South African Journal of Botany 171 (2024) 173–184

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Assessing structure, spatial patterning, and size class distribution of miombo woodland species along a precipitation gradient

Admore Mureva[a], Chipo Magombedze[a], Justice Muvengwi[b,*], Luke Jimu[a], Monicah Mbiba[b]

[a] Department of Natural Resources, Bindura University of Science Education, Private Bag, 1020 Bindura, Zimbabwe
[b] School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

ARTICLE INFO

Article History:
Received 14 March 2024
Revised 3 June 2024
Accepted 4 June 2024
Available online 12 June 2024

Edited by Dr. J. Fisher

Keywords:
Miombo woodland
Spatial pattern
Population structure
Ripley K function
Nearest neighbour

ABSTRACT

Our study investigates the intricate ecological mechanisms shaping miombo woodlands across a rainfall gradient in Zimbabwe. We comprehensively analysed vegetation structure, tree morphology, and spatial patterning across three distinct ecological regions characterized by varying mean annual precipitation (MAP). Results reveal that taller and larger trees are prevalent in the more humid site, while higher tree density is observed in the drier site. The spatial analysis highlights a significant aggregation of adult miombo species across all sites, with juveniles exhibiting a propensity to cluster around adult trees. These findings underscore the pivotal role of ecological gradients, such as precipitation, in shaping miombo woodland structure. However, the absence of clear spatial patterns across the rainfall gradient suggests that precipitation may have less influence on the spatial distribution of miombo trees. Understanding these complex ecological dynamics is essential for developing targeted conservation and management strategies that align with the unique attributes of miombo woodlands, critical ecosystems within the African landscape particularly vulnerable to global climate change.

1. Introduction

Tropical savanna covers approximately 20 % of the land surface with 65 % of this biome located in Africa (Shirima et al., 2011). The miombo woodlands are the most wide-ranging tropical savanna woodland formation in Africa covering an area of about 2.7 million km^2 in the southern, central and eastern parts of the continent including Angola, Democratic Republic of Congo, Malawi, Mozambique, Tanzania, Zambia and Zimbabwe (Campbell, 1996). The woodlands have immensely contributed to the maintenance and wellbeing of local communities by directly supporting the livelihoods of over 39 million people through the provision of food, firewood, pastures, and medicines (Shirima et al., 2011; Sileshi et al., 2007). The miombo woodland is adjacent to arid areas and deserts, and serves as a barrier to spreading desertification (Sileshi et al., 2007). It stores approximately 23 Mg C ha^{-1} making this ecosystem an important global sink of carbon for climate change mitigation (Shirima et al., 2011). Although they are of high economic, ecological and social importance, the miombo woodlands are under threat from anthropogenic activities and increased drought frequency due to climate change (Chidumayo, 2002; Sileshi et al., 2007; Zinyowera et al., 2021).

To better understand the significance of woodlands and the multifaceted challenges they face, it is crucial to implement a comprehensive and multidisciplinary approach that enhances our comprehension of their composition, size distribution, and spatial characteristics. Employing such an approach will facilitate the development of evidence-based policy interventions aimed at safeguarding this critical ecosystem and ensuring its sustainability for future generations. Developing effective management strategies relies on identifying the ecological mechanisms driving these ecosystems, and spatial pattern analysis can serve as a valuable instrument in revealing such mechanisms (Wiegand and Moloney, 2013).

Most studies in the miombo woodland have mainly focused on structure and composition (Banda et al., 2006; Giliba et al., 2011; Shirima et al., 2011), stand biomass (Mareya et al., 2018) carbon storage (Shirima et al., 2011) and on allometric models (Mugasha et al., 2013). However, there is little to no information on how miombo woodland species partition space. Spatial pattern and interactions of plants influence their population dynamics (Wiegand et al., 2000). The spatial distribution patterns of trees depend on the plant's biological characteristics at a small scale and on environmental heterogeneity, such as soil, water, light, and terrain, at large scales. Plants perform well at sites that provide optimal resources and conditions for germination and they interact positively or negatively with neighbours, which influences their survival and growth (Assédé et al.,

---

* Corresponding author.
E-mail address: justice.muvengwi@wits.ac.za (J. Muvengwi).

https://doi.org/10.1016/j.sajb.2024.06.003

2012; Berkowitz et al., 1995; Callaway and Walker, 1997). These interactions result in varying spatial patterns of plant distribution (Wiegand et al., 2000). For example, competition may result in the mortality of weaker individuals and thus increase the spacing between plants over time (Smith and Goodman 1987). Composition of any mature vegetation stand is shaped by competition (Clements et al., 1929; Wiegand et al., 2008) and/or facilitation among plant species (Mureva and Ward, 2016). Strong competition among woody species can result in a regular pattern of the shrubs, while weak competition and/or facilitation can also result in clustering, as can environmental heterogeneity (Meyer et al., 2008). Facilitation can be due to seed dispersal, nurse-plant syndrome, and environmental heterogeneity. A facilitative nurse-plant syndrome often refers to seedling establishment under canopies of adult trees. In such interactions, the seedlings profit from protection against harsh temperatures, higher available soil moisture and nutrients, and reduced soil compaction and erosion (Flores and Jurado, 2003). The nurse-plant syndrome has mainly been reported in arid and semi-arid regions (Chen et al., 2011; Schleicher et al., 2011). Indeed, the role of savanna trees such as *Vachellia karroo* in nucleation have been observed, producing species-rich bush clumps (O'Connor and Chamane, 2012; Jameson-Daniels et al., 2020).

If spatial processes of population dynamics have a strong effect on plant spatial patterns and distribution, then these spatial patterns contain information on population dynamics. It should be possible, therefore, to learn about population processes by investigating spatial patterns of plant distribution (Wiegand and Moloney, 2013). Spatial pattern analysis can be used to: (1) infer ecological mechanisms driving the plant population dynamics (Duncan, 1991; He and Duncan, 2000; Wiegand et al., 2000) (2) understand the genesis and maintenance of biodiversity patterns (Plotkin et al. 2000, He and Legendre 2002, Fang 2005), and (3) predict stand dynamics (Mateu et al. 1998, Stoyan and Penttinen 2000, Kokkila et al. 2002).

There are two common ways of determining spatial distribution of plants, namely point-pattern and nearest-neighbour analyses (Wiegand and Moloney, 2004; Muvengwi et al., 2016; Muvengwi et al., 2018a, Muvengwi et al., 2018b). In point-pattern analysis, the position of a plant in a plot is represented by a point, and the spatial pattern analysis indicates whether the distribution of the points is random, aggregated or regular (Wiegand and Moloney, 2004). However, spatial pattern analysis cannot detect competitive interactions that do not result in differential mortality of individual plants (Getzin et al., 2006). Nearest-neighbour analysis, on the other hand, may provide a useful tool for detecting subtle interactions, where competition may result in reduced growth rather than mortality (Getzin et al., 2006; Shackleton, 2002). Nearest-neighbour analysis shows that if competition is present there will be a substantial decrease in size of one or more competing neighbours (Shackleton, 2002). This analysis works on the premise that there is a positive correlation between a size index (usually canopy diameter) and distance between competing neighbours (Shackleton, 2002). It is therefore expected that large individuals should have smaller neighbours. In contrast, facilitation among plants may result in increased growth, resulting in a negative correlation size index and distance between competing neighbours (Schleicher et al., 2011).

In this study our objectives were to determine the population structure and spatial pattern of miombo woodland species across a rainfall gradient in Zimbabwe. We determined: (1) the spatial pattern of miombo tree species across a rainfall gradient, (2) the differences in spatial pattern of juvenile trees in relation to adult trees along a rainfall gradient and (3) the presence of both inter- and intra-specific tree competition through examination of the relationship between the total distance from the focal tree to its four closest neighbouring trees and the combined canopy cover of the focal tree and its four nearest neighbours.

We hypothesized that:

1. The spatial point pattern of miombo tree species was expected to be regular (indicating competition) in high precipitation areas and clustered (indicating facilitation) in low precipitation areas.
2. We expected juvenile miombo woody species to be clustered around large trees in low rainfall (indicating facilitation) and over-dispersed (indicating competition) around large trees in the high rainfall sites, respectively.
3. High rainfall might intensify competitive interactions due to the favourable growth conditions, possibly resulting in increased mortality and negative relationship between the total distance from the focal tree to its four closest neighbouring trees and the combined canopy cover of the focal tree and its four nearest neighbours, as predicted by the honeycomb Voronoi tessellations. Conversely, in areas with lower rainfall, plant-plant competition may be less pronounced due to the stressful environmental conditions (Maestre et al., 2009), with potential positive relationship between the total distance from the focal tree to its four closest neighbouring trees and the combined canopy cover of the focal tree and its four nearest neighbours, indicating weak interaction. Therefore, we expected reduced growth of neighbouring plants and minimum mortality.

2. Materials and methods

2.1. Study sites

Cecil Kop Nature Reserve, Zimbabwe, located at 18°57′S, 032°41′E, was established in 1977. The area receives an annual rainfall > 1000 mm and has minimum average temperature of 10 °C and an average maximum temperature of 23 °C. This 1500 ha reserve is a popular destination for bird enthusiasts. The soil profile predominantly consists of moderately shallow, greyish-brown, coarse-grained sands transitioning to similar sand loams, and further overlaying reddish-brown sandy loams. These soils are derived from granitic rocks (Campbell, Frost, Byron,1996). The area is protected, and a fire frequency of one fire in five years has been recorded. The reserve is dominated by *Julbernardia globiflora and Brachystegia spiciformis*. In addition to its rich avian life, the park houses two elephants *Loxodonta africana* (a mother and son), three zebras (*Equus quagga*), a giraffe (*Giraffa camelopardalis giraffa*), some kudu (*Tragelaphus strepsiceros*) and vervet monkey (*Chlorocebus pygerythrus*). This site is classified as region I in the study.

Mukuvisi Woodlands which is 263 ha in size is located on 17°50′S, 031°05′E, was founded in 1910. The area receives an average of 850 mm of rainfall per annum (Mbiba et al., 2021). The average minimum temperature of 16 °C and an average maximum temperature of 26 °C has been recorded (Muvengwi et al., 2021). The woodland is dominated by *Julbernardia globiflora and Brachystegia spiciformis*. The area records some occasional fires, with potential to modify tree structure (Muboko et al., 2014; Muvengwi et al., 2022). The area has ferric fluvisols-greyish brown sands and sandy-loam soils derived from granite rocks. Mukuvisi Woodlands serves as a green belt situated just 5 km east of Harare Central Business District (CBD). Mukuvisi Woodlands is home to various game animals, including eland (*Taurotragus oryx*), zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis giraffa*), wildebeest (Connochaetes taurinus), and impala (*Aepyceros melampus*) (Muvengwi et al., 2022). Mukuvisi woodlands is classified under region II in this study.

We sampled a protected woodlot 5 ha in size at Chisangano High School located at18° 52′S, 031°33′E in Chikomba District, Wedza. The area receives an average of 650 mm of rainfall per annum with a minimum temperature of 6 °C and an average maximum of 33 °C. The woodlot is dominated by *Julbernardia globiflora and Brachystegia* *spiciformis* and often experience occasional fires. The soil profile predominantly consists of moderately shallow, greyish-brown, coarse-grained sands transitioning to similar sand loams, and further overlaying reddish-brown sandy loams. These soils are derived from granitic rocks. Although smaller in size compared to the other two sites, it contributes valuable data on the diverse woodland ecosystems found in Zimbabwe (Fig. 1). The site does not have large herbivores and has been well protected from illegal harvesting. This site is a preserved miombo woodlot managed by a local school in region III.

2.2. Data collection

To ensure comprehensive assessment of woody plant interactions within different ecological regions of Zimbabwe, we selected two nature reserves in natural regions I and II and a protected woodlot from natural region III. There was no wood harvesting at the three sites. Within these selected sites, we marked two 20 × 20 m plots in relatively homogeneous patches to minimize the influence of visible landscape environmental heterogeneity, thus focusing on woody plant interactions within the specific site. Each plot contained a minimum of 50 individual woody plants, in accordance with recommendations by Wiegand and Moloney (2013), ensuring an adequate sample size for analysis. For precise location referencing, we employed a Cartesian plane with the origin set at (0, 0), marking the location of each woody plant within the 20 × 20 m plots. The x- and y-coordinates of each plant were determined using a tape measure, ensuring accurate spatial data collection. All woody plants within the plots, ranging from seedlings to adults, were considered for analysis. Adults were defined as individuals with a diameter at breast height (1.3 m) greater than 6 cm and/or a height exceeding 3 m. Sub-adults were characterized as individuals with a height greater than 0.3 m and less than 6 cm diameter at breast height (1.3 m), otherwise the individual was classified as a seedling for structural assessment purpose. These criteria, adapted from Gandiwa et al. (2011) and Walker (1976), allowed for consistent classification of individuals across the study sites. For each woody plant, comprehensive morphometric measurements were conducted, including height, basal diameter, and long and short perpendicular canopy diameters. Additional variables such as basal area and canopy cover were derived from these measured parameters, providing a comprehensive dataset for subsequent analysis and interpretation.

2.3. Data analysis

2.3.1. Tree structure analysis

Data on tree structural variables (height, basal diameter, and crown diameter) were tested for normality using Shapiro Wilk test. We analysed the tree structure variables using multivariate analysis of variance (MANOVA) followed by a pairwise Tukey honest significant difference (Tukey HSD) post hoc comparison for the different sites for significantly different variables. A MANOVA test was applied because its assumptions were fulfilled. Tree size class distribution was compared using the Kolmogorov-Smirnov test. Diameter and height size class distributions (SCDs) were computed according to (Condit et al., 1998). A least-squares linear regression was calculated with size-class midpoint as the independent variable and the number of individuals in that class (Ni) expressed per hectare as the dependent variable. Population structure was interpreted using the diameter and height SCD slopes (Everard et al., 1995). Negative slopes indicated recruitment; zero slopes indicated a balance between recruitment and mature trees whereas positive slopes indicated many mature trees without recruitment (Everard et al., 1995).

2.3.2. Spatial pattern analysis

The univariate point pattern was used to investigate the distribution pattern of adult miombo tree species in each region while the bivariate point pattern was used to investigate the association between adult plants (pattern 1) and juveniles' (pattern 2). The univariate method was used to determine whether the distribution of adult miombo species in different ecological regions can be considered as having a regular, random, or aggregated pattern. The bivariate method was used to determine the effect of adult species on the spatial distribution of juveniles which included, sub-adults, saplings and seedlings (Assédé et al., 2012).

In this study we used the pair correlation function $g(r)$, the expected point density at distance r from a typical point of the pattern, relative to the intensity of the pattern. For a random univariate pattern, the pair correlation function yields $g(r) = 1$. A value of $g(r) > 1$ indicates that the pattern is clustered while a $g(r) < 1$ value indicates that the pattern is uniform.

The bivariate K- function ($K_{12}(r)$) is the expected number of points of pattern 2 within a given distance r from an arbitrary point of pattern 1 divided by the intensity of pattern 2 points (Wiegand and

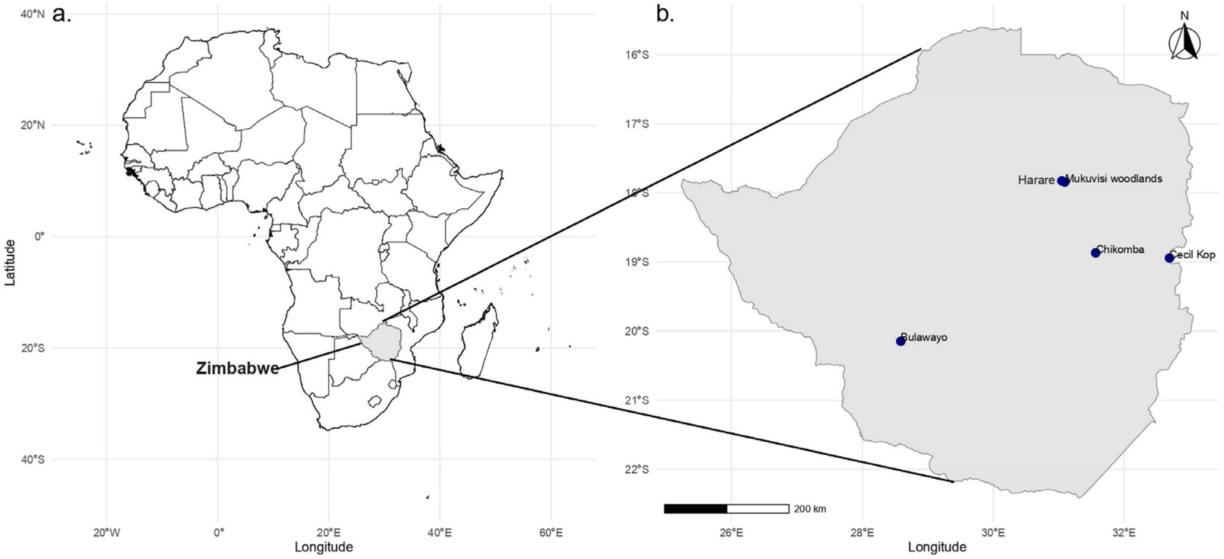

Fig. 1. Map showing location of Zimbabwe in Africa (a) and the study sites (Cecil Kop in region I, Mukuvisi woodlands in region II and Chikomba in region III) and two major cities, Bulawayo and Harare (b).

Moloney, 2004). The second-order bivariate estimate is defined as follows:

$$K_{12}(r) = (n_1 n_2)^{-1}\left|A\right|\sum_{i=1}^{n1}\sum_{j=1}^{n2} W_i^j \; lr(U_{ij}) \tag{1}$$

where n_1 and n_2 are populations from species 1 and 2 respectively in area *A*. Other terms are interpreted as in equation 4 above. However, in this study we used the pair correlation function $g_{12}(r)$ function which was determined as follows:

$$g_{12}(r) = \frac{dK_{12}(r)}{dr}/2\pi r \tag{2}$$

If patterns 1 and 2 are randomly associated, $g_{12}(r) = 1$. When there is facilitation, $g_{12}(r) > 1$. If the individuals are competing, $g_{12}(r) < 1$ (Gray and He, 2009). $K_{12}(r)$ is calculated as in equation 3 above.

The confidence envelopes for pair correlations statistics were estimated from 199 Monte Carlo simulations using the complete spatial randomness null model for univariate analysis and the toroidal shift null model for the bivariate analysis (Wiegand and Moloney, 2004). The confidence envelopes were estimated using the 5th lowest and the 5th highest values for each distance *r*. In the bivariate case, if the *g(r)* statistic exceeds the upper confidence limit, it indicates aggregation at the *r* spatial scales where the deviation occurs. If the function is below the lower confidence limit, it indicates spatial repulsion. When the function lies within the confidence limits, the distribution is considered random. To avoid the problems of Type I errors associated with multiple testing (Loosemore and Ford, 2006; Perry et al., 2006), significant departure from the null models was tested at $\alpha = 0.05$ using the Diggle-Cressie-Loosmore-Ford (DCLF) test with 199 Monte Carlo simulations.

2.3.3. Nearest-Neighbour analysis

We used nearest-neighbour analysis to infer fine-scale competition. Competition does not always lead to significant mortality and may only result in growth reduction in one or more neighbouring plants (Dale, 1999). We determined the correlation between the sum of canopy diameters of four nearest neighbours plus the canopy diameter of the focal tree and the sum of the distances from the four nearest neighbours to the focal tree. If the trees are directly competing, then the nearest-neighbour distance should be smaller for smaller trees than for large trees. A significant positive correlation between nearest-neighbour distances and tree sizes indicates competition and a significant negative correlation indicates facilitation.

3. Results

3.1. Tree density and structural variables

Adult tree height was significantly different ($F_{2,\ 389} = 69.8$, $p < 0.001$) among the three regions (Table 1). Region I (>1000 mm) had taller adult trees compared to the 850 ($p < 0.001$) and 650 ($p < 0.001$) mm MAP sites. Adult individuals at region II woodland were significantly taller compared with those in region III (Table 1). The juveniles were also significantly taller in the region I compared to region II and region III (Table 1). Individuals, however, were significantly taller in region II woodlands and region III woodland compared to region I.

Basal diameter was significantly different in adults ($F_{2,\ 389} = 12.35$, $p < 0.001$), sub-adults ($F_{2,\ 548} = 18.93$, $p = 0.008$) and juveniles ($F_{2,\ 526} = 12.35$, $p < 0.001$) across the three sites (Table 1). region I woodland had higher adult diameters compared with region II ($p < 0.001$) and region III woodlands ($p < 0.001$). The basal diameters of juvenile plants were smaller ($P < 0.001$) in region II compared to region I (Table 1).

Canopy diameter and canopy cover were significantly different for adults and sub-adults ($F_{2,\ 389} = 22.34$, $p = 0.001$, $F_{2,\ 389} = 17.25$, $p < 0.001$, respectively) across the regions. For sub-adults, canopy diameter was significantly different ($F_{2548} = 3.42$, $p = 0.03$) while canopy cover was marginally different ($F_{2,\ 548} = 2.65$, $p = 0.07$) across sites.

The Kolmogorov-Smirnov test showed that the diameter class distributions were significantly different between region I and region II woodlands ($D = 0.184$, $p < 0.001$). The diameter class distributions were also significantly different between region I and region III woodlands ($D = 0.193$, $p < 0.001$). The height class distributions were significantly different between region I and region II woodlands ($D = 0.222$, $p < 0.001$), region I and region III woodlands ($D = 0.194$, $p < 0.001$) and region II and region III woodlands ($D = 0.14$, $p < 0.001$). All the three miombo woodlands showed a typical inverse J-shaped diameter class distribution. The relative frequency of individuals between 0 and 4 cm in diameter was 56 %, 67 % and 64 % in the Regions 1, 2 and 3 respectively (Fig. 2). Individuals with diameters greater than 13 cm had a relative frequency of 15 % and 37 % in the region I and region II while they only contributed 1.7 % region III woodland (Fig. 2).

3.1.1. Univariate analysis of adult miombo species

The pair correlation function in region I showed that the miombo adult trees were significantly aggregated ($p < 0.05$) for both plots between 2 and 4 m (Figs. 3a&b; 4a&b). The highest average neighbourhood density for plot 1 in region I woodland was at 0.5 m (2 times higher than expected) while in plot 2 the highest density was at 3 m (1.5 times higher than expected) (Fig 4a&b, respectively). In region II woodland there was an aggregation up to 5 m ($p < 0.05$ for plot 1 and 2) (Figs. 3c&d; 4c&d). The average neighbour density for region II woodland plots was more than 2 times that expected at distances less than 0.5 m. In both plots in region III woodland, the pair correlation function showed aggregation up to 5 m ($p = 0.005$ and $p = 0.01$ for plot 1 and 2 respectively). The neighbourhood density was highest at short distances ($r < 1$) (Figs. 3e&f; 4e&f).

Table 1

Height (m), basal diameter (BD) (cm), basal area (BA) (cm^2), canopy diameter (CD) (m), canopy cover (CC) (m^2) of the major miombo species in different ecological regions within Zimbabwe compared using multivariate analysis of variance (MANOVA). Means were separated using Tukey honest significant difference (Tukey HSD) post hoc comparison. Values represent the means ± SE in each age class.

	region I			region II			region III		
	Juveniles	Sub-Adults	Adults	Juveniles	Sub-Adults	Adults	Juveniles	Sub-Adults	Adults
Height	0.32 ± 0.09^{a}	1.20 ± 0.69^{a}	5.77 ± 1.82^{a}	0.26 ± 1.32^{b}	1.61 ± 0.68^{ab}	4.26 ± 1.33^{b}	0.19 ± 0.11^{c}	1.64 ± 0.60^{b}	4.27 ± 4.35^{c}
BD	0.36 ± 0.41^{a}	2.67 ± 2.21^{a}	12.98 ± 6.92^{a}	0.85 ± 1.33^{b}	3.39 ± 2.11^{ab}	9.52 ± 4.45^{b}	0.46 ± 0.61^{a}	3.09 ± 1.58^{b}	6.788 ± 3.14^{c}
BA	——	9.44 ± 14.06^{a}	169.79 ± 252.47^{a}	——-	1.96 ± 5.02^{ab}	86.7 ± 70.42^{b}	——	9.44 ± 8.82^{b}	43.88 ± 40.4^{c}
CD	——	0.92 ± 0.62^{a}	3.04 ± 1.46^{a}	——-	1.07 ± 0.69^{a}	2.19 ± 1.24^{ab}	——-	0.95 ± 0.49^{a}	2.133 ± 0.95^{b}
CC	——-	0.95 ± 1.24^{a}	8.95 ± 9.53^{a}	——-	0.95 ± 0.49^{a}	4.97 ± 6.42^{b}	——	0.90 ± 0.89^{a}	4.27 ± 4.35^{b}

Means in the same row within the same age class with different superscripts are significantly different at $P = 0.05$.

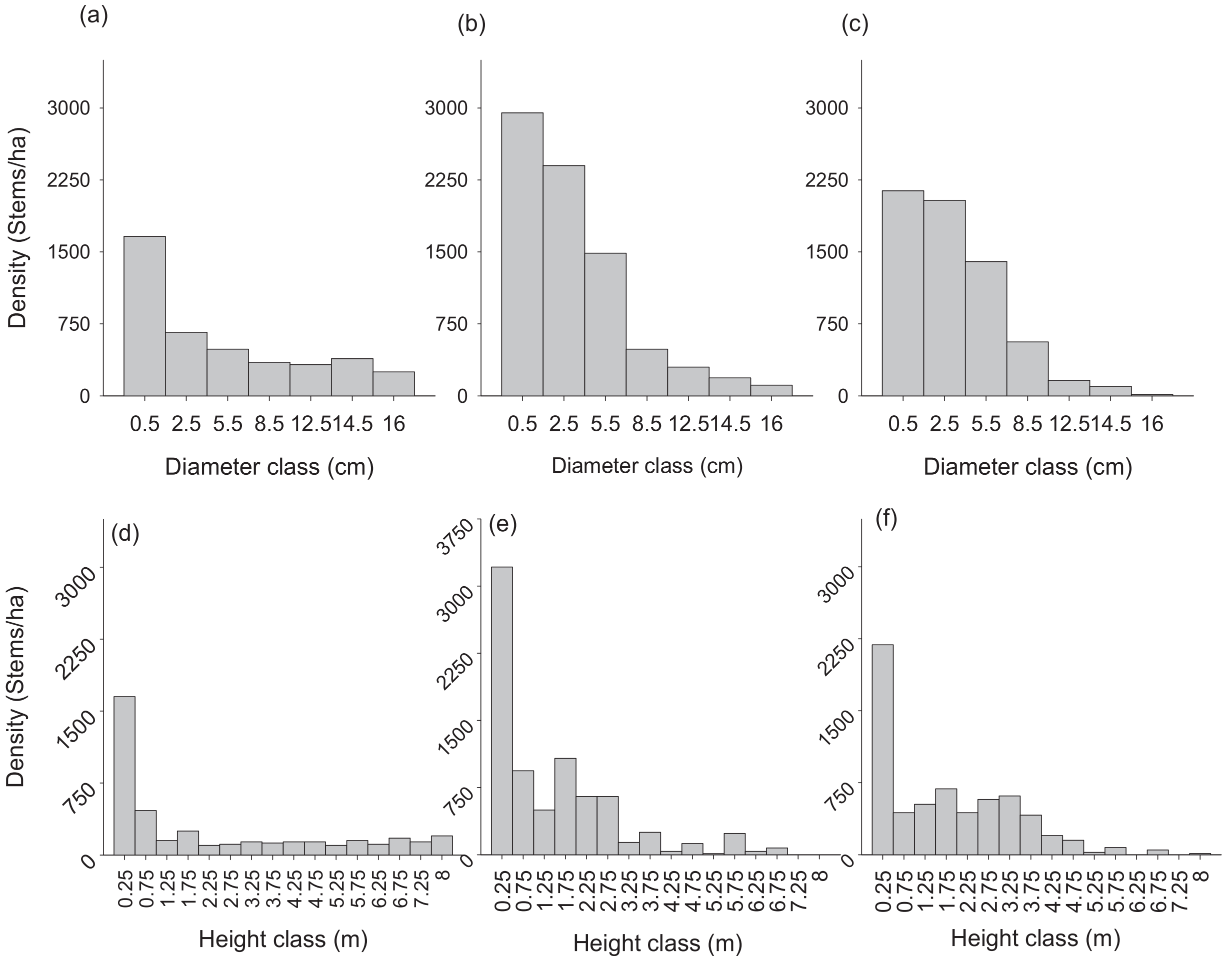

Fig. 2. Size class distributions (SCDs) according to diameter (a–c) and height (d–f)) of miombo species in the three ecological regions in Zimbabwe, region I (a and d), region II (b and e) and region III (c and f).

3.1.2. *Bivariate analysis of adults and juveniles*

The bivariate *L* function showed that region I juveniles were clustered around adults between 0.5 and 5 m ($p = 0.005$) in the two plots. The bivariate *L* function showed inconclusive results in region II woodland, with plot 1 showing significant ($p = 0.02$) aggregation of juveniles around adults between 2 and 5 m, while in plot 2 juveniles were significantly ($p = 0.005$) dispersed from their adult counterparts between 2 and 5 m (Fig 5c and d, respectively). In region III woodland the bivariate *L* function was also inconclusive with one plot showing clustering of juveniles around adults while the other plot showed that juveniles were randomly distributed around the adults.

The bivariate pair correlation function indicated that juveniles were aggregated around adults in both plots in region, with plot 1 showing aggregation ($p = 0.005$) between 0 and 2 m while plot 2 showed aggregation between 0.5 and 5 m ($p = 0.005$). In region I woodland the bivariate pair correlation function showed that the juveniles in plot one were generally randomly distributed around the adult trees, while in plot 2 the juveniles were over dispersed (between 1 and 5 m) around the adult plants. In region III the juveniles in one plot were aggregated between 1 and 5 m ($p = 0.005$) around adult plants while in the other plot there was random distribution ($p = 0.73$) of juveniles around adult plants (Fig. 6).

3.1.3. *Nearest-Neighbour analysis*

There were significant correlations between sum of the distance to the nearest neighbour and the sum of the canopy diameters of the focal individual and its neighbours in the study plots (Fig. 6). However, although the *p*-values were significant (because of the large number of data points), the relationships explained very little (< 5 %) of the variation in all the plots (Fig. 7).

4. Discussion

Adult and juvenile trees had significantly larger structural variables (height, basal and canopy diameter) in the most humid site (region I) than in region II and region III. Tree density, was however, highest in region II and lowest in region I site contrary to our prediction which expected density to be highest in region III site. High moisture content that prevails in humid regions as well as high levels of nutrient cycling (Schimel et al., 1985) enhance plant performance, leading to large trees dominating our wetter site (Homeier et al., 2010; Takyu et al., 2002). Because of the high moisture availability, plants in our region I study site tend to compete, eliminating weaker individuals resulting in a low-density stand (Mureva and Ward, 2016; Muvengwi et al., 2018). High tree density in the region III woodland may have led to intense competition with potential to lower plant growth (in terms of canopy diameter and diameter at breast height), with trees investing more in height due to competition for light (Nagashima and Hikosaka, 2011; Nishimura et al., 2010; Weiner and Thomas, 1992). However, the investment in height of trees in low precipitation areas is limited by resource availability.

The high recruitment observed in our region III site compared to the most humid site demonstrated that in low precipitation areas there is less mortality dependent competition and bigger plants tend to facilitate seedlings and juveniles to escape from the harsh environment through provision of shade, water, and nutrients (Getzin et al.,

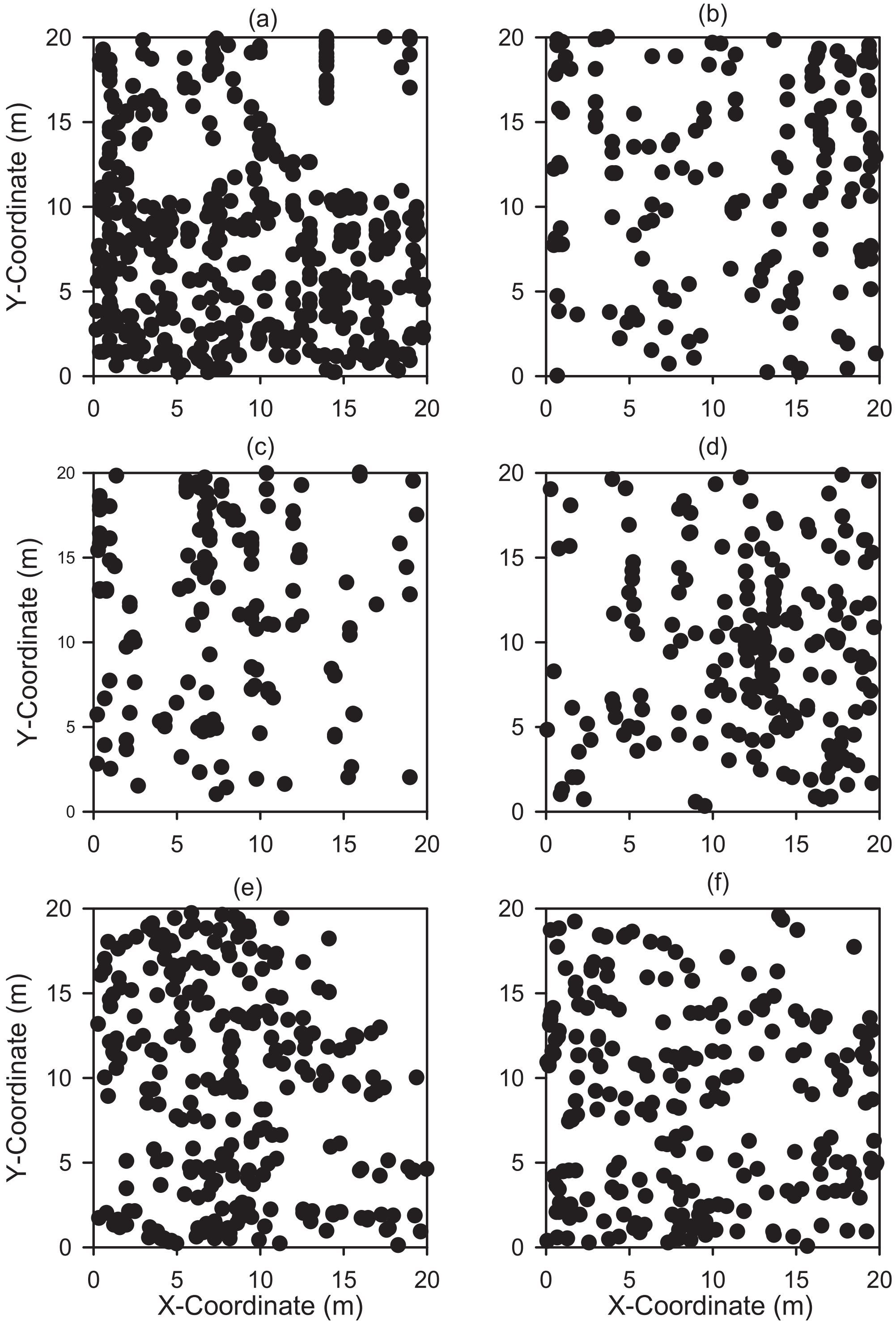

Fig. 3. Spatial distribution of trees in sampled regions of Zimbabwe, region I; (a) and (b), in region II (c) and (d) and in region III woodlands (e) and (f). Black circles represent locations of individual trees in the sampled plots.

2006; Maestre et al., 2003; Pillay and Ward, 2012). Another probable explanation for the high density of seedlings and juveniles in the drier site, is that, under tree canopy, there is low evapotranspiration demands and competition for soil water (Holmgren et al., 1997) resulting in high seedling survival in arid regions compared to humid regions. Although recruitment was significantly higher in the low precipitation areas, all our study sites showed a size class distribution conforming to the inverse J size-class distribution indicating high density of juveniles compared to adults (Everard et al., 1995). These findings suggest that the Miombo woodlands may be fine grained forests and the species may be shade tolerant as they are able to regenerate under canopy cover (Everard et al., 1995).

The aggregation of adult tree species shown in this study was contrary to our prediction for the region I woodland, however the prediction agreed with our region III site. Our findings in the high rainfall area, are in agreement with Pillay and Ward (2012) who found a similar spatial pattern (aggregation) of adult savanna trees in humid regions, although they were focusing on *Acacia* (*Vachellia*) species.

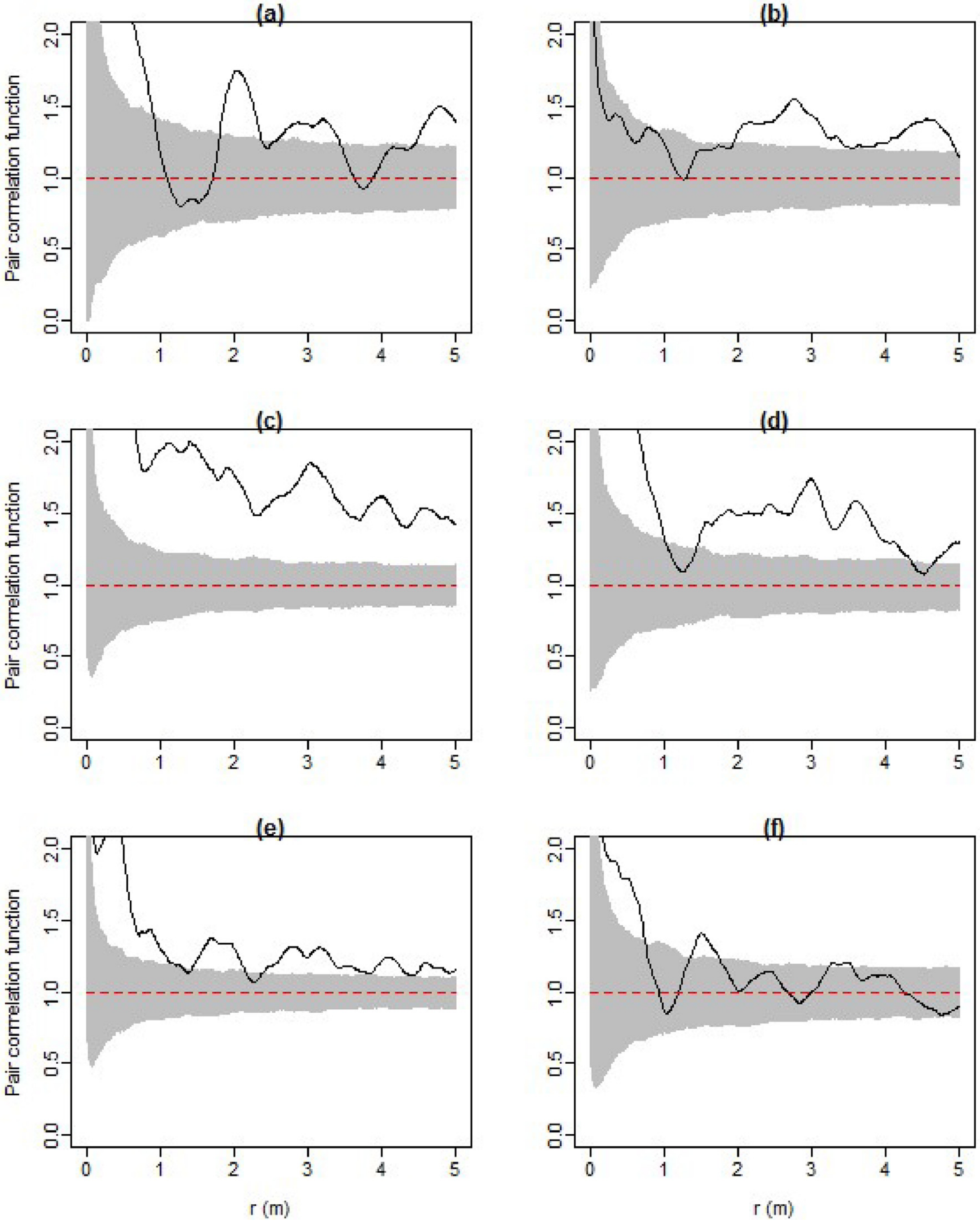

Fig. 4. Spatial distribution of adult miombo trees in the sampled regions of Zimbabwe, region I (a and b), region II (c and d), and region III woodlands (e and f) using the univariate pair correlation function. Significant departure from the null model of complete spatial randomness (CSR) is indicated by the dark line falling below or above the 99 % confidence limits (grey shaded area), determined from the 5th lowest and 5th highest values among 199 Monte Carlo simulations.

This suggests absence of extreme inter- and intra-specific competition, which leads to death of plants. A regular distribution of trees is usually due to density-dependent mortality and occurs when trees compete for limited resources. Intense competition may result in mortality of aggregated individuals, resulting in regular distribution of trees in accordance with the honeycomb rippling model (Ward, 2005; Wiegand et al., 2005). Adult individuals, therefore, should be more evenly spaced than juveniles. Even distribution will only occur when competition leads to sufficient mortality within a stand of trees (Stoll and Bergius, 2005). In some cases, competition may not be sufficient to cause mortality but rather reduces growth. In agreement with our studies, Pillay and Ward (2012) and Getzin et al. (2006) failed to find any evidence of spatial regularity in *Vachellia karoo* and *Pseudotsuga menziesii* var. *menziesii* stands, respectively. However, the two studies detected important competitive interactions via size correlations. In our study the correlation between canopy diameters and nearest neighbour distance was weak, suggesting relatively weak competitive interactions of adult miombo species.

The aggregated distribution of the juvenile plants observed in this study can be due to several ecological processes such as facilitation, seed dispersal and environmental heterogeneity. Facilitation has been reported in arid and semi-arid environments and is regarded as

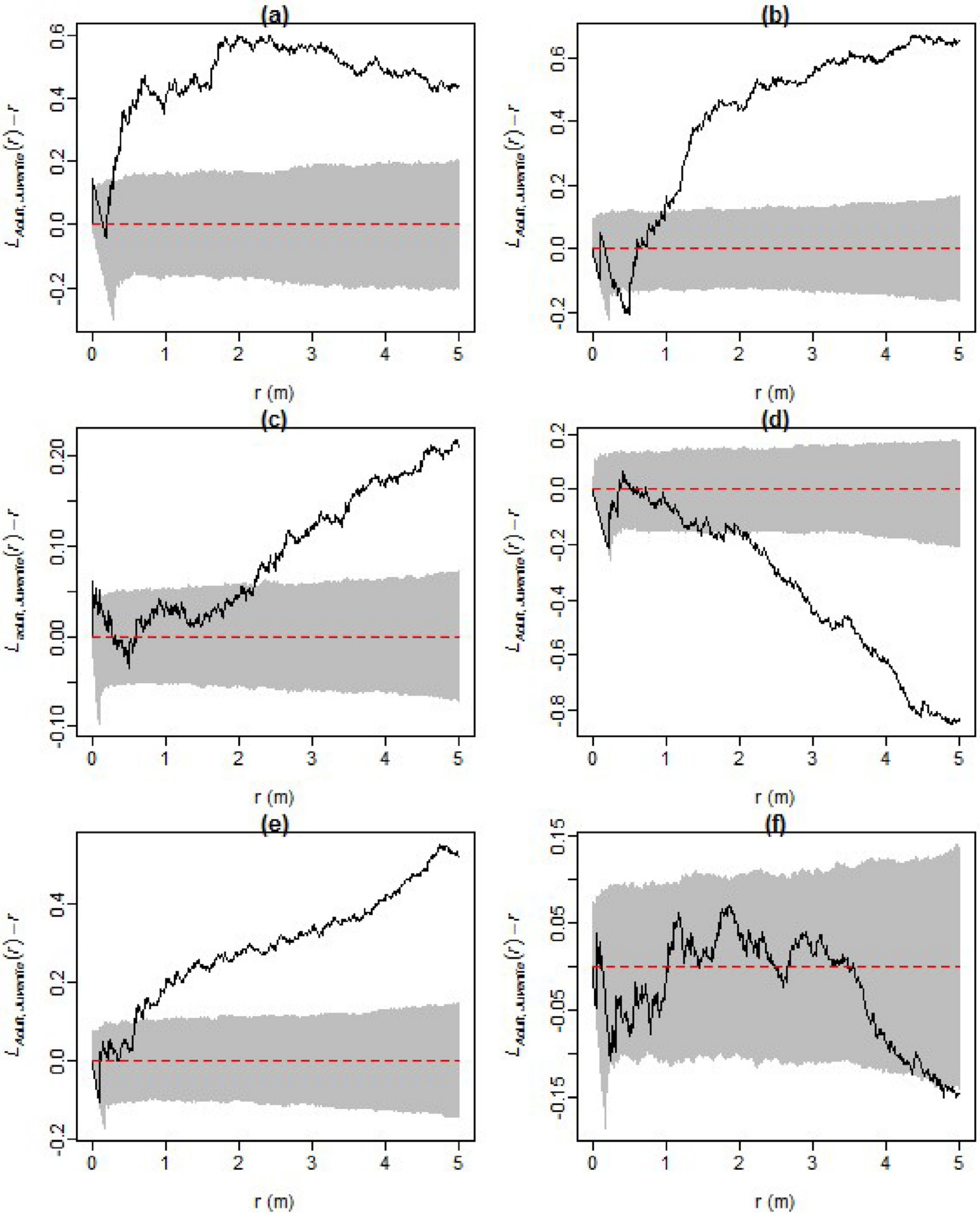

Fig. 5. Bivariate $L_{12}(r)$ function (square root transformation of the bivariate Ripley $K_{12}(r)$ function) showing the analysis of the interaction between adults and juvenile miombo tree species in sampled regions of Zimbabwe, region I (a) and (b), in region II (c) and (d) and in region III woodlands (e) and (f); r (m) is the distance scale in metres. The observed pattern (solid black line) within, above or below the 95 % Monte Carlo Simulation envelopes (grey area) indicate random, aggregated and regular, respectively.

a response to patchy precipitation events in arid savannas (Holmgren et al., 1997; Schleicher et al., 2011) which is uncommon in high rainfall areas (Eisinger and Wiegand, 2008; Ward, 2009). Facilitation occurs when a nurse plant has an established canopy beneath which conditions for seed germination and seedling survival are enhanced, e.g. due to increased water availability, more nutrients in the soil, or reduced grazing pressure (Flores and Jurado, 2003). On the other hand, directed seed dispersal results in spatial plant associations similar to those caused by nurse plant effects when wind-dispersed seeds are trapped beneath (apparent nurse) plants or when animal dispersed seeds preferentially defecated beneath (apparent nurse) plants (Chen et al., 2011; Dean et al., 1999). Finally, external factors cause environmental variables to be unevenly distributed in space and/or time. If local environments (e.g. soil nutrient concentrations) are favourable to the investigated species, these species will tend to aggregate even in the absence of mutualistic interactions (Barot et al., 1999; Maestre et al., 2003).

Understanding the influence of a rainfall gradient on miombo species spatial point patterns, size class distribution, and structure provides valuable insights for ecosystem management and conservation, particularly in the context of climate change. Our findings suggest that the distribution and characteristics of miombo woodlands are strongly influenced by local environmental conditions, with varying responses along a precipitation gradient. Given that tree height and other structural attributes were significantly influenced by the rainfall gradient, climate change scenarios predicting alterations in

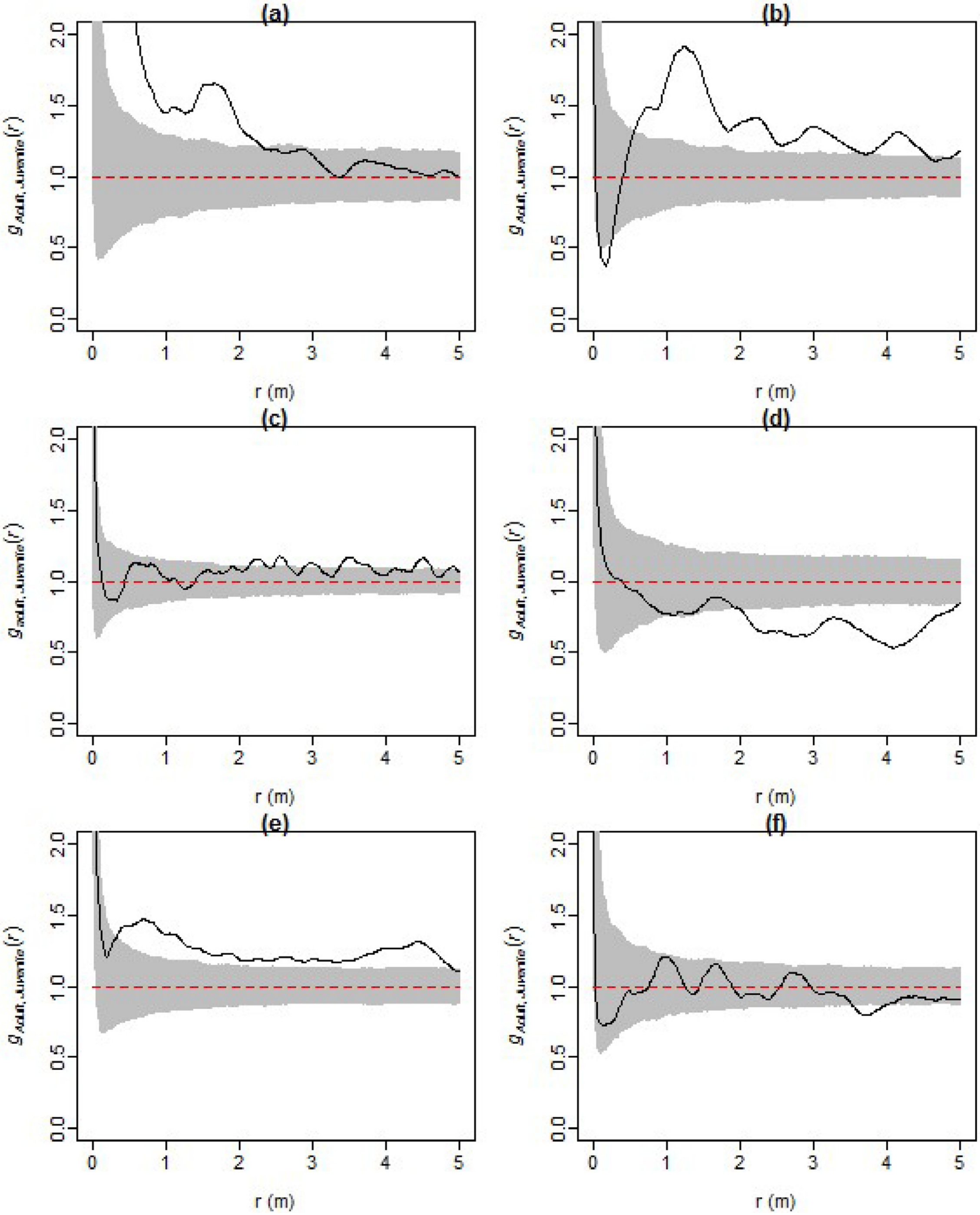

Fig. 6. Bivariate pair correlation function showing the analysis of the interaction between adults and juvenile miombo tree species in the sampled regions of Zimbabwe, region I; (a) and (b), in region II (c) and (d) and in region III woodlands (e) and (f), r (m) is the distance scale in metres. The observed pattern (solid black line) within, above or below the 95 % Monte Carlo Simulation envelopes (grey area) indicate random, aggregated and regular, respectively.

precipitation patterns could have profound effects on miombo woodland structure. With anticipated shifts in rainfall regimes, particularly in drier regions experiencing increased aridity and moisture stress, we might expect changes in tree density, size class distribution, and spatial patterns. For instance, reduced precipitation could lead to decreased tree growth and recruitment, impacting the overall structure and composition of miombo woodlands. Conversely, areas experiencing increased rainfall may see enhanced tree growth and density, potentially altering species interactions and community dynamics.

To inform evidence-based management strategies for miombo woodlands under future climate scenarios, it is imperative to implement adaptive management approaches that account for potential shifts in tree species composition, structure, and function in response to changing precipitation patterns. There is need to prioritize conservation efforts in areas exhibiting high tree density and recruitment, especially in regions prone to increased aridity and potential vegetation shifts and finally establish long-term monitoring programs to track changes in miombo woodland structure and dynamics, enabling timely interventions and adaptive responses to climate-induced alterations.

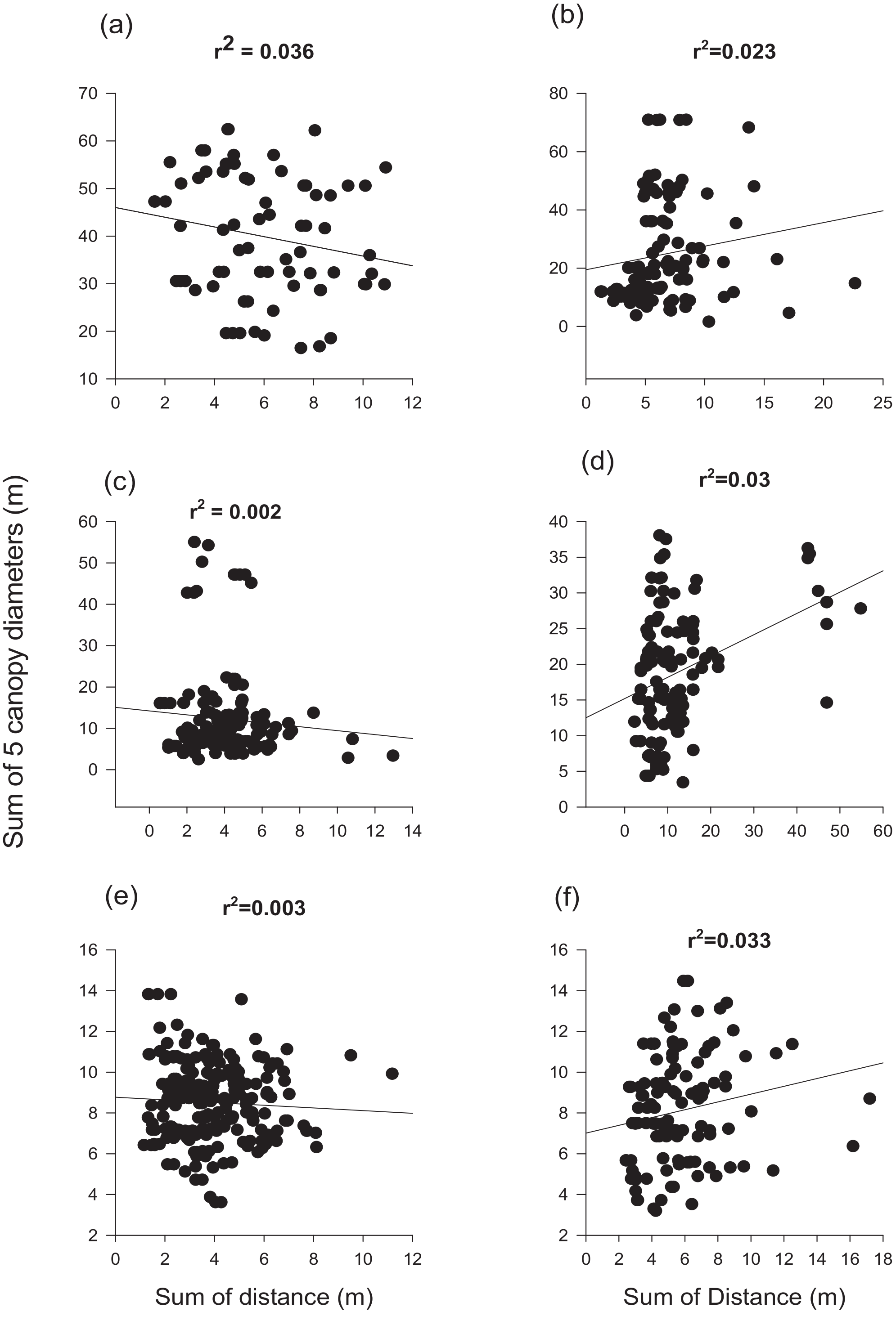

Fig. 7. The nearest neighbour analysis in region I; (a) and (b), in region II (c) and (d) and in region III woodlands (e) and (f) in miombo woodlands in Zimbabwe.

5. Conclusion

Our study investigated the influence of a rainfall gradient on spatial point patterns, size class distribution, and structural variables of miombo species. We found that adult miombo species were significantly clustered across the three study sites, with aggregation of juveniles around adults observed consistently. Trees in the high rainfall site exhibited the largest structural variables (height, diameter at breast height, canopy diameter, and canopy cover) compared to sites with medium and lower rainfall. This underscores the strong influence of rainfall on miombo tree structure, suggesting that regions experiencing high rainfall may struggle to sustain large trees, with potential implications for ecosystem services and overall function in the face of climate change. Interestingly, tree density was higher in the least humid site. Both univariate Ripley's *L* and pair correlation functions supported these findings. However, our analysis suggests that while rainfall gradient is important for shaping miombo woodland structure, its influence on the spatial patterning of tree species may be minimal. We propose that biological mechanisms, such as seed dispersal and nurse syndrome, may play a more critical role than environmental factors in shaping miombo woodland dynamics and distribution patterns.

Declaration of competing interest

The authors declare that they have no conflict of interest.

CRediT authorship contribution statement

Admore Mureva: Writing – review & editing, Conceptualization. **Chipo Magombedze:** Writing – review & editing, Data curation, Conceptualization. **Justice Muvengwi:** Writing – original draft, Formal analysis, Conceptualization. **Luke Jimu:** Writing – review & editing, Conceptualization. **Monicah Mbiba:** Writing – review & editing, Conceptualization.

References

Assédé, E., Adomou, A., Sinsin, B., 2012. Relationship between stand regime and population structure of Pseudocedrela kotschyi (Meliaceae) and Terminalia macroptera (Combretaceae) in the Biosphere Reserve of Pendjari (Benin, West Africa). Int. J. Biodivers. Conserv. 4, 427–438.

Banda, T., Schwartz, M.W., Caro, T., 2006. Woody vegetation structure and composition along a protection gradient in a miombo ecosystem of western Tanzania. For. Ecol. Manag. 230, 179–185.

Barot, S., Gignoux, J., Menaut, J.-C., 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. Ecology 80, 1987–2005. https://doi.org/10.1890/0012-9658(1999)080[1987:DOASPT]2.0.CO;2.

Berkowitz, A.R., Canham, C.D., Kelly, V.R., 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. Ecology 76, 1156–1168. https://doi.org/10.2307/1940923.

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78, 1958–1965. https://doi.org/10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2.

Chen, J., Liu, J., Yang, X., Wang, Y., Yu, X., 2011. The structure and spatial patterns of three desert shrub communities in the western Ordos Plateau: implications for biodiversity conservation. J. Food, Agric. Environ. 9, 714–722.

Chidumayo, E., 2002. Changes in miombo woodland structure under different land tenure and use systems in central Zambia. J. Biogeogr. 29, 1619–1626. https://doi.org/10.1046/j.1365-2699.2002.00794.x.

Clements, F.E., Weaver, J.E., Hanson, H.C., 1929. Plant Competition, an Analysis of Community Functions. Carnegie Institute, Washington, DC, U.S.A.

Condit, R., Sukumar, R., Hubbell, S.P., Foster, R.B., 1998. Predicting population trends from size distributions: a direct test in a tropical tree community. Am. Nat. 152, 495–509. https://doi.org/10.1086/286186.

Dale, M.R.T., 1999. Spatial Pattern Analysis in Plant Ecology. Cambrige University Press, Cambridge, United Kingdom. https://doi.org/10.1017/CBO9780511612589.

Dean, W.R.J., Milton, S.J., Jeltsch, F., 1999. Large trees, fertile islands, and birds in arid savanna. J. Arid Environ. 41, 61–78. https://doi.org/10.1006/jare.1998.0455.

Duncan, R.P., 1991. Competition and the coexistence of species in a mixed podocarp stand. J. Ecol. 79, 1073–1084. https://doi.org/10.2307/2261099.

Eisinger, D., Wiegand, K., 2008. SERGE: a spatially explicit generator of local rainfall in southern Africa. S. Afr. J. Sci. 104, 37–42 S0038-23532008000100010&lng=en.

Everard, D.A., Midgley, J.J., Van Wyk, G.F., 1995. Dynamics of some forests in KwaZulu-Natal, South Africa, based on ordinations and size-class distributions. S. Afr. J. Bot. 61, 283–292. https://doi.org/10.1016/S0254-6299(15)30548-2.

Flores, J., Jurado, E., 2003. Are nurse-protégé interactions more common among plants from arid environments? J. Veg. Sci. 14, 911–916. https://doi.org/10.2307/3236989.

Gandiwa, E., Chikorowondo, G., Zisadza-Gandiwa, P., Muvengwi, J., 2011. Structure and composition of Androstachys johnsonii woodland across various strata in Gonarezhou National Park, southeast Zimbabwe. Trop. Conserv. Sci. 4, 218–229.

Getzin, S., Dean, C., He, F., Trofymow, A.J., Wiegand, K., Wiegand, T., 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. Ecography 29, 671–682. https://doi.org/10.1111/j.2006.0906-7590.04675.x.

Giliba, R.A., Boon, E.K., Kayombo, C.J., Musamba, E.B., Kashindye, A.M., Shayo, P.F., 2011. Species composition, richness and diversity in miombo woodland of Bereku Forest Reserve, Tanzania. J. Biodiversity 2, 1–7.

Gray, L., He, F., 2009. Spatial point-pattern analysis for detecting density-dependent competition in a boreal chronosequence of Alberta. For. Ecol. Manag. 259, 98–106. https://doi.org/10.1016/j.foreco.2009.09.048.

He, F., Duncan, R.P., 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. J. Ecol. 88, 676–688. https://doi.org/10.1046/j.1365-2745.2000.00482.x.

Holmgren, M., Scheffer, M., Huston, M.A., 1997. The interplay of facilitation and competition in plant communities. Ecology 78, 1966–1975 10.1890/0012-9658(1997)078[1966:TIOFAC]2.0.CO;2.

Loosemore, N.B., Ford, E.D., 2006. Statistical inference using the G or K point pattern spatial statistic. Ecology 87, 1925–1931. https://doi.org/10.1890/0012-9658(2006)87[1925:SIUTGO]2.0.CO;2.

Maestre, F.T., Cortina, J., Bautista, S., Bellot, J., Vallejo, R., 2003. Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semiarid degraded ecosystem. Ecosystems 6, 630–643. https://doi.org/10.1007/s10021-002-0222-5.

Mareya, H.T., Tagwireyi, P., Ndaimani, H., Gara, T.W., Gwenzi, D., 2018. Estimating tree crown area and aboveground biomass in miombo woodlands from high-resolution RGB-Only imagery. Forest 16, 18.

Mbiba, M., Mazhude, C., Fabricius, C., Fritz, H., Muvengwi, J., 2021. Bird species assemblages differ, while functional richness is maintained across an urban landscape. Landsc. Urban Plan. 212. https://doi.org/10.1016/j.landurbplan.2021.104094.

Meyer, K.M., Ward, D., Wiegand, K., Moustakas, A., 2008. Multi-proxy evidence for competition between savanna woody species. Perspect. Plant Ecol. Evol. Syst. 10, 63–72.

Mugasha, W.A., Eid, T., Bollandsås, O.M., Malimbwi, R.E., Chamshama, S.A.O., Zahabu, E., Katani, J.Z., 2013. Allometric models for prediction of above-and belowground biomass of trees in the miombo woodlands of Tanzania. For. Ecol. Manag. 310, 87–101.

Mureva, A., Ward, D., 2016. Spatial patterns of encroaching shrub species under different grazing regimes in a semi-arid savanna, eastern Karoo, South Africa. Afr. J. Range Forage Sci. 33, 1–13. https://doi.org/10.2989/10220119.2016.1148775.

Muvengwi, J., Fritz, H., Mbiba, M., Ndagurwa, H.G.T., 2022. Land use effects on phylogenetic and functional diversity of birds: significance of urban green spaces. Landsc. Urban Plan. 225. https://doi.org/10.1016/j.landurbplan.2022.104462.

Muvengwi, J., Mbiba, M., Chikumbindi, J., Ndagurwa, H.G.T., Mureva, A., 2018. Population structure and spatial point-pattern analysis of a mono stand of Acacia polyacantha along a catena in a savanna ecosystem. For. Ecol. Manag. 409, 499–508. https://doi.org/10.1016/j.foreco.2017.11.056.

Muvengwi, J., Davies, A.B., Parrini, F., Witkowski, E.T.F., 2018. Geology drives the spatial patterning and structure of termite mounds in an African savanna. Ecosphere 9, e02148. https://doi.org/10.1002/ecs2.2148 10.1002/ecs2.2148.

Muvengwi, J., Mbiba, M., Ndagurwa, H.G.T., Kabvuratsiye, N., 2016. Pulsing hydrology and topography determine the structure and spatial distribution of Cubitermes mounds in a savanna ecosystem. Catena 145, 99–106. https://doi.org/10.1016/j.catena.2016.05.009.

Nagashima, H., Hikosaka, K., 2011. Plants in a crowded stand regulate their height growth so as to maintain similar heights to neighbours even when they have potential advantages in height growth. Ann. Bot. 108, 207–214. https://doi.org/10.1093/aob/mcr109.

Nishimura, E., Suzaki, E., Irie, M., Nagashima, H., Hirose, T., 2010. Architecture and growth of an annual plant Chenopodium album in different light climates. Ecol. Res. 25, 383–393. https://doi.org/10.1007/s11284-009-0666-6.

O'Connor, T.G., Chamane, S.C., 2012. Bush clump succession in grassland in the Kei Road region of the Eastern Cape, South Africa. Afr. J. Range Forage Sci. 29 (3), 133–146. https://doi.org/10.2989/10220119.2012.74477.

Perry, G.L.W., Miller, B.P., Enright, N.J., 2006. A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. Plant Ecol. 187, 59–82. https://doi.org/10.1007/s11258-006-9133-4.

Pillay, T., Ward, D., 2012. Spatial pattern analysis and competition between *Acacia karroo* trees in humid savannas. Plant Ecol. 213, 1–11. https://doi.org/10.1007/s11258-012-0115-4.

Schleicher, J., Wiegand, K., Ward, D., 2011. Changes of woody plant interaction and spatial distribution between rocky and sandy soil areas in a semi-arid savanna, South Africa. J. Arid Environ. 75, 270–278. https://doi.org/10.1016/j.jaridenv.2010.10.003.

Shackleton, C., 2002. Nearest-neighbour analysis and the prevelance of woody plant competition in South African savannas. Plant Ecol. 158, 65–76. https://doi.org/10.1023/A:1014795505362.

Shirima, D.D., et al., 2011. Carbon storage, structure and composition of miombo woodlands in Tanzania's Eastern arc mountains. Afr. J. Ecol. 49, 332–342.

Sileshi, G., Akinnifesi, F.K., Ajayi, O.C., Chakeredza, S., Kaonga, M., Matakala, P., 2007. Contributions of agroforestry to ecosystem services in the miombo eco-region of eastern and southern Africa. Afr. J. Environ. Sci. Technol. 1, 68–80.

Stoll, P., Bergius, E., 2005. Pattern and process: competition causes regular spacing of individuals within plant populations. J. Ecol. 93, 395–403. https://doi.org/10.1111/j.0022-0477.2005.00989.x.

Walker, S., 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. S. Afr. J. Wildl. Res. 6, 1–32.

Ward, D., 2005. Do we understand the causes of bush encroachment in African savannas? Afr. J. Range Forage Sci. 22, 101–105. https://doi.org/10.2989/10220110509485867.

Ward, D., 2009. The Biology of Deserts. Oxford University Press, Oxford.

Weiner, J., Thomas, S.C., 1992. Competition and allometry in three species of annual plants. Ecology 73, 648–656. https://doi.org/10.2307/1940771.

Wiegand, K., Jeltsch, F., Ward, D., 2000. Do spatial effects play a role in the spatial distribution of desert-dwelling Acacia raddiana? J. Veg. Sci. 11, 473–484. https://doi.org/10.2307/3246577.

Wiegand, K., Saltz, D., Ward, D., Levin, S.A., 2008. The role of size inequality in self-thinning: a pattern-oriented simulation model for arid savannas. Ecol. Model. 210, 431–445. https://doi.org/10.1016/j.ecolmodel.2007.08.027.

Wiegand, K., Ward, D., Saltz, D., 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. J. Veg. Sci. 16, 311–320. https://doi.org/10.1111/j.1654-1103.2005.tb02369.x.

Wiegand, T., Moloney, A.K., 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104, 209–229. https://doi.org/10.1111/j.0030-1299.2004.12497.x.

Wiegand, T., Moloney, K.A., 2013. Handbook of Spatial Point-Pattern Analysis in Ecology. CRC Press, New York.

Zinyowera, N.I., Ndagurwa, H.G.T., Muvengwi, J., 2021. Changes in miombo woody assemblage along a disturbance gradient in a smallholder tobacco production communal land, northeast Zimbabwe. For. Ecol. Manag. 502 (June), 119718. https://doi.org/10.1016/j.foreco.2021.119718.