

Pinpointing baobab (*Adansonia digitata* [Linn. 1759]) population hotspots in the semi-arid areas of Tanzania

Upendo L. Msalilwa^{1,2}  | Linus K. Munishi^{1,2}  | Edna E. Makule^{2,3} | Patrick A. Ndakidemi^{1,2}

¹Department of Sustainable Agriculture, Biodiversity, and Ecosystem Management, The Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania

²Centre for Research, Agricultural Advancement, Teaching Excellence and Sustainability (CREATES) in Food and Nutrition Security, The Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania

³Department of Food and Nutritional Sciences, The Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania

Correspondence

Upendo L. Msalilwa, Department of Sustainable Agriculture, Biodiversity, and Ecosystem Management, The Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania.
Email: msalilwau@nm-aist.ac.tz

Funding information

British Ecological Society (BES); Rufford Small Grants Foundation, Grant/Award Number: 24376-1; Centre for Research, Agricultural Advancement, Teaching Excellence and Sustainability in Food and Nutrition Security (CREATES-FNS) at the Nelson Mandela African Institution of Science and Technology (NM-AIST)

Abstract

The impact of unsustainable land-use conversions, changes in climate and anthropogenic activities on abundance and distribution of baobab populations was assessed in semi-arid regions of Tanzania. Baobabs were sampled in plots of 1 km long and a 50 m wide, which were carried out in 337 grids located in different land-use types. Transects for each land-use type were located using a stratified random sampling technique to compare baobab population variations and occurrences in semi-arid areas of Tanzania. Baobab density was found to be highest in strictly protected areas and the lowest density in unprotected areas, suggesting that anthropogenic activities coupled with local management practices within land-uses may be influencing its viability in semi-arid areas. In species like this, with less and slow recruitment rate, it takes a long time to bring the population to recovery when substantial disturbance and overutilisation have reduced the populations to certain levels. Thus, increased human and climate change pressures on land are likely to drive the species to extinction in these fragmented populations.

Résumé

L'impact des conversions non durables de l'utilisation des terres, des changements climatiques et des activités anthropiques sur l'abondance et la répartition des populations de baobabs a été évalué dans les régions semi-arides de Tanzanie. Les baobabs ont été échantillonnés dans des parcelles de 1 km de long et de 50 m de large, réalisées dans 337 grilles situées dans différents types d'utilisation du sol. Des transects pour chaque type d'utilisation des terres ont été localisés à l'aide d'une technique d'échantillonnage aléatoire stratifié afin de comparer les variations et les occurrences de la population de baobabs dans les zones semi-arides de Tanzanie. La densité de baobab était la plus élevée dans les zones strictement protégées et la plus faible dans les zones non protégées, ce qui suggère que les activités anthropiques associées aux pratiques de gestion locales dans les utilisations des sols peuvent influencer sa viabilité dans les zones semi-arides. Dans des espèces comme celle-ci, où le taux de recrutement est faible et lent, il faut beaucoup de temps pour rétablir la population lorsque des perturbations importantes et une surutilisation ont réduit les populations à certains niveaux. Ainsi, les pressions croissantes exercées par l'homme sur les terres

et les changements climatiques pourraient entraîner l'extinction de l'espèce dans ces populations fragmentées.

KEYWORDS

Adansonia digitata, density, population, semi-arid region, Tanzania

1 | INTRODUCTION

The baobab (Malvaceae: *Adansonia digitata* [Linn. 1759]) is a species native to the Sudano-Zambesian drier areas that receive a range of 200–800 mm of rain annually, with its lifespan range estimates varying between 1,000 and 2,000 years (Sidibe & Williams, 2002; Wickens, 1982). It is a large, deciduous tree that can reach 25 m high, and its germination rate is generally low due to physical dormancy of the seeds (Baskin & Baskin, 2001; Muthane & Gyanchand, 1980). Typically, *A. digitata* is distributed in the savannahs of Africa where it functions as a keystone species making an important contribution to ecosystem functioning and people's livelihoods for food, fibre and medicine (Lisao, Geldenhuys, & Chirwa, 2018; Sanchez, Osborne, & Haq, 2010; Schumann, Wittig, Thiombiano, Becker, & Hahn, 2012; Venter & Witkowski, 2010). The tree is harvested by humans for food, fodder and medicinal purposes. Elephants (*Loxodonta africana*) also tend to eat its fruits and commonly strip the bark, potentially acting as agent of dispersal while at the same time increasing the vulnerability of baobab trees to diseases and increase mortality rates of trees with smaller stem diameters, respectively (Romero et al., 2001; Wilson, 1998).

While the baobab generates various products that are bartered and sold in urban and informal markets across Africa (Venter & Witkowski, 2010), these food products form an important source of income, especially in the dry season or at times of drought and are increasingly being commercialised and exported around the world, with pressures on its use growing. To manage the species and its associated products sustainably, a thorough understanding of the spatial distribution of the species, along with an understanding of the effects of land-use and environment factors on baobab density in these areas, is required.

Land degradation is a major threat to sustainable management of biodiversity, and unsustainable land conversions and changes in climate and human populations have been predicted to increase pressure on baobab populations in their range areas (Schumann, Wittig, Thiombiano, Becker, & Hahn, 2010; Van den Bilcke, Smedt, Simbo, & Samson, 2013). Furthermore, international interest in nontimber forest products (NTFP) has resulted in an increase on the utilisation pressures in the species, which can potentially affect its abundance and distribution in the areas where it occurs. Despite the importance of the baobab to local communities in the semi-arid regions of Tanzania, data on the distribution of the species are limited and no known study quantifying the distribution hotspots of baobabs in Tanzania. Also, the factors influencing on

baobab populations in its range areas are not well understood. The main objective of this study was to compare baobab population variations and occurrences in three different land-use types across semi-arid areas of Tanzania. The specific objectives of the study were (a) to determine the current distribution, occurrence and variation of baobab densities in different land-uses in the semi-arid areas of Tanzania and (b) to assess how variations among land-use systems and across the precipitation, temperature and altitudinal gradient affect the abundance and distribution of baobabs in the semi-arid areas of Tanzania.

2 | METHODS

2.1 | Study area description

The study area was the semi-arid zone in Tanzania (Latitude: 2°39'5.225"S, Longitude: 34°8'29.364"E and Latitude: 8°2'53.048"S, Longitude: 35°3'18.731"E) and comprised of strictly protected areas (National Parks and Forest Reserves), nonstrictly protected areas (Game Controlled Areas, Game Reserves, Open Areas and Wildlife Management Areas) and unprotected areas (croplands, pastures and settlements; Figure 1). Dudley (2008) defined strictly protected areas as the area set aside to protect biodiversity and also possibly geological/geomorphological features, where human visitation, use and impacts are strictly controlled and limited to ensure protection of the conservation values. In this study, the strictly protected areas are the conservation areas that do not allow for resource extraction that may lead to biodiversity loss including baobab harvest. Nonstrictly protected areas here referred to those areas (e.g. Game Open Areas) that allow resource extraction with potential degradation of biodiversity. Unprotected areas (e.g. village lands and settlements) are the areas where unregulated resource extraction is practiced, and human visitation, use and impacts are not limited such as farms, residential areas and grazing areas. The semi-arid regions of Tanzania cover about 22% of the Tanzanian total land area (World Bank, 1994), which is used by almost 30% (population density of approximately 62 people per square kilometre) of the human population. Semi-arid areas cover about 22% of the Tanzanian total land area (World Bank, 1994), which is used by about 30% (population density of approximately 62 people per square kilometre) of the human population. The semi-arid areas were delineated by ODA/NRI in relation to Tanzania's administrative regions (LRDC, 1987; NRI, 1991, 1996). This classification has been used widely by the World Bank amongst others (World Bank, 1994).

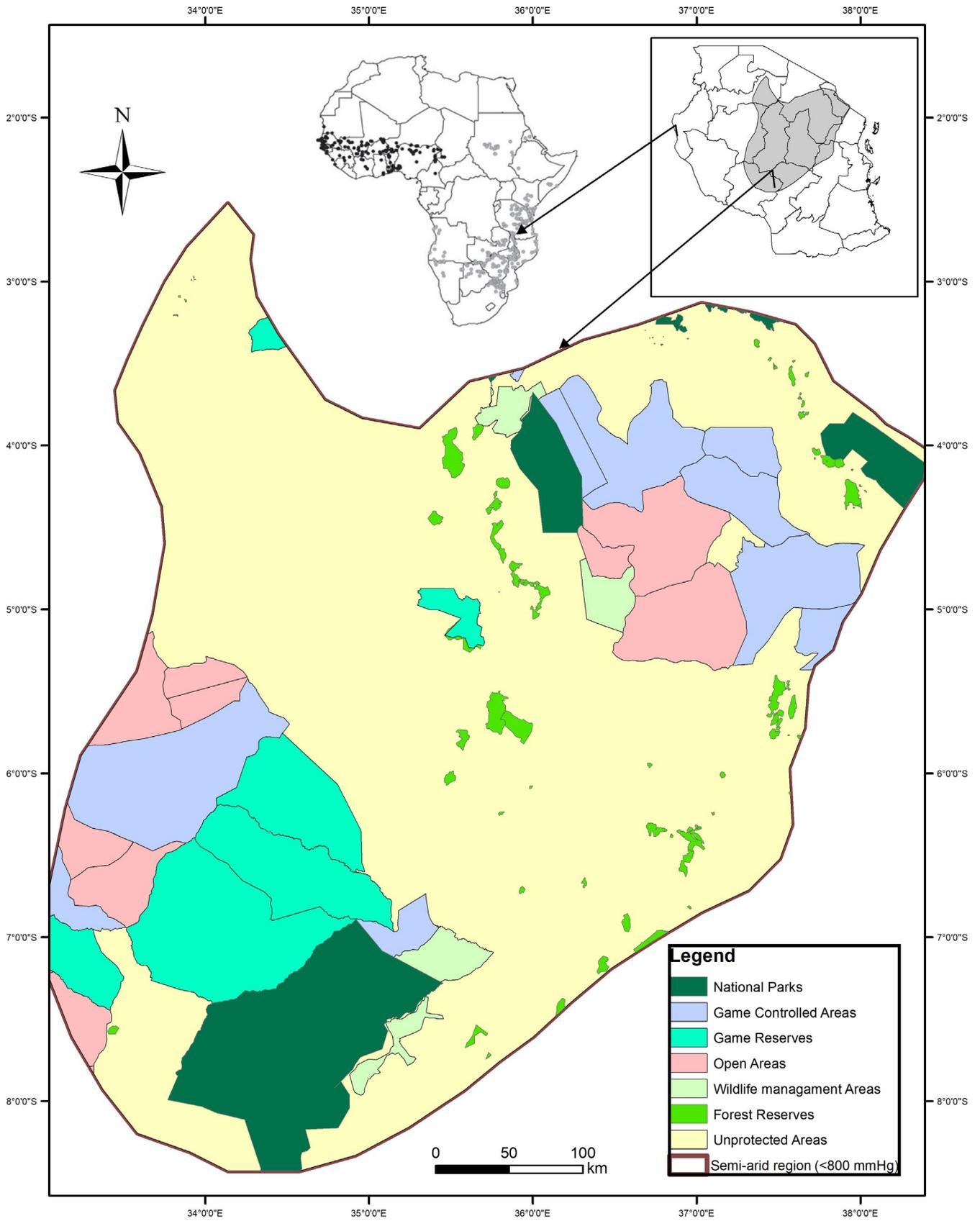


FIGURE 1 Map showing all land-use types within the study area in Tanzania

2.2 | Data collection

2.2.1 | Prefield work

Before the main field data collection, a reconnaissance survey was carried out in the study area. The main aim was to get the actual information about the terrain characteristics, land-use systems and baobab distribution as well as to reconcile the reality with the information obtained from topographic map. After the reconnaissance survey, the information generated was used to design and establish sampling points and sample size as described in the section below. The focus of this study was on baobab distribution in certain land-use types other than government's gazetted towns, urbans, formal settlements and cities. Therefore, land-use was restricted to forms of human management of vegetation that turns out to affect baobab species. land-use in this study therefore referred to (a) strictly protected areas; (b) nonstrictly protected areas and (c) unprotected areas.

Using the map for the study area, the coordinates of all sampled points were plotted on maps and imputed in a Global Positioning System (GPS). The nearest land-use to a sample point was firstly located by using the combination of digitized land-use map of the study area, sampled points map and the topographic map. At each land-use type, the sampled point was navigated, following the GPS reading until the GPS direction became perpendicular to the direction that could be used to reach the desired point. The size of each grid was calculated during reconnaissance survey to ensure proportionate distribution of the sample points, which is a requirement of stratified random sampling (de Grijter, Brus, Bierkens, & Knotters, 2006).

2.2.2 | Sampling strategy

Using a topographic map of the study area in combination with some level of knowledge of the site about the baobab distribution in different major land-use types, the study area was marked into grids of 20 km × 20 km. A stratified systematic random sampling design was used whereby grids were selected randomly from maps for each of the three land-use types. Each grid was 20 km × 20 km, and a plot size of 1 km long and 50 m wide (i.e. 5 ha) was established in the northwestern corner of the grids using one strip transect. For a given sampling error, stratification ensures reduced number of sampling units and improved precision (Kent & Cooker, 1992). Based on the background hypothesis for this study, it was assumed that each grid is uniform in terms of baobab density and each land-use type was uniform. The climate map was constructed from more than 30 years of rainfall and temperature data to reflect the distinctive patterns/gradients of this across the study area.

A total of 337 grids were surveyed for this study, with the number of surveyed plots in each land-use type being determined by their relative sizes. Using the grid count located within the study area, the respective areas surveyed in strict protected area, non-strict protected area and unprotected area were 23,200 km²,

46,400 km² and 65,200 km², respectively. Strictly protected area had 21 plots; nonstrictly protected areas 26 plots and unprotected areas had 68 plots that were surveyed during the study period, covering approximately 40% of the entire semi-arid areas. In each of these plots, information on the number of baobab stems and land-uses was recorded. All baobab plants in each transect were counted. The GPS coordinates obtained during field survey were used to locate the actual plots where the main baobab survey carried out. The 337 points were confirmed to lie within semi-arid areas after being overlaid on the climatic maps of Tanzania that were reconstructed from long-term rainfall and temperature data spanning 30 years (TMA, 2014).

2.3 | Data analysis

We compared baobab population variations and occurrences in three different land-use types (which were generated from the recent map of Tanzania and validated in the field) across semi-arid regions of Tanzania. Using the coordinates and the baobab counts in each of the sampled plots, the distribution (i.e. occurrence of baobab in the study area), abundance (variation in extent of occurrence of baobabs classified into high, medium and low) and density (number of baobabs per unit area) in the major land-use types were constructed. The distribution, abundance (high, medium and low) and density of baobabs were compared between the three land-use types in the study area. These aspects were also compared between different gradients of rainfall and altitude in the study area. Mapping (Figures 2, 4 and 5) and descriptive statistics of each aspect were firstly done to compare the hotspots, distribution and mean densities, within and between land-use types and the rainfall and altitudinal gradients. Baobab numbers were converted into densities (baobab stems/ha) as follows:

Baobab stem density = Number of individual trees/Area of the plot

A one-way analysis of variance (ANOVA) followed by Fisher's Least Significant Difference (LSD, $p < .05$) test was used to compare baobab densities between the three land-use types. A general linear model (GLM), in SPSS version 17.0 (IBM Corp), was used to determine the effects of environmental variables on baobab density whereby land-use type was used as fixed/random factor with rainfall, temperature and elevation as covariates. Relationships between environmental variables (rainfall, temperature and elevation) and baobab density were analysed using Pearson's correlation analysis.

3 | RESULTS

3.1 | Baobab abundance and distribution in Tanzania

The survey findings recorded distinct and wide spatial variations of baobabs across different land-use types (Figure 2). The most evident from the results were the varied distribution and hotspots of baobab across the study area and in land-use categories. Most of the baobab populations concentrated in the central regions (Dodoma and Singida) running from the southern central parts to the northern

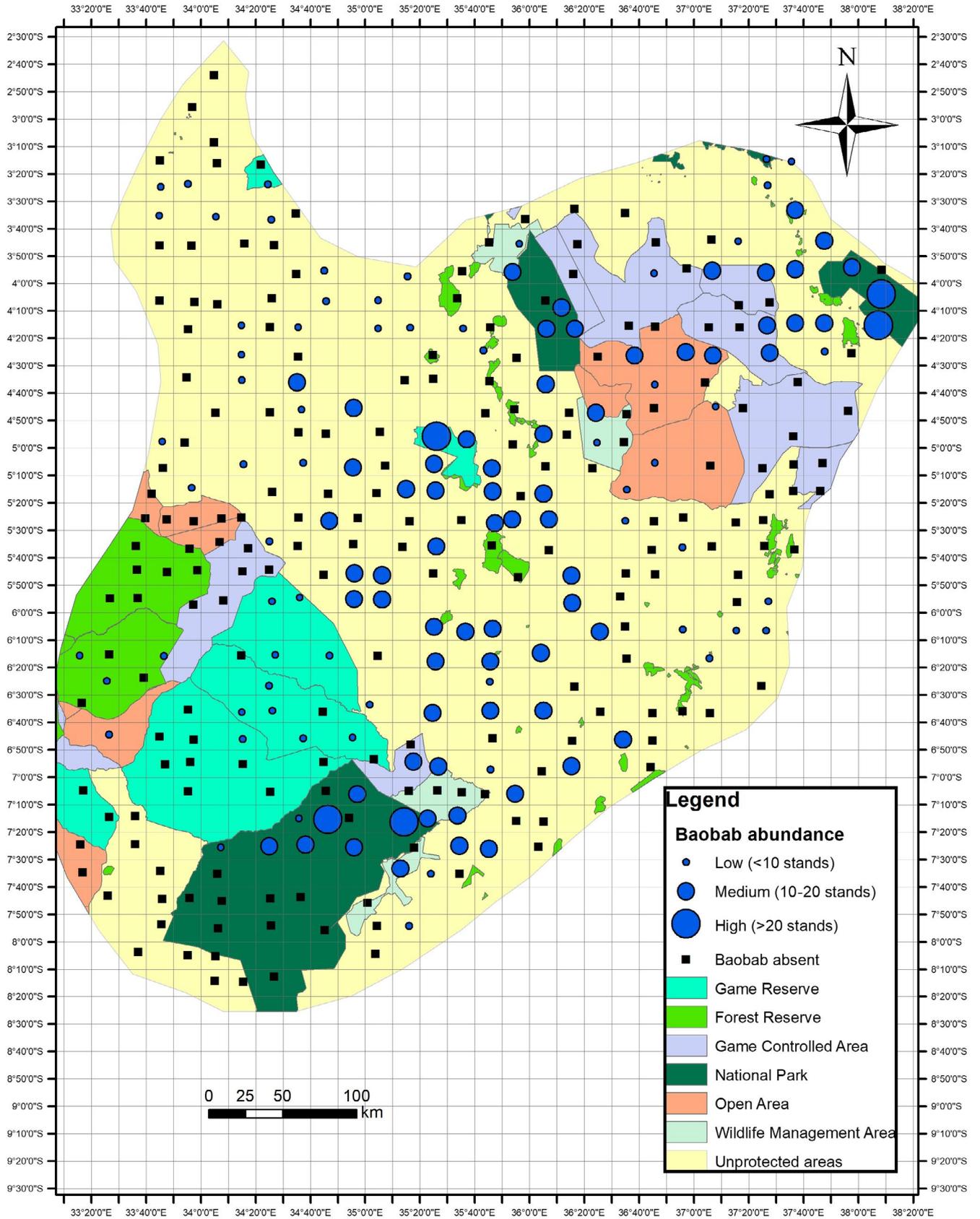


FIGURE 2 Map showing abundance of baobabs in the surveyed grids in the semi-arid region

central parts (Figure 2). The result also indicated that baobab population and distribution are increasingly being isolated and fragmented mainly within strictly protected areas of varying size, habitat and environmental diversity. Furthermore, it was detected that strictly protected areas are areas of baobab hotspots. In addition, it was noted that the hotspots reflected a gradient of elevation, rainfall and land-use types.

3.2 | Variations of baobab density among land-use types

A total of 115 grids (34.12%) of the 337 surveyed grids had baobabs in the surveyed area, and the mean density was 1.86 ± 1.10 stems per ha across all land-use types in the study area. However, baobab density varied substantially and significantly ($F_{2,115} = 5.436$, $p = .006$) across land-use types after controlling for rainfall, temperature and elevation. Baobab densities did not vary significantly within land-use types in the semi-arid areas. There was no significant ($F_{1,21} = 0.117$, $p = .736$) difference in baobab density within strictly protected areas. There was no significant ($F_{1,26} = 1.744$, $p = .187$) difference in baobab density within nonstrictly protected areas.

As summarised in Table 1, the highest baobab density (2.45 ± 1.29 stems per ha) was observed in strictly protected areas. Nonstrictly protected areas had an average density of 1.62 ± 1.04 stems per ha. The lowest density (1.52 ± 1.00 stems per ha) was recorded in unprotected areas (Figure 3). Based on post hoc LSD multiple comparisons, baobab densities varied significantly across land-use types in the semi-arid region. Baobab density was greater for strictly protected areas than in the nonstrictly and unprotected areas, and this density differed significantly between strictly protected areas and unprotected areas ($p = .004$). Furthermore, there was a significant ($p = .003$) difference in baobab density between strictly and nonstrictly protected areas. However, no significant ($p = .687$) difference in baobab density was observed between nonstrictly protected and unprotected areas.

3.3 | Variations of baobabs with environmental factors

Baobab distribution showed different responses to the environmental variables studied. There was a significant ($F_{1,115} = 22.289$, $p < .001$) main effect of rainfall on baobab density across the semi-arid region. There was a significant ($r = -.16$, $p = .04$) negative correlation between baobab density and rainfall suggesting that baobab density declines with increasing rainfall (>800 mm). As shown in Figure 4, regardless of land-use, rainfall ranges of between 500 and 650 mm per annum are key to the distribution of baobabs in the semi-arid regions of Tanzania. Also, there was no significant ($F_{1,115} = 1.515$, $p = .221$) main effect of temperature on baobab density (Figure 4). It was observed that baobab density was highest in areas with the mean temperature between 28 and 30°C (Figure 5). However, there was no significant ($r = -.06$, $p = .24$) correlation between baobab density and temperature.

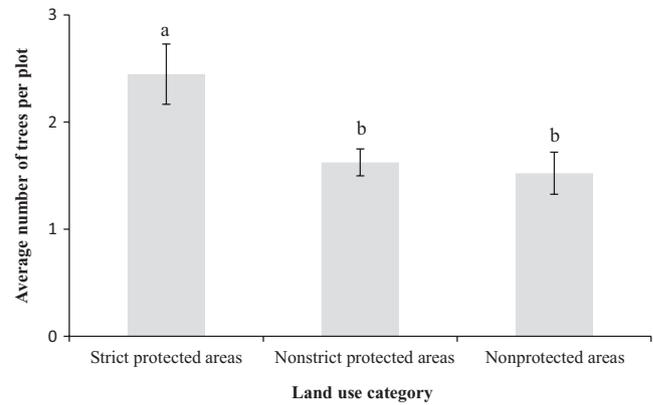


FIGURE 3 Mean density (number of individuals/ha, \pm SE) of *Adansonia digitata* in different land-use types, bars marked with different letters (a and b) are significantly different ($p = .05$)

There was a significant ($F_{1,115} = 8.201$, $p < .005$) main effect of elevation on baobab density across the semi-arid region. Also, there was a significant ($r = -.37$, $p < .001$) negative correlation between baobab density and elevation suggesting that baobab density declines with increasing elevation.

There was a significant interaction between land-use \times rainfall on baobab density ($F_{2,115} = 3.763$, $p < .027$). In addition, there was a significant interaction between land-use and elevation on baobab density ($F_{2,115} = 4.513$, $p = .013$). Furthermore, a significant ($F_{2,115} = 7.845$, $p = .001$) interaction between land-use \times temperature on baobab density was found. There was a significant ($F_{1,115} = 20.759$, $p < .001$) rainfall \times elevation interaction on baobab density was observed. Furthermore, there was a significant ($F_{1,115} = 26.277$, $p < .001$) rainfall \times temperature interaction on baobab density was observed. Also, a significant ($F_{1,115} = 4.616$, $p = .034$) elevation \times temperature interaction on baobab density was observed. However, no significant ($F_{1,115} = 1.455$, $p = .231$) rainfall \times temperature \times elevation interaction on baobab density was observed. There was a significant interaction between land-use \times rainfall \times temperature \times elevation on baobab density ($F_{2,115} = 3.680$, $p = .029$).

4 | DISCUSSIONS

4.1 | Variations of baobab density with land-use

Our results indicate that baobab density and distribution are sensitive to both land-use types and environmental factors. Land-use intensification has been predicted to increase pressure on baobab populations in the future (Schumann et al., 2010, 2012; Wilson, 1998). Land-use is known to impact on baobab population structure (Schumann et al., 2012; Venter & Witkowski, 2010). A study by Schumann et al. (2010) that compared stands in a protected area with those of surrounding communal area revealed that the land-use type has an impact on the population structure of the baobab. We found an uninformative distribution of baobabs in the semi-arid regions of Tanzania. However, baobab density varied substantially and significantly across land-use types.

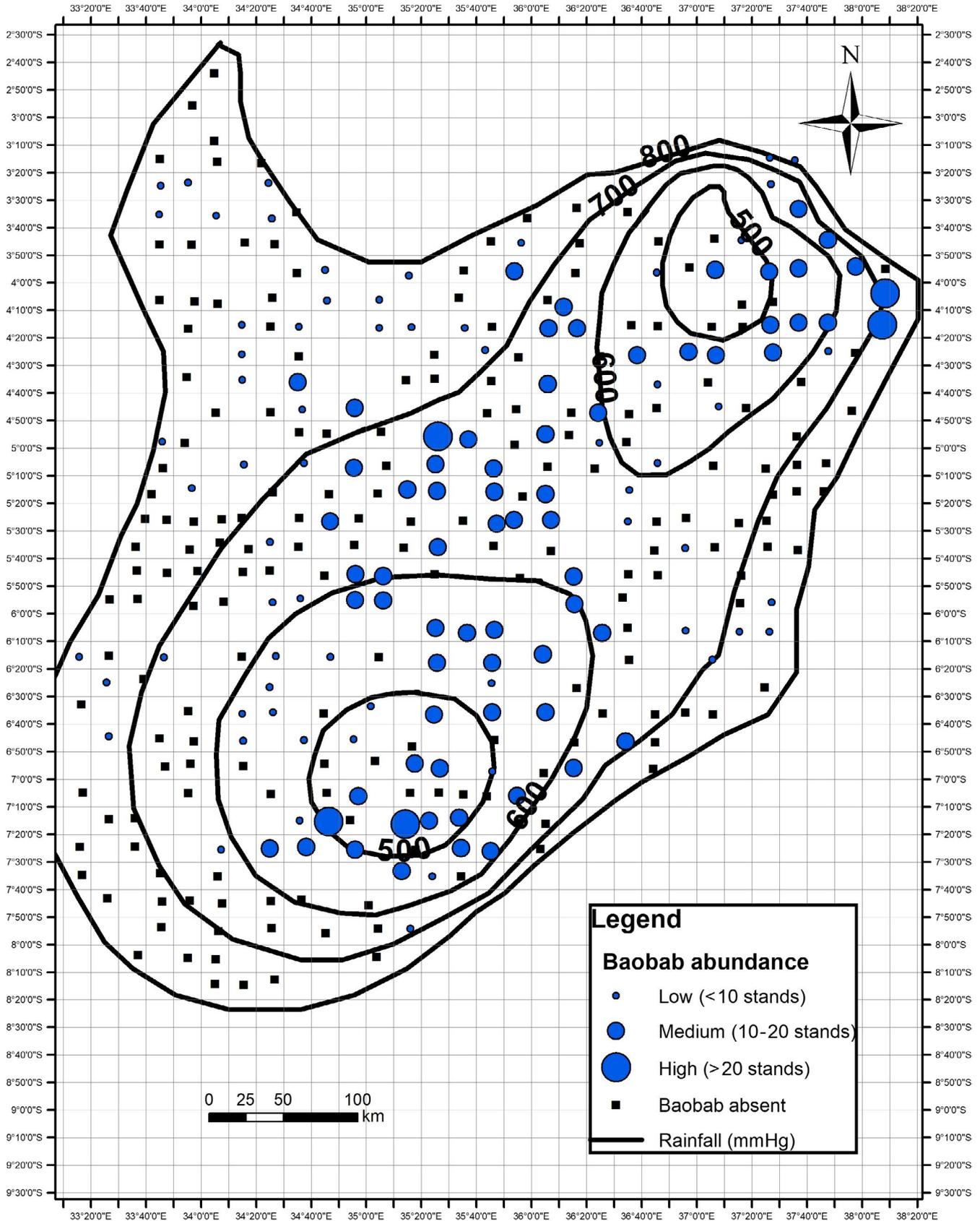


FIGURE 4 Map showing effects of rainfall on baobabs distribution in the surveyed grids in the semi-arid region

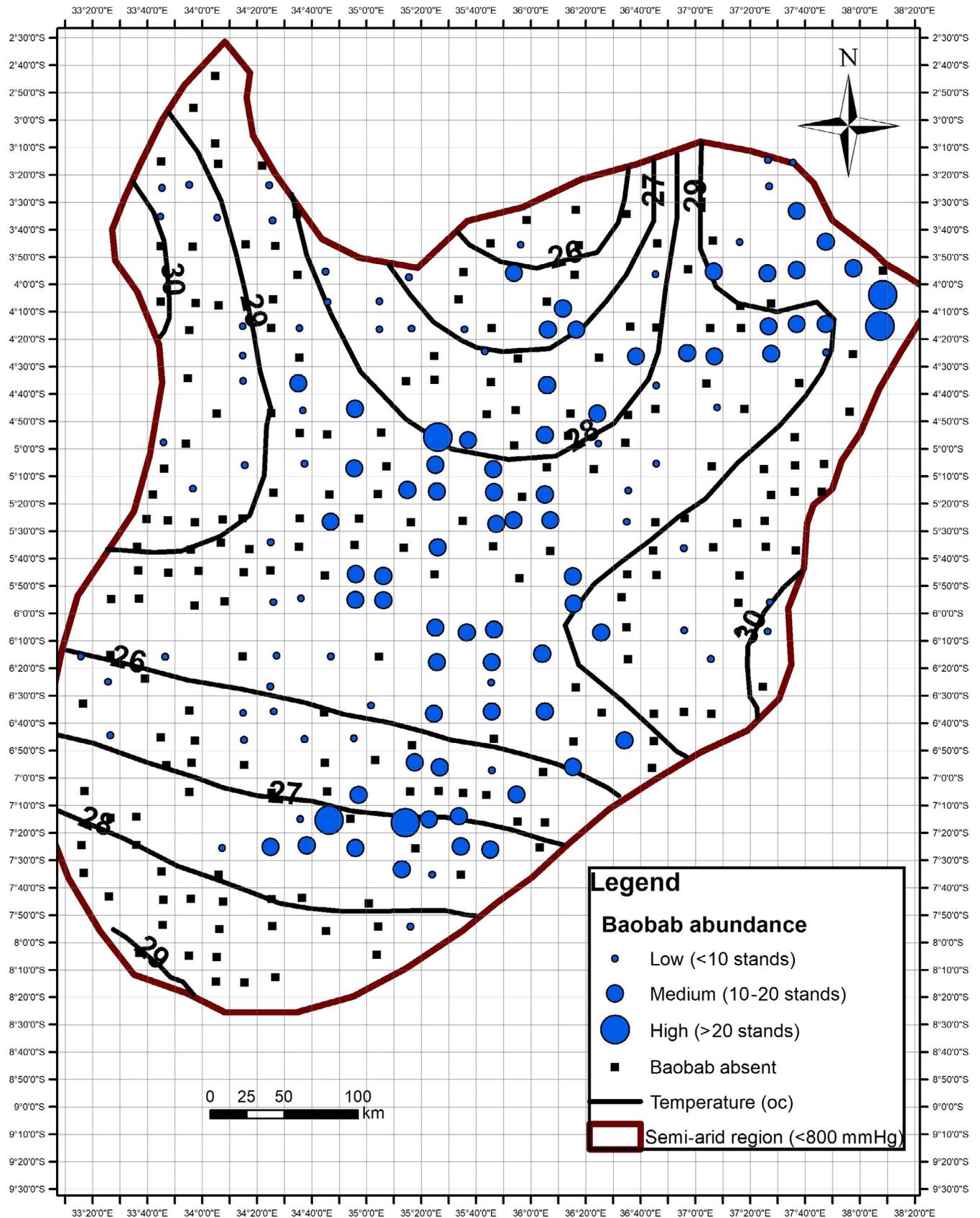


FIGURE 5 Map showing effects of temperature on distribution of baobabs in the surveyed grids in the semi-arid regions

TABLE 1 Baobab density in different land-use types in the semi-arid regions of Tanzania

land-use type	Sample size (N)	Average abundance	Average stems per ha	SE
Strictly protected areas	21	12.24	2.45	0.28
Nonstrictly protected areas	26	8.12	1.62	0.20
Unprotected areas	68	7.16	1.52	0.13

Most of the baobab populations concentrated in the central regions (Dodoma and Singida), which fall into unprotected areas running from the southern central parts (Iringa) to the northern central parts (Manyara and Kilimanjaro), which fall into protected areas. Dodoma and Singida areas had more baobab populations probably due to a combination of environmental factors that favour the growth of the baobab species and the protection due to economic and social importance of the baobab products to the local communities living in those areas (Aluko, Kinyuru, Chove, Kahenya, & Owino, 2016; Sidibe & Williams, 2002).

The overall mean density for the three sampled land-use types was variable and ranged 1.52–2.45 baobab stems per ha. This is within the range of recorded baobab densities in other African countries (Ndoro, Mashapa, Kativu, & Gandiwa, 2014; Venter & Witkowski, 2010). The observed lowest baobab density in unprotected areas likely due to land-use changes resulting from increased human populations. Increased domestic animal numbers may also be responsible for low density in unprotected areas. Low densities of baobab in unprotected areas could be attributed to livestock browsing and trampling, clearing new fields, digging up seedlings to eat taproots, fire, and overharvesting of fruit and leaves. Other studies (e.g. Assogbadjo, Kakaï, Edon, Kyndt, & Sinsin, 2011; Chirwa, Chithila, Kayambazinthu, & Dohse, 2006; Dhillion & Gustad, 2004) have found that low baobab densities in human-dominated areas were attributed to livestock browsing and trampling, clearing new fields, fire, and overharvesting of fruit and leaves.

The population of baobab trees in unprotected areas was widely spread with more exposure to disturbances caused by human activity. High human densities, infrequent domestic use of baobab fruit and lack of seedling protection may have a negative effect on density in unprotected areas. The people in central regions appear to have a stronger 'baobab culture' than the people in other regions, which may be the reason for the high baobab populations in the central regions. Duvall (2007) reports that the Manika-speaking people of West Africa effectively disperse baobab seed by collecting and using large quantities of fruit, the seeds of which are discarded around villages, where they germinate. There is also a culture of actively protecting seedlings from livestock, thus increasing the recruitment success of baobabs near human habitation (Assogbadjo et al., 2011; Dhillion & Gustad, 2004; Duvall, 2007). The protection is due to the benefits that the local communities derived from the mature trees (Lisao et al., 2018).

It may be possible that in some parts within protected areas, lack of baobab recruitment was caused by elephants browsing.

Previous studies (Barnes, Barnes, & Kapela, 1994; Swanepoel, 1993; Wilson, 1998) have documented the distribution and population structure of *A. digitata*, which was determined by the elephant population densities. In their study, Barnes et al. (1994) revealed that baobab tree densities dropped between 1976 and 1982 due to elephant browsing in Ruaha National Park, Tanzania, while the same was reported in Lake Manyara in 1969 and 1981 (Douglas-Hamilton, 1973; Owen-Smith, 1988). Abundant livestock in unprotected areas may account for the low baobab density in comparison with other land-use types, whereas elephants are highly associated with baobab populations and believed to negatively affect baobab populations (Edkins, Kruger, Harris, & Midgley, 2008). They have been observed to reduce baobab densities by destroying young baobab trees by trampling or feeding on them (Barnes, 1980; Edkins et al., 2008; Ndoro et al., 2014). According to the Southampton Centre for Underutilized Crops, ICUC (2006), baobabs need to be protected against animals, especially during the juvenile stage. The semi-arid areas of Africa are facing intractable challenges related to practical pathways to social and environmental sustainability in rangelands. The rangelands make up ~90% of habitat for the species, and the rangeland area is currently undergoing enormous change including shifts from large communal to partitioned private tenure, coupled with the effects of climate change (Venter & Witkowski, 2010).

4.2 | The effect of environmental factors on baobab distribution

Our results suggest that out of the climatic variables investigated, rainfall is the main factor determining baobab distribution in Tanzania. Temperature also influences the distribution of a number of several species, although it explains much less of the variation. Insight into how individual species' distribution and abundance are influenced by environmental factors is critical (Condit, Engelbrecht, Pino, Perez, & Turner, 2013). At a large scale, rainfall has been shown to influence species distribution (Amisshah, Mohren, Bongers, Hawthorne, & Poorter, 2014; Engelbrecht et al., 2007; Toledo et al., 2012), whereas at smaller scales, soil fertility, topography and irradiance can affect species distribution (John et al., 2007; Mashapa, Zisadza-Gandiwa, Gandiwa, & Kativu, 2013). Most tropical forests show seasonal variation in rainfall, and species drought performance and physiological drought tolerance have therefore been found to determine the distribution of tropical species (Baltzer, Davies, Bunyavejchewin, & Noor, 2008; Engelbrecht et al., 2007).

We analysed the distribution of baobabs in relation to environmental variables and determined the relative importance of rainfall and temperature to their distribution. Baobab distributions were more strongly influenced by rainfall than by temperature. Other studies also found that rainfall is the main driver of large-scale distribution patterns of tropical plant and tree species (Amissah et al., 2014; Bongers, Poorter, Rompaey, & Parren, 1999; Maharjan et al., 2011; Toledo et al., 2012). Temperature may have an indirect effect on plant growth. Short-term leaf-level measurements in a number of tropical forest regions showed that net carbon assimilation declines with an increase in daytime temperatures (Doughty & Goulden, 2008). In many countries where seasonal variability in temperature is large compared with daily variation, an increase in temperature may affect the distribution of a limited number of species (Vasseur et al., 2014). However, in areas with larger temperature variation, increases in temperature are likely to shift the distribution of plant species (Amissah et al., 2014; Toledo et al., 2012).

Baobabs are dominant and originate in the dry tropical ecosystems. Sidibe and Williams (2002) argued that the extent of the distribution of the baobabs is probably determined by its relatively wide-ranging ecological tolerance. It usually grows at low altitudes (450–700 m), at mean annual rainfall of 150–1,500 mm (Wickens, 1982). *Adansonia digitata* occurs on well-drained soils, from clay to sand, and is often spared when land is cleared for cultivation (Wickens & Lowe, 2008). It has been demonstrated that vegetation structure and composition vary continuously along environmental gradients (Gauch & Whittaker, 1972; Oksanen & Minchin, 2002) especially when the gradient is long such as the rainfall gradient in Tanzania. The observed significant differences in baobabs stand density across the semi-arid regions of Tanzania were also related to environmental factors. The highest baobabs stem densities were observed in areas with a relatively medium (500–800 mm) annual rainfall. High annual rainfall may, therefore, not necessarily be the primary factor in determining high baobabs densities. Wetter areas have relatively high baobab densities in comparison with dry areas (Edkins et al., 2008; Mashapa et al., 2013; Mpofo, Gandiwa, Zisadza-Gandiwa, & Zinhiva, 2012). We found a significant main effect of rainfall on baobab density across the semi-arid region. It appears that baobab density declines with increasing rainfall above 800 mm. Regardless of land-use, rainfall ranges of between 500 and 650 mm per annum are key to the distribution of baobabs in the semi-arid regions of Tanzania.

Studies that have evaluated the response of tropical plant species to individual environmental gradients have focused on soil nutrients, rainfall and water availability, but far less attention has been paid to the role of temperature (Amissah et al., 2014). Seasonal variation in temperature is rather minor across most tropical forests, but recent studies suggest that small changes in temperature are likely to affect plants species distribution patterns (Amissah et al., 2014; Wright, 2010), although there are still few data to support this point. Determination of individual species response curves to a range of climatic variables is imperative to identify the climatic variables that are biologically most relevant to individual plant

species, as they can help to predict the possible consequences of climate change for tropical forests (Amissah et al., 2014; Borchert, 1998). Although we did not find a significant main effect of temperature on baobab density, we learned that baobab density was highest in areas with the mean temperature between 28 and 30°C. Temperature seasonality is important for plants species growth and hence for their distribution, because most annual net primary production of plants in seasonal forests is concentrated in the months with high rainfall and growth is likely to be most sensitive to temperature variability during this time of the year (Amissah et al., 2014; Vlam, Baker, Bunyavejchewin, & Zuidema, 2014). We also observed a significant main effect of elevation on baobab density suggesting that baobab density declines with increasing elevation (>1,000 m asl).

4.3 | Structural and climatic differences among land-use categories

Largely dry, the semi-arid extends well into highland zones to North and South and displays various elevation gradients due to prevalence of volcanic and other activities below the Earth's surface (Millennium Ecosystem Assessment, 2005). Local landscapes at various scales are distinguished by substantial geological heterogeneity, dissected landforms and resultant steep gradients of precipitation and vegetation, as reflected by results of baobab abundance and distribution. The consequent pronounced fragmentation of habitats and sharp juxtaposition of distinct landscape and use types, combined with climatic oscillations in geological time, may have contributed to major variations observed in this study. The study further indicates that baobab population and distribution are increasingly being isolated and fragmented mainly within strictly protected areas of varying size, habitat and environmental diversity. Thus, the ability to sustain the species in the absence of active management is increasingly becoming constrained. The field survey in the study area recorded that wide spatial variations of baobab densities were distinct across land-use and environmental gradient. The most evident from the results are the varied densities and distribution and hotspots of baobab across the study area and in particular land-use categories.

In many of the semi-arid areas, a high density of baobab co-existed with extensive overlap in the land-use/rainfall/extensive long-term elephant migratory routes, effectively clustered in strictly protected areas, known to harbour many elephants and located in and at extreme end of climate-elevation continuum (Wato et al., 2018). The proportion of different intensities of occurrence/hotspot of baobab population indicated environmental/ land-use distinctions across semi-arid region. They have been described as being dissimilar largely because of their use, structural and boundary elevation. For example, residence and annual movements of the elephants delineate the semi-arid ecosystem, of which most of the time elephants are confined in the strictly protected areas and other nonstrictly protected areas with sporadic movements between locations (Wato et al., 2018). Consequently, elephants are able to act as

dispersers more in the strictly protected areas where availability and access of baobab by elephants can be made. Elephants, for example, regularly migrate across the National Park boundaries to habitats that are not protected.

The geographic distributions of baobab are documented but less understood. On local scale, this is the first and most comprehensive and rigorously quantitative study that measured its distribution and abundance in semi-arid regions of Tanzania in relation to land-use types. Application of GIS technology to these data identified key hotspots that segregated this population to various locations across environmental and land-use types. The hotspots reflected a gradient of elevation, rainfall and land-use types. Occupying in strictly protected areas, the management policies are designed such that they stabilize the densities in such land-use types whereas disappearance and low densities may be traced to the activities of humans. Although some other background factors such as edaphic factors, dissected topography and dispersal agents (elephants) may be independent of human beings. Many protected areas are intensively managed; thus, claims of high plant and animal biomasses not unique. Elephant populations that have been censused regularly in these areas have in fact indicated high numbers compared with other land-use types, providing room for dispersal of baobab seeds within and around such areas lease (Barnes et al., 1994; Owen-Smith, 1988; Swanepoel, 1993). The distribution of baobabs varies with geomorphology and climate in the semi-arid regions of Southern Africa including Tanzania (Wickens & Lowe, 2008). This suggests that most baobab populations tend to grow in arid-eutrophic soil types of savannahs that are likely to be found in low-rainfall, open grasslands (Wickens, 1982).

In the past, the herbivores in the semi-arid areas used to consist of particularly elephant (*L. africana*) and buffalo that then contributed 75% or more of total animal biomass interacting closely with baobab species and in areas where elephant populations had shown a sign of overpopulation, and managers were posed a dilemma for managing populations due to worries of regulating/reducing tree abundance (Douglas-Hamilton, 1973). While in the past, both trees and elephant densities have been shown to be highest in strict protected areas such as national parks (Douglas-Hamilton, 1973), results of from other studies (e.g. Kupika, Shakkie, Edson, & Gumbie, 2014) indicated that elephants target large baobabs with girth ≥ 5 m. Thus, Kupika et al.'s (2014) study suggests that damage of baobab by elephants in these areas is not necessarily detrimental to succumb to mortality. Baobabs act as biomass of high quality forage and high density and principal forage plants for elephants. Baobab seeds are dispersed by elephants and can be transported long distances elsewhere, which germinate easily after passing through the alimentary canal of elephants. There is a potential for damage and clearance of plant species, which could at some point, if no action is taken lead to local extinction. The current land-use intensifications likely due to increased cultivation may lead to an increasing pressure on baobab population in the future and display a conservation concern over the long term. Therefore, there is need to adopt management strategies

that guarantee the continuous existence of this economically important plant species.

5 | CONCLUSIONS

Our results clearly show that an understanding of baobab population hotspots in Tanzania is of paramount importance if we are to sustainably conserve the species. The variations in land-use types have been important in shaping their abundance and distribution. Unsustainable land-use type conversions, changes in climate and anthropogenic activities can play major roles in reducing abundance and distribution of baobab populations. The semi-arid regions of Tanzania harbour one of the important baobab populations in savannah regions, which are continuously threatened by changes land-use changes and unsustainable utilisation of baobabs. We found evidence of population variations both in density and occurrence among land-uses with the highest baobab density being observed in strictly protected areas and the lowest density recorded in unprotected areas. The results suggest that anthropogenic activities coupled with habitat fragmentation and population pressure may be contributing to reduction and occurrence of baobabs populations in unprotected areas across the semi-arid savannah ecosystem. A comparison of baobab density between nonstrictly protected and unprotected areas showed a significant difference, which suggests that environmental factors play a lesser role than land-use and anthropogenic changes in influencing the observed variation in hotspots, distribution and densities within land-use and across the landscape in semi-arid savannahs. In long-lived species like baobabs, with less and slow recruitment rate, it takes long time to bring population to recovery when substantial disturbance and overutilisation. Therefore, there is need for management authorities to develop strategies that can ensure not only sustainable utilisation of the species but also further implement actions protecting the species in all land-use types. In the event of increased human population and pressure due to climate change and other triggers, unsustainable land-use conversions are likely to drive the local extinction of baobabs in these fragmented populations.

ACKNOWLEDGEMENTS

The authors are grateful to the Centre for Research, Agricultural Advancement, Teaching Excellence and Sustainability in Food and Nutrition Security (CREATES-FNS) at the Nelson Mandela African Institution of Science and Technology (NM-AIST) for the financial support. We thank Rufford Small Grants Foundation and British Ecological Society (BES) for the research financial support. Upendo Msalilwa is thankful to her employer, Tanzania Forestry Research Institute (TAFORI), for granting her a study leave for PhD studies.

ORCID

Upendo L. Msalilwa  <https://orcid.org/0000-0002-5775-3500>

Linus K. Munishi  <https://orcid.org/0000-0003-0188-8630>

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

- Aluko, A., Kinyuru, J., Chove, L. M., Kahenya, P., & Owino, W. (2016). Nutritional quality and functional properties of baobab (*Adansonia digitata*) pulp from Tanzania. *Journal of Food Research*, 5(5), 23–31. <https://doi.org/10.5539/jfr.v5n5p23>
- Amisshah, L., Mohren, G. M. J., Bongers, F., Hawthorne, W. D., & Poorter, L. (2014). Rainfall and temperature affect tree species distribution in Ghana. *Journal of Tropical Ecology*, 30, 435–446. <https://doi.org/10.1017/S026646741400025X>
- Assogbadjo, A. E., Kakaï, R. G., Edon, S., Kyndt, T., & Sinsin, B. (2011). Natural variation in fruit characteristics, seed germination and seedling growth of *Adansonia digitata* L. in Benin. *New Forests*, 41(1), 113–125. <https://doi.org/10.1007/s11056-010-9214-z>
- Baltzer, J. L., Davies, S. J., Bunyavejchewin, S., & Noor, N. (2008). The role of desiccation tolerance in determining tree species distributions along the Malay-Thai Peninsula. *Functional Ecology*, 22, 221–231. <https://doi.org/10.1111/j.1365-2435.2007.01374.x>
- Barnes, R. F. W. (1980). The decline of the baobab tree in Ruaha National Park, Tanzania. *African Journal of Ecology*, 18, 243–252. <https://doi.org/10.1111/j.1365-2028.1980.tb01053.x>
- Barnes, R. F. W., Barnes, K. L., & Kapela, E. B. (1994). The long-term impact of elephant browsing on baobab trees at Msembe, Ruaha National Park, Tanzania. *African Journal of Ecology*, 32, 177–184. <https://doi.org/10.1111/j.1365-2028.1994.tb00569.x>
- Baskin, C., & Baskin, J. (2001). *Seeds: Ecology, biogeography, and evolution of dormancy and germination* (p. 666). San Diego, CA: Academic Press.
- Bongers, F., Poorter, L., Van Rompaey, R. S. A. R., & Parren, M. P. E. (1999). Distribution of twelve moist forest canopy tree species in Liberia and Cote d'Ivoire: Response curve to a climate gradient. *Journal of Vegetation Science*, 10, 371–382.
- Borchert, R. (1998). Responses of tropical trees to rainfall seasonality and its long-term changes. *Climatic Change*, 39, 381–393.
- Chirwa, M., Chithila, V., Kayambazinthu, D., & Dohse, C. (2006). *Distribution and population structures of Adansonia digitata in some parts of Ntcheu, Dedza and Mangochi Districts, Malawi*. Zomba, Malawi: FRIM.
- Condit, R., Engelbrecht, B. M., Pino, D., Perez, R., & Turner, B. L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences of the United States of America*, 110(13), 5064–5068.
- de Groot, J., Brus, D. J., Bierkens, M. F. P., & Knotters, M. (2006). *Sampling for natural resource monitoring* (p. 334). Berlin, Germany: Springer-Verlag Berlin Heidelberg.
- Dhillon, S. S., & Gustad, G. (2004). Local management practices influence the viability of the baobab (*Adansonia digitata* Linn.) in different land use types, Cinzana, Mali. *Agriculture, Ecosystems & Environment*, 101(1), 85–103. [https://doi.org/10.1016/S0167-8809\(03\)00170-1](https://doi.org/10.1016/S0167-8809(03)00170-1)
- Doughty, C. E., & Goulden, M. L. (2008). Are tropical forests near a high temperature threshold? *Journal of Geophysical Research*, 113, G00B07. <https://doi.org/10.1029/2007JG000632>
- Douglas-Hamilton, I. (1973). On the ecology and behaviour of the Lake Manyara elephants. *East African Wildlife Journal*, 11, 401–403. <https://doi.org/10.1111/j.1365-2028.1973.tb00101.x>
- Dudley, N. (2008). *Guidelines for applying protected area management categories*. Gland, Switzerland: IUCN.
- Duvall, C. S. (2007). Human settlement and baobab distribution in southwestern Mali. *Journal of Biogeography*, 34(11), 1947–1961. <https://doi.org/10.1111/j.1365-2699.2007.01751.x>
- Edkins, M. T., Kruger, L. M., Harris, K., & Midgley, J. J. (2008). Baobabs and elephants in Kruger National Park: Nowhere to hide. *African Journal of Ecology*, 46, 119–125. <https://doi.org/10.1111/j.1365-2028.2007.00798.x>
- Engelbrecht, B. M., Comita, L. S., Condit, R., Kursar, T. A., Tyree, M. T., Turner, B. L., & Hubbell, S. P. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, 447, 80–82. <https://doi.org/10.1038/nature05747>
- Gauch, H. G., & Whittaker, R. H. (1972). Coenocline simulation. *Ecology*, 53, 446–451. <https://doi.org/10.2307/1934231>
- International Centre for Underutilized Crops (ICUC) (2006). *Technique manual for small scales processor* (p. 94). Southampton, UK: International Center for Underutilized Crop (ICUC).
- John, R., Dalling, J. W., Harms, K. E., Yavitt, J. B., Stallard, R. F., Mirabello, M., ... Foster, R. B. (2007). Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, 104(3), 864–869.
- Kent, M., & Cooker, P. (1992). *Vegetation description and analysis. A practical approach*. London, UK: Belhaven Press.
- Kupika, O. L., Shakkie, S., Edson, G., & Gumbie, A. (2014). Impact of African elephants on baobab (*Adansonia digitata* L.) population structure in northern Gonarezhou National Park, Zimbabwe. *Tropical Ecology*, 55(2), 159–166.
- Land Resources Development Centre (1987). *Tanzania, profile of agricultural potential*. Surbiton, UK: LRDC, Overseas Development Administration.
- Lisao, K., Geldenhuys, C. J., & Chirwa, P. W. (2018). Assessment of the African baobab (*Adansonia digitata* L.) populations in Namibia: Implications for conservation. *Global Ecology and Conservation*, 14, e00386.
- Maharjan, S. K., Poorter, L., Holmgren, M., Bongers, F., Wieringa, J. J., & Hawthorne, W. D. (2011). Plant functional traits and the distribution of West African rain forest trees along the rainfall gradient. *Biotropica*, 43, 552–561. <https://doi.org/10.1111/j.1744-7429.2010.00747.x>
- Mashapa, C., Zisadza-Gandiwa, P., Gandiwa, E., & Kativu, S. (2013). Abundance and structure of African baobab (*Adansonia digitata*) across different soil types in Gonarezhou National Park, Zimbabwe. *International Journal of Biodiversity and Conservation*, 2013, 1–7.
- Millennium Ecosystem Assessment (2005). *Ecosystems and human well-being: Desertification synthesis*. Washington, DC: World Resources Institute.
- Mpofu, E. E., Gandiwa, E., Zisadza-Gandiwa, P., & Zinhiva, H. (2012). Abundance, distribution and status of African baobab (*Adansonia digitata* L.) in dry savanna woodlands in southern Gonarezhou National Park, southeast Zimbabwe. *Tropical Ecology*, 53, 119–124.
- Muthane, K. D., & Gyanchand, , Arora, G. D. (1980). Silvical studies on indigenous and exotic tree species in Rajasthan desert. In H. S. Mann, (Ed), *Arid zone research and development* (pp. 339–343). Jodhpur, India: Scientific Publishers.
- Ndoro, O., Mashapa, C., Kativu, S., & Gandiwa, E. (2014). A comparative assessment of baobab density in northern Mana Pools National Park. *Zimbabwe African Journal of Ecology*, 53, 109–111. <https://doi.org/10.1111/aje.12189>
- NRI (1991). *Tanzania: Profile of agricultural potential*. Chatham, UK: Natural Resources Institute.
- NRI (1996). *Tanzania renewable natural resources profile*. Chatham, UK: ODA/NRI.
- Oksanen, J., & Minchin, P. R. (2002). Continuum theory revisited: What shape are species responses along ecological gradients? *Ecological Modelling*, 157, 119–129. [https://doi.org/10.1016/S0304-3800\(02\)00190-4](https://doi.org/10.1016/S0304-3800(02)00190-4)
- Owen-Smith, R. N. (1988). *Megaherbivores: The influence of a very large body size on ecology*. Cambridge, UK: Cambridge University Press.
- Romero, C., Dovie, D., Gambiza, J., Luoga, E., Schmitt, S., & Grundy, I. (2001). *Effects of commercial bark harvesting on Adansonia digitata*

- (Baobab) in 131 Save-Odzi Valley, Zimbabwe, with considerations for its management (IES Working Paper No. 18). Harare, Zimbabwe: Hotspring Working Group.
- Sanchez, A. C., Osborne, P. E., & Haq, N. (2010). Identifying the global potential for baobab tree cultivation using ecological niche modeling. *Agroforestry Systems*, 80(2), 191–201. <https://doi.org/10.1007/s10457-010-9282-2>
- Schumann, K. W., Wittig, R., Thiombiano, A., Becker, U., & Hahn, K. (2010). Impact of land-use type and bark- and leaf-harvesting on population structure and fruit production of the baobab tree (*Adansonia digitata* L.) in a semi-arid savanna, West Africa. *Forest Ecology and Management*, 260, 2035–2044. <https://doi.org/10.1016/j.foreco.2010.09.009>
- Schumann, K. W., Wittig, R., Thiombiano, A., Becker, U., & Hahn, K. (2012). Uses, management and population status of the baobab in eastern Burkina Faso. *Agroforestry Systems*, 85, 263–278. <https://doi.org/10.1007/s10457-012-9499-3>
- Sidibe, M., & Williams, J. T. (2002). *Baobab. Adansonia digitata. Fruits for the future 4* (p. 100). Southampton, UK: International Centre for Underutilised Crops.
- Swanepoel, C. (1993). Baobab damage in Mana Pools National Park, Zimbabwe. *African Journal of Ecology*, 31, 220–225. <https://doi.org/10.1111/j.1365-2028.1993.tb00535.x>
- TMA (Tanzania Meteorological Agency) (2014). *Past and current trends in climate in Tanzania: An analysis of the 1960-1990 and 1971-2000 baseline periods in select stations*. Analysis report prepared for the Centre for Climate Change Studies (CCCS) (Unpublished).
- Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balcázar, J., Chuviña, J., ... Poorter, L. (2012). Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology*, 100, 253–263. <https://doi.org/10.1111/j.1365-2745.2011.01890.x>
- Van den Bilcke, N., De Smedt, S., Simbo, D. J., & Samson, R. (2013). Sap flow and water use in African baobab (*Adansonia digitata* L.) seedlings in response to drought stress. *South African Journal of Botany*, 88, 438–446.
- Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D. G., McCann, K. S., ... O'Connor, M. I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society*, 281, 20132612.
- Venter, S., & Witkowski, E. (2010). Baobab (*Adansonia digitata* L.) fruit production in communal and conservation land-use types in Southern Africa. *Forest Ecology and Management*, 261, 630–639. <https://doi.org/10.1016/j.foreco.2010.11.017>
- Vlam, M., Baker, P. J., Bunyavejchewin, S., & Zuidema, P. A. (2014). Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees. *Oecologia*, 174, 1449–1461. <https://doi.org/10.1007/s00442-013-2846-x>
- Wato, Y. A., Prins, H. H. T., Heitkönig, I. M. A., Wahungu, G. M., Ngene, S. M., Njumbi, S., & van Langevelde, F. (2018). Movement patterns of African elephants (*Loxodonta africana*) in a semi-arid savanna suggest that they have information on the location of dispersed water sources. *Frontiers in Ecology*, 6, 167. <https://doi.org/10.3389/fevo.2018.00167>
- Wickens, G. E. (1982). The baobab: Africa's upside-down tree. *Kew Bulletin*, 37, 173–209. <https://doi.org/10.2307/4109961>
- Wickens, G. E., & Lowe, P. (2008). *The baobabs: Pachycauls of Africa, Madagascar and Australia*. London, UK: Springer.
- Wilson, R. T. (1998). Vital statistics of the baobab (*Adansonia digitata*). *African Journal of Ecology*, 26, 197–206. <https://doi.org/10.1111/j.1365-2028.1988.tb00971.x>
- World Bank (1994). *Tanzania agricultural sector memorandum volume II: Main report*, July 29, 1994.
- Wright, S. J. (2010). The future of tropical forests. *Annals of the New York Academy of Sciences*, 1195, 1–27. <https://doi.org/10.1111/j.1749-6632.2010.05455.x>

How to cite this article: Msalilwa UL, Munishi LK, Makule EE, Ndakidemi PA. Pinpointing baobab (*Adansonia digitata* [Linn. 1759]) population hotspots in the semi-arid areas of Tanzania. *Afr J Ecol.* 2019;00:1–13. <https://doi.org/10.1111/aje.12709>