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RESEARCH ARTICLE

Rocky outcrops form islands of high and unique tree biodiversity within an ocean of grass in Serengeti National Park

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Abstract

African savannahs are characterised by a high plant diversity, partly resulting from a high turnover in community compositions across space. However, it is poorly understood what is driving this spatial turnover in plant communities. Here, we investigate to which extent the presence of rocky outcrops (also called kopjes) explains the community composition of trees in an African savannah, and how we can understand the responses of tree species to rocky outcrops by their functional traits. Along a precipitation gradient, we visited 24 sites in Serengeti National Park (Tanzania). At each site, we characterised tree communities, as well as their functional traits, in both a kopje and an adjacent open savannah plot (matrix plot). We found that kopjes harboured elevated tree abundances and species richness. Their dominant trees were more often evergreen, had a higher specific leaf area, a lower leaf nitrogen content and a lower spine density, than dominant trees in the savannah matrix. Differences in tree communities between kopjes and savannah matrix plots were generally the largest at sites with low precipitation. Our results indicate that kopjes are strong drivers of tree biodiversity, possibly due to locally increased soil moisture and low fire frequencies. The uniqueness of kopje tree communities may have important implications for higher trophic levels and ecosystem functioning.

KEYWORDS
biodiversity, functional traits, heterogeneity, kopjes, precipitation, rocky outcrops, savannah, Serengeti, trees

Résumé

Les savanes africaines sont caractérisées par une grande diversité végétale, résultant en partie d'une forte variation de la composition des communautés dans l'espace. Toutefois, les facteurs à l'origine de cette évolution spatiale des communautés végétales sont mal compris. Nous étudions ici dans quelle mesure la présence d'affleurements rocheux (également appelés kopjes) explique la composition de la communauté d'arbres dans une savane africaine, et comment nous pouvons comprendre les réponses des espèces d'arbres aux affleurements rocheux par leurs caractéristiques fonctionnelles. Le long d'un gradient de précipitations, nous avons

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visité 24 sites dans le parc national du Serengeti (Tanzanie). Sur chaque site, nous avons déterminé les communautés d'arbres, ainsi que leurs caractéristiques fonctionnelles, à la fois dans un kopje et dans une parcelle de savane ouverte adjacente (parcelle matricielle). Nous avons constaté que les kopjes abritaient une abondance d'arbres et une richesse d'espèces élevées. Leurs arbres dominants étaient plus souvent sempervirents, avaient une surface foliaire spécifique plus élevée, une teneur en azote foliaire plus faible et une densité d'épines plus faible que les arbres dominants de la matrice de la savane. Les différences des communautés d'arbres entre les kopjes et les parcelles matricielles de savane étaient généralement les plus importantes dans les sites à faibles précipitations. Nos résultats indiquent que les kopjes sont de puissants facteurs de biodiversité arboricole, peut-être en raison de l'humidité accrue du sol et de la faible fréquence des incendies. Le caractère unique des communautés d'arbres des kopjes peut avoir des incidences importantes sur les niveaux trophiques supérieurs et le fonctionnement de l'écosystème.

1 | INTRODUCTION

African savannahs are famous for their high biodiversity (Mittermeier et al., 1998), including their diversity of herbaceous as well as woody plants (Byers, 2001). Part of this high biodiversity is driven by a high turnover in species composition across space (Anderson et al., 2004, 2015; Davies et al., 2023; McNaughton, 1983), which is partly driven by gradients in precipitation, wildfires, herbivory and termite mounds (Anderson et al., 2008, 2015; Reed et al., 2009; Rugemalila et al., 2016; van der Plas et al., 2013). In addition, another factor that can contribute to habitat heterogeneity in African savannahs is the presence of rocky outcrops (Anderson et al., 2008; Poelchau & Mistry, 2006).

In African savannahs, rocky outcrops, also known as 'kopjes' (Figure 1), are relatively rare landscape elements (covering less than 1% of the ground surface; Herlocker, 1976), but they add considerable abiotic heterogeneity to the landscape. First, when precipitation falls on kopjes, most of the water accumulates between cracks, which thereby form local patches with relatively high water availability. As a result, plant species that, due to higher water requirements, are unable to survive the dry season in most of the savannah might potentially grow on kopjes. Second, it has been suggested that the vegetation on kopjes escapes fires since the bare rocks act as a fire break (Hoeck, 1975). Third, kopjes provide shade and oversight opportunities for large predators, making them a popular resting site for these (Durant et al., 2010; Hopcraft et al., 2005). As a result, kopjes might be avoided by many herbivorous mammal species, making herbivory pressure lower. Because of these strong environmental differences between kopjes and 'matrix' sites, overall, kopjes may provide relatively 'benign' conditions for woody plants, and some have suggested that kopje may therefore strongly contribute to biodiversity in African savannahs (e.g. Anderson et al., 2008). Yet, few formal studies have compared diversity patterns between kopje and matrix sites. The only studies that formed exceptions found that kopjes harboured unique bird and herbaceous plant species (Poelchau & Mistry, 2006; Trager & Mistry, 2003). However, we are still missing formal studies on whether and, if so, how tree communities differ between kopje and matrix sites.

One approach to gain understanding of the potential drivers of differences in species compositions among sites is the study of plant functional traits (McGill et al., 2006). Functional traits determine the habitat requirements of species as well as their competitive capacity and ability to tolerate or escape natural enemies. Therefore, functional traits can be used to understand how different sites within a landscape act as different 'habitat filters', whereby only species with certain traits can tolerate local abiotic conditions (Díaz et al., 1998; Keddy, 1992). For example, plant species without spines are typically

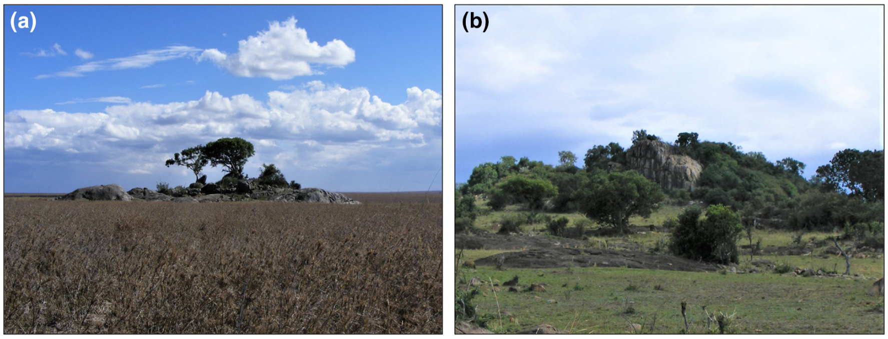

FIGURE 1 Two kopjes in Serengeti National Park (SNP). (a) A kopje in the southern plains, where trees are hardly present in the surrounding vegetation. (b) A kopje more north in SNP, where average annual precipitation is higher and trees are also present in the surroundings. Photos made by Fons van der Plas.

more heavily browsed than species with a high spine density (Cooper & Owen-Smith, 1986), potentially making species without spines only able to occur on kopjes if these have lower herbivore densities.

Importantly, we also expect that effects of kopjes on tree communities depend on spatial variation in precipitation. Water availability is one of the most important limiting factors for plant growth in savannahs, so it is no surprise that many plant species respond strongly to precipitation gradients (Reed et al., 2009). In general, higher precipitation areas support higher densities of trees (Anderson et al., 2015; Sankaran et al., 2005), as well as more tree species (Anderson et al., 2008; Davies et al., 2023; Eshete et al., 2011). As a result, we expect that kopjes, especially, will have strong effects on tree abundances, species composition and species richness in dry sites, where low water availability would normally strongly constrain tree establishment in savannah vegetation but where water availability within rock cracks can still be relatively high. In contrast, we expect that with higher precipitation, the effects of kopjes on tree abundances, species composition and species richness are more moderate, as even in the savannah matrix, water availability is relatively high.

To test these ideas, we surveyed tree communities at 24 kopjes and 24 adjacent matrix plots positioned along a precipitation gradient in Serengeti National Park (SNP). Additionally, we measured several functional traits (specific leaf area, leaf area, leaf nitrogen content and spinescence) and collated data on leaf habit (deciduous/evergreen) from existing literature. With these data, we investigated the following questions: (i) how do tree species composition, species richness and abundances respond to habitat type (kopje vs. adjacent site); (ii) can traits be used to understand how habitat filtering drives tree community responses to habitat type and (iii) to what extent do effects of habitat type interact with precipitation patterns?

2 | MATERIALS AND METHODS

2.1 | Study region

Serengeti National Park (SNP) is a protected area in northwestern Tanzania (34° to 36° E and 1° to 3° 30′ S). There is a strong gradient in mean annual precipitation, ranging from <500 mm in the southeast to over 900 mm in the northwest (Figure 2; data from http://www.grid.unep.ch/data/data.php). This precipitation gradient coincides with transitions in main habitat types, with treeless plains in the southeast, savannah vegetation in the centre and woodlands becoming more common in the northwest (Reed et al., 2009). At smaller scales, rocky outcrops add to the habitat heterogeneity in SNP.

2.2 | Plot selection

We surveyed tree communities in paired plots (kopje vs. matrix) along a gradient in annual precipitation. Although the precipitation gradient in SNP spans from 500 to 900 mm, we studied a gradient from ~650 to ~750 mm, as (i) in drier sites, no trees are present in the matrix vegetation due to a shallow soil hardpan (Sinclair, 1979), and (ii) because the wettest sites are devoid of kopjes (Figure 2). In total, we studied 24 'kopje plots' and 24 adjacent, equal-sized 'matrix' plots in October–December 2010 (Figure 2). Kopjes were at least 62.5 m away from each other, with a mean nearest neighbour distance of 1433 m and the furthest kopjes being over 67 km away from each other (Figure 2). We sampled vegetation within the smallest rectangle that could be drawn around a kopje. The area of these plots ranged from 285 to 2000 m^2, with an average size of 588 m^2. Between 50 and 100 m from the kopje plot (randomly chosen distance), in a random direction, we visited a matrix plot, which had the same size and shape as the associated kopje plot. We ensured that the matrix plot was not within 50 m of another kopje.

2.3 | Tree community survey

In each plot, we surveyed all individual woody plants that were at least 0.5 m in height and identified them as species. Initial identification was performed using Van Wyk and Van Wyk (1997) and the Seronera Research Station herbarium collection. We later standardised species names using the 'Leipzig Catalogue of Vascular Plants' (Freiberg et al., 2020), using the 'lcvp_search' function of the LCVP package (https://github.com/idiv-biodiversity/LCVP) in R-4.1.0 (R Core Team, 2021). Additionally, we estimated the height of each individual to a precision of 0.5 m.

2.4 | Plant traits

In each plot, we measured four traits for each observed tree species: specific leaf area (SLA, i.e. the area of a fresh leaf divided by its dry weight), individual leaf area (LA), leaf nitrogen content (N) and spine density. These traits were selected for their functional relevance regarding a photosynthetic efficiency-leaf longevity trade-off (SLA and N; Reich et al., 1997; Wright et al., 2004), tolerance to drought and nutrient stress (LA and SLA; Westoby et al., 2002), leaf attractiveness to herbivores (N; Cooper & Owen-Smith, 1985; Mattson, 1980) and defence against large herbivores (spine density; Gowda, 1996; Cooper & Owen-Smith, 1986).

Each of these four traits was measured for each observed species within each plot. To measure SLA and LA, 10 leaves of each species in each plot were picked at breast height (or lower for shorter trees). Together with a reference square with a known area, these leaves were put on a sheet and photographed in the field. Because many leaves fold during sunny and hot weather, we picked the leaves and placed them in a shaded location for at least 15 min before photographing. The program ImageJ (Abramoff et al., 2004) was used to calculate the total area of photographed leaves in cm^2. By dividing this by the number of leaves, the individual LA was calculated. The leaves were oven-dried at 70°C for at least 24 h, after which the

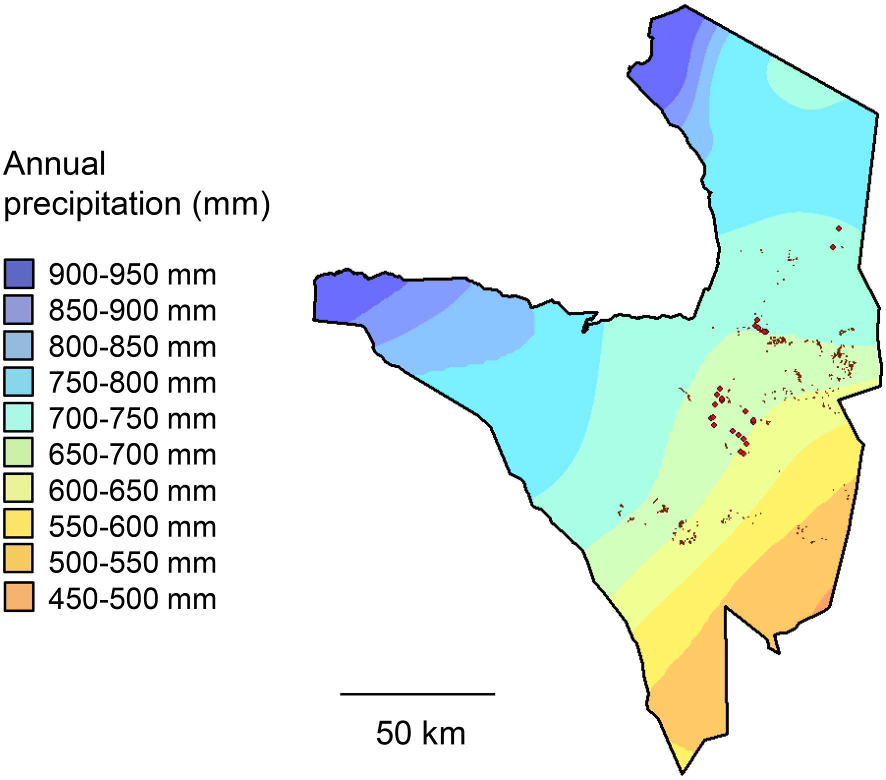

FIGURE 2 Map of Serengeti National Park, with kopjes indicated in brown, and surveyed sites by red dots. The background colour gradient indicates spatial variation in annual precipitation.

weight was measured. SLA was calculated by dividing the total leaf area of fresh leaves by the total dry weight. Spine density was measured by taking at least five randomly selected branches at breast height (or lower, for lower trees) between 10 and 20 cm and counting the number of spines. Density was then quantified as the number of spines per 10 cm. For leaf N content measurements, we collected bulk samples of fresh leaves from each species. These were dried and ground with a bullet grinder. We measured leaf N content for a subset of the samples (11%) using a Carlo-Erba NA 1500 (Carlo-Erba, Milan, Italy). Leaf N concentrations of the other samples were estimated using a spectrophotometer (Bruker MPA NIR) and an associated calibration, based on the combined chemically measured samples from this and a previous study (van der Plas et al., 2013). Samples (i.e. leaves and branches) for SLA, LA, spine density and leaf N concentration were collected from 1 to 5 individuals on each plot, depending on tree availability (many species only occurred with a single individual within a plot).

In addition to the above plant traits, we also collated information on leaf habit, that is whether trees are deciduous or evergreen. Leaf habit data was collated at the species level, based on various published sources (see Supplementary Data).

2.5 | Data analyses

Based on the tree surveys and the trait data, we quantified the following eight variables for each plot: tree species richness, tree density, rarefied species richness, the proportion of evergreen trees and the community-weighted mean (CWM; Violle et al., 2007) of SLA, LA, N and spine density. Species richness was quantified as the number of woody species within a plot, while density was quantified as the total number of observed tree individuals within the plot, divided by the plot area. We also calculated rarefied species richness based on an abundance level of 10 following Hurlbert's (1971) formulation, using the 'rarefy' function in the 'vegan' package (Oksanen et al., 2024) in R-4.1.0 (R Core Team, 2021). The proportion of evergreen trees was quantified as the proportion of tree individuals that are evergreen, weighted for the height of the tree individuals. To quantify CWM values of SLA, LA, N and spine density, we first quantified average trait values for each tree species within each plot. In cases where data were missing (with 12%, 20%, 19% and 7% of missing observations for SLA, LA, N and spine density, respectively), average trait values (across plots) of the given tree species were assigned, which reduced the proportion of missing values to 5%, 13%, 6% and 4% for SLA, LA, N and spine density, respectively. We then quantified CWMs using the equation: $\text{CWM} = \sum_{i=1}^{S} T_i H_i$ (Violle et al., 2007), where S is the number of species, T_i the trait value of species i and H_i the summed heights of all trees of species i within a given plot, divided by the summed height of all trees of all species, so that H_i is a proxy of relative biomass (suitable when diameter data are not available; Mukuralinda et al., 2021). In addition, for each pair of kopje and associated matrix plot (i.e. a pair of kopje plot and matrix plots that were located at the same site), we also quantified the dissimilarity in their species composition using three different measures: the Jaccard distance, the Bray-Curtis distance and the Raup-Crick distance (Anderson et al., 2010). The Jaccard distance quantifies, based on presence-absence data, the proportion of species that are not shared between two communities. The Bray-Curtis distance is based on abundance (rather than presence-absence) data and is a measure of how similar different plots are in their species composition and relative abundances (Bray & Curtis, 1957). Last, we also quantified the Raup-Crick distance, which is similar to the Jaccard distance but corrects for differences in species richness (Anderson et al., 2010). All distance measures were quantified using the 'ecodist' function in the 'vegan' package (Oksanen et al., 2024) in R-4.1.0 (R Core Team, 2021).

We then analysed to what extent the above variables (species richness, density, rarefied richness, proportion of evergreen trees and CWMs of SLA, LA, N and spine density) are related to habitat type (kopje vs. matrix plot) and precipitation and their interactive effects using General Linear Mixed Models (GLMMs). In 'full' GLMMs, (rarefied) species richness, density, the proportion of evergreen trees or CWMs of SLA, LA, N and spine density were treated as the response variables, habitat type (kopje vs. matrix), annual precipitation and their interaction were treated as fixed factors, and site (given the paired design, where each kopje was adjacent to a matrix plot) was treated as a random factor. In the model of species richness, we also included the log-transformed area of the plot as a fixed factor, as species-area relationships are typically non-linear but become linear on a log-log scale (Brown, 1995; Preston, 1962). To meet the assumption of normality, in some cases data transformations were required: species richness, density and LA were log-transformed, and the proportion of evergreen trees was asin-transformed. In addition to full GLMMs, also four simplified models were performed, in which (i) the interaction effect between habitat type and annual precipitation was omitted, (ii) only annual precipitation, (iii) only habitat type was included as a fixed factor or (iv) an 'intercept only' model without fixed factors. The richness model deviated from the other models in that the logged area was also included in all cases. We also investigated to what extent differences in CWM values of traits between kopje and matrix plots could be driven by trait plasticity within species by running GLMMs where raw trait values were treated as the response variable, habitat type was treated as a fixed factor and site and species were treated as random factors. All above models were fitted with a maximum likelihood procedure using the lmer function of the lme4 package (Bates et al., 2015) in R-4.1.0 (R Core Team, 2021), and we selected a final model based on the lowest Akaike Information Criterion. We quantified the marginal (proportion of variance explained by fixed factors only) and conditional (combined fixed and random effects) R^2 values (sensu Nakagawa & Schielzeth, 2012), using the 'r.squaredGLMM' function of the MuMIn package (Barton, 2020). We also investigated whether Jaccard distance, Bray-Curtis distance or Raup-Crick distance among paired matrix and control plots were associated with precipitation, using simple linear models with the amount of precipitation as the predictor variable.

3 | RESULTS

In total, 41 woody species were observed during this study, with 37 found on kopjes and 18 found on matrix plots (Supplementary Data). Twenty-three species were exclusively found on kopje plots, and four species exclusively on matrix plots. The five most frequently observed species were *Commiphora schimperi* (present in 34 plots), *Grewia bicolor* (present in 23 plots), *Turraea fischeri* (present in 22 plots), *Cordia ovalis* (present in 20 plots) and *Vachellia tortilis* (in 20 plots). Of these, *Grewia bicolor* and *Cordia ovalis* were exclusively found on kopje plots.

Species richness was significantly higher on kopje plots (mean = 11.5 species, standard error [SE] = 0.68) than on matrix plots (mean = 3.3 species, SE = 0.47), and increased with annual precipitation. This increase was stronger on matrix plots, so that the difference in species richness between kopje plots and matrix plots was largest at sites with low precipitation (Figure 3a; Table 1). Similarly, tree density was significantly higher on kopje plots (mean = 15.28, SE = 2.28) than on matrix plots (mean = 3.92, SE = 1.52). Tree densities increased with annual precipitation on

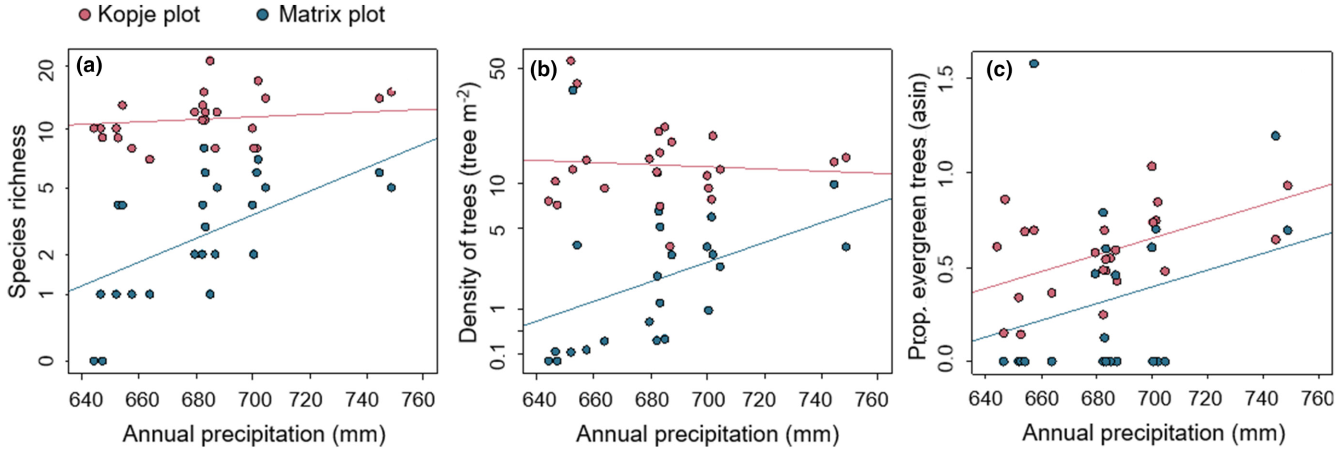

FIGURE 3 Species richness (a), tree density (b), and the proportion of evergreen trees (c) vary among habitat types and along a precipitation gradient. Note that species richness is shown on a log-transformed axis, while the proportion of evergreen trees is asin-transformed.

TABLE 1 GLMM summaries.

Response	Intercept	Habitat type	Precipitation	Habitat x prec.	Log area	R^2_m	R^2_c
Log richness	−5.845 (2.757)	8.628 (2.586)	0.012 (0.003)	−0.011 (0.004)	−0.186 (0.129)	0.759	0.790
Rarefied richness[a]	−28.139 (6.425)	27.395 (8.957)	0.046 (0.009)	−0.035 (0.013)		0.696	0.705
Log density	−7.897 (3.638)	11.527 (5.145)	0.013 (0.005)	−0.015 (0.008)		0.570	0.570
Asin Habit	−2.689 (1.395)	0.257 (0.087)	0.004 (0.002)			0.206	0.387
CWM of SLA	60.644 (2.327)	12.299 (3.181)				0.245	0.264
Log CWM of LA	−18.267 (5.020)	15.036 (6.296)	0.031 (0.007)	−0.018 (0.009)		0.747	0.763
CWM of N	6.305 (1.434)	−0.600 (0.094)	−0.005 (0.002)			0.457	0.564
CWM of SD	7.333 (0.877)	−5.971 (1.214)				0.350	0.350

Note: The ‘response’ column gives the response variable of a given model, and the ‘intercept’, ‘habitat type’, ‘precipitation’, ‘habitat type × precipitation’ and ‘log area’ columns give the effect sizes and standard errors of the respective fixed factors, if they were included in the final model. As the model selection was based on AIC values, p values are not given, although, as a rule of thumb, when effect sizes are in absolute magnitude over two times as large as standard errors, the effect should be significant. Explanation of acronyms: Asin = asin transformation, CWM = community-weighted mean, SLA = specific leaf area, LA = individual leaf area, N = nitrogen, SD = spine density.

[a] Rarefied to an abundance level of 10. Note that as some (eleven) plots had a lower abundance, of five even had an abundance of 0 or 1, for some plots rarefied richness was based on extrapolation rather than interpolation.

control plots but slightly decreased with precipitation on kopje plots, so that at the highest level of precipitation, abundances hardly varied among habitat types (Figure 3b; Table 1). Rarefied species richness was also significantly higher on kopje plots (mean = 6.64, SE = 0.13) than on matrix plots (mean = 3.35, SE = 0.43) and also increased with rainfall (Table 1).

The proportion of evergreen trees was higher on kopjes (mean = 0.317, SE = 0.039) than on matrix plots (mean = 0.192, SE = 0.062), and both on control and kopje plots, this proportion increased with annual precipitation (Figure 3c; Table 1). Furthermore, CWMs of each trait differed among habitat types, and CWMs of some traits additionally changed with precipitation (Figure 4; Table 1). Specifically, the CWM of SLA was higher on kopjes (mean = 72.9 $cm^2 g^{-1}$, SE = 1.94) than on matrix plots (mean = 60.6 $cm^2 g^{-1}$, SE = 2.62), but did not change with annual precipitation (Figure 4a; Table 1). The CWM of LA was higher on kopjes (mean = 3.92 cm^2, SE = 0.60) than on matrix plots (mean = 0.53 cm^2, SE = 0.13) and increased with annual precipitation, although this increase was strongest on matrix plots, so that at high precipitation, the difference in LA between kopje and matrix plots was relatively smaller than in drier areas (Figure 4b; Table 1). The CWM of N content was lower on kopjes (mean = 2.62%, SE = 0.05) than on matrix plots (mean = 3.21%, SE = 0.10) and decreased with annual precipitation (Figure 4c; Table 1). Last, the CWM of spine density was lower on kopjes (mean = 1.36 spines 10 cm^{-1}, SE = 0.28) than on matrix plots (mean = 7.33 spines 10 cm^{-1}, SE = 1.23), but did not change with annual precipitation (Figure 4a; Table 1).

Our analyses to test for trait differences among kopje and matrix sites *within* the same species indicated no differences in average values of spine density (kopje effect = −0.332, $p = 0.425$) or LA (kopje effect = 118.4, $p = 0.493$). Leaf N content was, within the same species, slightly lower on kopje trees than on matrix trees (kopje effect = −0.163, $p = 0.027$), although the variance explained by habitat type was low (marginal $R^2 = 0.004$). Similarly, SLA content was, within the same species, slightly higher on kopje trees than on matrix trees (kopje effect = 8.564, $p = 0.008$), although not much variance was explained by habitat type (marginal $R^2 = 0.021$).

On average, kopjes and matrix plots strongly differed in their community composition, as reflected by the average Jaccard distance of 0.904 between paired kopje and matrix plots, an average Bray-Curtis distance of 0.837 and an average Raup-Crick distance of 0.630. Irrespective of the distance metric used, compositional dissimilarity among paired kopje and matrix plots did not respond to the precipitation gradient (all $p > 0.05$; Figure 5).

4 | DISCUSSION

We investigated the interactive effects of habitat type (kopje vs. matrix savannah) and annual precipitation on the diversity and functional composition of tree communities. We found that tree densities and diversity were substantially higher on kopje plots than in matrix vegetation. Furthermore, trees on kopjes had on average larger leaves, higher SLA, lower leaf N content, fewer spines and a higher fraction of evergreen trees. Many of these differences in tree communities between kopjes and matrix plots were smaller in areas with high annual precipitation.

Key abiotic differences between kopjes and matrix savannah that are relevant for tree communities include the availability of soil water and wildfire frequency. Most of the precipitation that falls on rock surfaces runs off towards the limited spaces within kopjes with a soil layer, such as in cracks. As a result, in specific spaces, relatively high amounts of water are available (Poelchau & Mistry, 2006), which creates better growing conditions for trees in an environment where water is a key limiting resource. Furthermore, as boulders can act as firewalls, kopjes are expected to burn less frequently than vegetation in the savannah matrix (Poelchau & Mistry, 2006). It is therefore likely that increased water availability, as well as reduced fire frequency (two factors

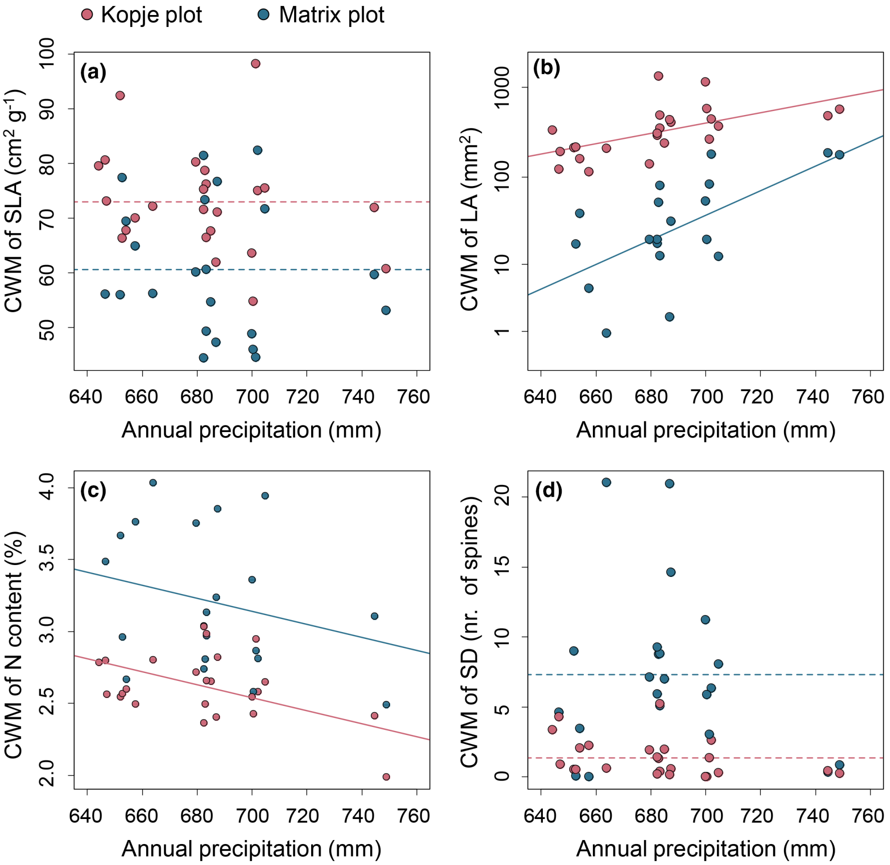

FIGURE 4 Responses of the CWM of specific leaf area (SLA) (a), individual leaf area (LA) (b), leaf nitrogen (N) content (c) and spine density (SD) (d) to habitat type and annual precipitation. Note that LA is shown on a log-transformed *y* axis. Continuous lines indicate significant precipitation effects, while dashed lines represent mean values for SLA (a) and SD (d) on kopjes and matrix plots with non-significant precipitation effects.

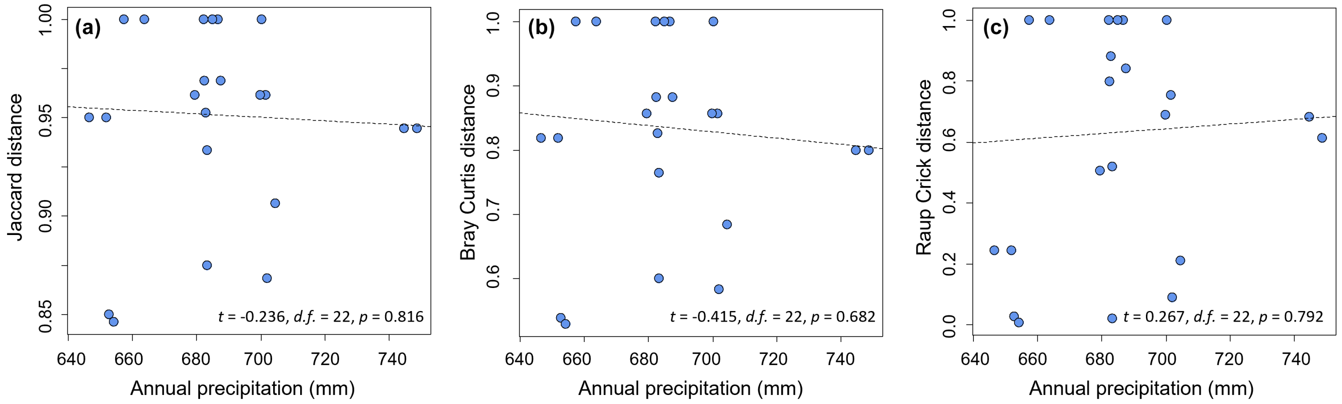

FIGURE 5 Relationships between different measures of compositional dissimilarity between paired kopje and matrix plots (a: Jaccard distance, b: Bray-Curtis distance, c: Raup-Crick distance) and annual precipitation were non-significant.

normally limiting tree densities and diversity in savannahs; Davies et al., 2023; Eshete et al., 2011; Rugemalila et al., 2016), contribute to the comparatively high tree densities and tree diversity. The elevated levels of species richness on kopje sites are likely not just resulting from sampling effects, as analyses on rarefied richness (based on an abundance level of 10) showed qualitatively similar results. Some care has to be taken with the interpretation of our rarefaction analysis, however, as the low abundances on some matrix plots (eleven plots had an abundance level below 10) meant that some rarefied richness values were actually based on extrapolation and hence may be less accurate. It is also important to emphasise that some of the species that we did not observe in the savannah matrix, such as *Grewia bicolor*, actually do occur, albeit with low abundances, in savannahs. With 24 sampled sites, it was inevitable that some species occurring in savannahs were not present in our matrix plots. Another limitation of our study is that we could not study the effects of fire frequency directly. While some maps on fire occurrences in the Serengeti exist (Dempewolf et al., 2007), these are at a too coarse resolution (250 m) to be useful in our study. While we are not aware of other studies assessing tree communities on African kopjes, our results are in line with some studies on other continents that also observed increased tree biodiversity on rocky outcrops (Abreu et al., 2012). In contrast, other studies conducted in areas where matrix vegetation consisted of woodlands did not find elevated tree biodiversity or abundance on outcrops (Chozas et al., 2021).

Trees on kopjes on average had bigger leaves, a higher SLA and a lower spine density and leaf N concentration. This was mostly due to differences in species composition between kopje and matrix plots rather than trait plasticity, as within-species trait differences between habitat types were minor. In addition, kopjes had a lower percentage of deciduous trees. Deciduous trees conserve water in the dry season, which may be particularly beneficial in the matrix vegetation, which lacks places where high amounts of water are concentrated. Furthermore, fires especially suppress the recruitment of large, broad-leaved (often evergreen) tree species (Sharam et al., 2006), which may explain the comparatively low dominance of evergreen tree species with large leaves in the matrix vegetation. We also found that mean spine density and leaf nitrogen concentrations were higher in the matrix vegetation, largely because of the high abundances of spiny, nitrogen-fixing Mimosaceae species (e.g. *Senegalia* and *Vachellia* species). It is well known that various large predator species, including lions and leopards, are positively associated with kopjes (Durant et al., 2010; Hopcraft et al., 2005). Due to a 'landscape of fear' effect (Atkins et al., 2019; Chamaillé-Jammes et al., 2019; Laundré et al., 2001), many herbivores may avoid the use of kopjes or areas with a high woody cover and be more abundant in the more open matrix vegetation, where it therefore pays for trees to construct spines to avoid browsing (Ford et al., 2014). The high dominance of nitrogen-fixing trees in savannahs is often explained as a response to the continuous removal of nitrogen from ecosystems resulting from frequent fires (Vitousek et al., 2013), which also explains the lower need for nitrogen fixation on less flammable kopje vegetation. There may be additional differences between kopje and matrix-associated trees that were not studied here. For example, at least some of the tree species that were associated with kopjes, such as *Ficus glumosa*, have fleshy fruits that are eaten by birds and monkeys (van Wyk & van Wyk, 1997). Some of these animals are associated with kopje habitats (Trager & Mistry, 2003) or other locations with high tree densities and may facilitate the spread and germination of these seeds (Sharam et al., 2009) between different kopjes. Hence, the study of fruit and seed-related traits would likely have yielded additional insights into how dispersal processes have contributed to observed differences in tree communities between kopje and matrix sites.

We also found that tree abundances, diversity and the dominance of species with particular traits, changes along an annual precipitation gradient, even though this precipitation gradient is relatively moderate (ranging from ~650 to 750 mm/year). Both tree density and diversity increased with annual precipitation, in line with other studies (Anderson et al., 2015; Eshete et al., 2011; Rugemalila et al., 2016). Rainfall is one of the most limiting factors for plant growth in savannahs (Kraaij & Ward, 2006), and in wetter areas, trees better persist in competition with grasses (Holdo & Nippert, 2023). Additionally, the driest sites in SNP are characterised by a shallow, impermeable hardpan (Sinclair, 1979) that roots cannot penetrate, explaining the near-absence of trees in the driest matrix sites we studied. There, tree communities were dominated by species with deciduous, small, leaves with a high N content. Deciduous leaves are particularly adaptive in areas with low precipitation, in which the shedding of leaves can be an effective way to reduce transpiration and conserve water. The positive relationship between precipitation and leaf size that we found mirrors global relationships and can be explained by the increased transpiration rates of large leaves (Wright et al., 2017). A possible explanation for increased leaf N content with higher precipitation (also observed by, e.g. Olff et al., 2002) is that in more productive environments, plant-available nitrogen gets diluted over a higher amount of plant biomass. In line with our hypothesis, we also found that differences in some properties of tree communities among kopjes and matrix sites decreased with increasing precipitation. For example, differences between kopjes and matrix sites in species abundance, species richness and the community-weighted means of some of the traits we studied declined with increasing precipitation. As discussed above, a key difference between kopjes and matrix sites is that in the former habitat type, water tends to concentrate at specific places (in cracks between rocks), causing sites with locally high availability. This may be especially impactful for tree communities in those areas of the landscape where precipitation is normally most limited, making kopjes a particularly important habitat for trees in the driest savannah sites. However, contrary to expectations, dissimilarity in species compositions between kopje and matrix sites did not change with precipitation. Dissimilarity values were in general very high and close to theoretical maxima, limiting variation in dissimilarity values, which could have explained this lack of a pattern along the precipitation gradient.

With their high abundances and high diversity of tree species and the uniqueness of these species in terms of functional traits, kopjes form some kind of 'islands' within grass-dominated habitats. This has important consequences for both local and larger-scale ecosystem functioning. The comparatively high cover of trees on kopjes provides habitat for various other organisms. For example, it may in part explain the high abundances of frugivorous and nectivorous bird species found on kopjes (Trager & Mistry, 2003). Furthermore, by providing shade, kopjes may form attractive resting sites for predators such as lions (Durant et al., 2010; Hopcraft et al., 2005). While tree abundances are high on kopjes, the relatively low cover of nitrogen-fixing trees may make the trees less attractive for most browser species than the trees that dominate in the matrix vegetation. This may deter especially small and intermediately sized ungulate species (Hopcraft et al., 2010). Furthermore, it is possible that, with their high amounts of green, non-grassy biomass, kopjes also form key habitat for invertebrate herbivores and their predators, although further research is needed to test this. The high amount of relatively N-poor green biomass, combined with the low fire frequency, also has the consequence that more leaf litter biomass accumulates on the ground (personal observation), which may be slow to decompose due to the low nitrogen concentration (Cornwell et al., 2008). This litter layer may, however, also provide key habitat for various soil and ground-dwelling organisms.

In summary, we have shown that in the Serengeti, kopjes are key habitat features that support high numbers and a high diversity of functionally unique tree species within a mostly grassy matrix. This is particularly true in the driest sites of savannahs, where tree densities are very low and kopjes form some of the rare habitat features that still support the growth of trees. These tree communities provide key habitats for other organisms. With their likely important impact on various ecosystem processes, kopjes thereby form a unique habitat feature that, despite its relatively low cover, substantially adds to the wider scale heterogeneity and biodiversity in African savannahs.

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CONFLICT OF INTEREST STATEMENT

The authors do not have any conflict of interest to share.

DATA AVAILABILITY STATEMENT

All data and R scripts will be uploaded on a public repository (e.g. Dryad or Figshare) after acceptance of the manuscript.

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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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