must balance tree conservation with trying to reduce woody encroachment, highlighting the need for park-wide vegetation monitoring systems.

## Divergent roles of elephant bulls and herds

Elephants had divergent correlation with tree cover and density: Male bulls were negatively associated with tree cover and density, while herds were positively associated. These contrasting trends likely reflect behavioral and spatial differences. Elephants, despite being mixed feeders, have been linked to changes in fire occurrence (Smit & Archibald, 2019). Although all elephants damage trees by tearing off leaves and branches, stripping the bark, or pushing over entire trees, several studies have confirmed that bulls have a higher impact on woody plants than females (Asner et al., 2016; Henley & Cook, 2019). This behavior is not strictly due to foraging but might reflect displacement aggression or a form of intra- or intersexual display of dominance during the reproductive "musth" cycles (Midgley et al., 2005). In KNP, bulls are known to favor open areas on basalts around artificial water points over densely vegetated riverine areas compared to herds which, instead, prefer areas close to rivers (Abraham et al., 2021). This pattern may partly reflect habitat preferences, though the greater visibility of lone bulls in open basalt areas than in more vegetated granites could also contribute to a minor detection bias. Therefore, our results most likely reflect a preference of nonreproductive bulls for areas further away from rivers, where tree density is sparser and canopy cover is reduced, as confirmed in other studies (Smit et al., 2007).

On the other hand, the positive association with herds most likely reflects a preference of female elephants for habitat types close to rivers, and thus more densely covered by trees. Herds are indeed known to congregate along river courses during the dry season due to the higher water turnover rates of females and calves (due to the smaller body size) (Smit et al., 2007), and also because riverine forests provide greater availability and quality of forage and possibly protective cover against predation risk (real or perceived) by humans (Stokke & Du Toit, 2002). However, recently, it has been shown that in KNP, bulls are increasingly occupying areas closer to rivers while herds are expanding uplands, indicating that there may no longer be a clear bulls–herds segregation (MacFadyen et al., 2019). For this reason, since the space and resource use are changing, monitoring tree distribution systematically will be essential to further clarify the potential bulls–herds impacts on savanna vegetation. This study provides a baseline and presents a method which can be repeated over time to monitor tree and elephant dynamics over time and investigate how tree cover and density are correlated to elephant bulls and herds.

### Remote sensing approach: Strengths and limitations

Remote sensing tools like Collect Earth, when validated through ground truth or LiDAR data, offer a cost-effective approach for monitoring trees over large areas. Yet, some limitations need to be acknowledged. A key challenge is the difficulty in detecting small trees and shrubs lower than 3 m, which may lead to an underestimation of tree cover and density, especially in savannas. Previous studies have validated Collect Earth estimates with ground truth data. For example, in a global analysis on drylands, Bastin et al. (2017) obtained an 8.32% error, while Riccardi et al. (2020) collected ground truth plots on the arid island of Socotra, Yemen, obtaining an error of 8% tree cover, with a maximum disagreement of one cover class above or below (e.g., 10%–19% instead of 20%–29%), and 11% error for tree density. In this study, LiDAR data provided an effective and statistically significant substitute for ground truthing, as shown in other previous studies (Asner et al., 2016; Strydom et al., 2023). The RMSE (8.89%) is consistent with previous studies, and the analysis confirmed that most of the trees that were being recorded by the operators were above 3 m and not only 5 m and above, further supporting the reliability of this method for monitoring tree cover and density in savanna ecosystems. Despite these limitations, Collect Earth, when complemented with ground truthing or LiDAR validation, provides an efficient, accessible, and effective approach to assess tree distribution systematically across large areas such as KNP and can be used to monitor both tree loss and woody encroachment over time.

## CONCLUSION AND MANAGEMENT IMPLICATIONS

This study provides the first park-wide spatial assessment of tree cover and density in KNP using Collect Earth supported by LiDAR validation. The findings highlight how tree distribution is correlated to a complex combination of abiotic and biotic factors, with geology and fire-return interval emerging as the strongest predictors. Furthermore, we show how elephant bull and herd density relate to tree cover and density differently; however, because the elephant data predate the tree density and tree cover data, these relationships likely reflect longer term patterns rather than immediate impacts on tree distribution.

By establishing a robust, replicable methodology and providing a validated baseline for tree cover and density, this study offers a tool that can contribute to ongoing long-term monitoring conservation programs in KNP (Coetsee, Smit, et al., 2023; Ferreira et al., 2017; van Wilgen et al., 2022). Collect Earth is designed for tree assessments, often with 5 m as a threshold to define trees. However, our validation using LiDAR confirmed that it effectively captures woody vegetation taller than 3 m, making it a cost-effective and systematic tool to also assess woody encroachment of trees above 3 m across savanna landscapes.

As environmental pressures such as climate change, fire regime shifts, and herbivore dynamics continue to change, open-source and accessible monitoring tools will be essential for maintaining landscape resilience and informing evidence-based decision-making in KNP. This approach and methodology can be extended to other savanna systems facing similar ecological pressures, offering a tool to monitor both land-cover and land-use changes across dryland protected areas.

## AUTHOR CONTRIBUTIONS

**Tullia Riccardi:** Conceptualization; methodology; data collection; statistical analysis; visualization; writing—original draft preparation. **Giacomo D'Ammando:** Conceptualization; methodology; statistical analysis; writing—reviewing and editing. **Lucy Wilson:** Methodology; data collection; statistical analysis; writing—reviewing and editing. **Fabio Attorre:** Conceptualization; methodology; statistical analysis; writing—reviewing and editing. **Andrew Davies:** Methodology; data collection; writing—reviewing and editing. **Alessio Farcomeni:** Methodology; statistical analysis, writing—reviewing and editing. **Sandra MacFadyen:** Methodology; data collection; statistical analysis; writing—reviewing and editing. **Tercia Strydom:** Methodology; data collection; writing—reviewing and editing. **Izak P. J. Smit:** Methodology; data collection; writing—reviewing and editing. **Luca Malatesta:** Conceptualization; methodology; data collection; statistical analysis; supervision; writing—reviewing and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data on tree cover and tree density obtained using Collect Earth (Riccardi et al., 2025) are available from Figshare: https://doi.org/10.6084/m9.figshare.30042691. The rainfall dataset (MacFadyen, 2018) is available from Zenodo: https://doi.org/10.5281/zenodo.10691170. Requests to access additional environmental data should be directed to SANParks through the SANParks Biodiversity Information Management System (BIMS): https://bims.sanparks.org.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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