

Small-Scale Spatial Patterns of *Copernicia alba* Morong near Bahia Negra, Paraguay

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ABSTRACT

We assessed the spatial distribution of *Copernicia alba* Morong. In the study area, a lowland palm savanna floodplain, *C. alba* is the only overstorey species. We hypothesized *C. alba* would be randomly distributed within natural stands. Palms were tallied in six randomly located 0.25 ha plots and analyzed using a first-order, Ripley's K function to assess the distribution of juvenile, adult, and total palm populations. While the total population had either aggregated or random distributions, when analyzing juvenile and adult population separately, we found juveniles were consistently more aggregated than the adults.

Keywords: Ripley's K-Function; First Order Analysis; Floodplain; Fire; Chaco; Monotypic Stands; Disturbance Ecology; Population Dynamics

1. Introduction

The spatial distribution of plant species is considered an important ecological subject as distribution results from and mediates complex ecological processes [1]. Studies of the spatial distribution of palms and trees may be purely descriptive, (this was especially true for the early theoretical development of spatial distribution models) [2,3]; they are designed to elicit the underlying ecological mechanisms for the patterns [4,5], or observe or infer changes in and the dynamics of spatial distribution over time [1,4,6]. Frequently studies contain elements from all three purposes; for example, it is the underlying ecological processes that may drive temporal changes in species distribution [1,7,8].

Ecologists have hypothesized that plant distribution may be based on seed dispersal patterns [4,9], underlying heterogeneity of local environment [1,10], competition or facilitation between plants—both within and between species [5-7,11], climate [12], and relative abundance of a species within the plant community [13]. Ecological factors influencing plant distributions may include moisture availability [14], soil heterogeneity [1,15], topography [16,17], inter-specific competition [18-22], and seed dispersal [11,23-25]. The plant's role in temporal succession, intraspecific competition, along with forest struc-

ture have also been explored as variables [22,26,27] specific to the plant rather than its environment and can be scale dependent [11].

Physical patterns within the landscape such as soil, moisture or topography may generate patterns that are dissimilar from the pattern that would develop in a more uniform landscape [28]. For example, seedlings and juveniles of *Borassus aethiopum*, an African savanna palm, are more aggregated than adults and the aggregated clusters tend to occur on sites with better nutrient status [1]. In general, spatial heterogeneity of resources [29,30] and species diversity [31] may increase aggregation. A single plant species may aggregate when growing in heterogeneous landscapes and in dense enough stands to generate competition between plants even when the pattern for all species combined is not aggregated [32].

Populations may have different distributions at different scales [2,5,11,13]. Plants may be aggregated at larger scales but plant competition generates a more regular pattern at smaller scales [3]. In the early stages of plant establishment species may benefit from the protection or the amelioration of soil properties provided by a more mature plant, fostering aggregation of plants. This is especially true in arid and semi-arid environments [6].

Skellam's [3] paper on theoretical random distributions of plants assumed an open environment, one recently disturbed so that initially there is no inter-specific

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competition and one where the plants' environment is uniform. Most studies of spatial distribution include more than one species and some form of spatial heterogeneity. For example, in a study of different tropical forests almost all species were aggregated and none were dispersed; however, the number of species in the forest ranged from 70 to over 800 [33]. Pillay and Ward's study [34] of the small woody tree *Acacia karroo* is an exception; all trees in their study plots were *Acacia karroo*. The purpose of our study was to examine the spatial distribution of *Copernicia alba* (Arecaceae) without the confounding influences of inter-specific overstory competition or a heterogenous environment. Our study location contained only one overstory species, *Copernicia alba*, and the study plots were located on uniform flat section of the Chaco of Paraguay near Bahía Negra, but distant from the Rio Paraguay. We used Ripley's K function as it allows for independent testing for random, aggregated or dispersed distribution at different scales. Our null hypothesis was that species would be randomly distributed at all measured scales.

2. Methods

2.1. The Gran Chaco Basin

The Chaco is part of a Pleistocene Epoch lake that deposited a thick layer of fine-grained sediment and poorly drained soils along the Chaco's northeastern edge [35,36]. Fire is a historically common disturbance agent in the dry and humid Chaco and throughout the neighboring Pantanal wetland [37,38]. The Paraguay River system supports a landscape of monotypic stands of naturally regenerated palm forest intermixed with riparian edges rich in species characteristic of the Brazilian Amazon, Cerado, and Humid Chaco [35,39-43].

2.2. The Study Area

The study area is located between the Pantanal wetlands and the Humid Chaco forest, approximately 13 km west of the Paraguay River, W20°04'5", S58°17'16", with elevations of 82 - 85 m. Temperature ranges from 12°C - 40°C with an average rainfall of 995 mm/year [44,45]. The rainy season is from September to April, with December and January having the greatest rainfall [45,46]. The dry season is from August to October when hot northerly winds and wild fires are more common [47]. The region has a return fire interval of one to five years. Key informants described the study area as being grazed in the 1970s by approximately 3000 cattle and palms were harvested until a major flood had forced owners to move to higher lands. The land is currently operated as a biological reserve maintained by Guyra Paraguay, a non-profit organization.

Plot locations were chosen randomly within the study

area and were located within 0.5 km of two focal points. Each plot was a 50 × 50 m quadrat. The plots are not replicates and statistical analysis was performed on each plot separately.

C. alba dominates both the overstory and the midstory throughout the study area. The understory is codominated by members of Poaceae and Fabaceae family (*Acacia* and *Albizia* genera). Members of the Verbenaceae, Asteraceae, and Apocynaceae families can also be found in the understory.

2.3. *Copernicia alba*

C. alba is 10 to 13 meters tall, with a maximum height of 25 m [48-51]. It is monoecious and generally does not produce flowers or seeds until it reaches at least 3 m in height [52,53]. *C. alba* blooms between the months of August to October [46,53,54]. Fruits are 1.0 to 1.5 cm in diameter [50,55]. The rachises that carry seeds grow from the center of the crown and can range from 0.5 m to 2 m in length. Fruit are produced irregularly throughout the seasons and the majority of individuals drops their seed fruits in the late dry season (winter) with the onset of sporadic rainfalls, strong northern winds, and fire season [46,54]. In the open canopied savanna *C. alba* is exposed to strong winds that could aid in dislodging the light fruits [56]. *C. alba*'s role with many of the endangered fauna and migratory birds has received limited study. Birds, small rodents, and native herbivores such as the greater rhea (*Rhea Americana*) and white-lipped peccary (*Tayassu pecari*) could play a role in dispersing seed [4,53,56,57]. Other studies have shown that herbivory may increase aggregation [4] or lead to a more regular dispersion, especially in more diverse plant communities [58]. The corky vascular meristems of palms make them resistant to most savanna fires while secondary adventitious roots sustain the palm in times of flooding [11].

Copernicia alba Morong has been documented from latitudes 14°S to 27°S and longitudes 56°03'W to 66°00'W, along the Pilcomayo and Paraguay Rivers. Mature palms occupy the overstory in both forest and grassland habitats. Within forests, *C. alba* can codominate the overstory and midstories. Throughout the Chaco *C. alba* is associated with planar alluvial flood zones that cycle between floods and long periods of drought [46, 53,59-61].

2.4. Study Design

A preliminary trip to the savanna was made in April of 2010 and the first dataset was collected from Plots 1 - 3 during the middle of the dry season (winter) 2010. Field measurements for Plots 4 - 6 were taken during the end of a light drought in November, 2010.

Within each plot all palms with a stem height of at

least 1 m were located using a handheld global positioning system (GPS) (Garmin Etrex, Garmin Ltd., Kansas, USA). Several sets of ground-truthed points showed that the measurements were accurate within 1 to 2 m. Diameter at breast height (DBH) was recorded only for palms of at least 1.5 m in height and lacking thick petiole sheaths which would bias diameter measurements. Any palms completely defoliated or showing signs of stem damage were included in the data set, however dead palms were excluded. We define juveniles in this study as having established stem heights greater than or equal to 1.0 m and less than 3.5 m. Adults have stem heights greater than or equal to 3.5 m. Heights do not include crowns, but were measured to the stem apex. The hypsometer technique was used to measure the heights of palms greater than or equal to 5 m while the height of shorter palms were measured directly using a flagged pole that was 3 m in height. Herbarium samples were submitted to Universidad Nacional de Asunción to assist in identification.

2.5. Data Analysis

The transformed Ripley's K function, $L(r)$, tests for complete spatial randomness in the distribution of palms (*i.e.*, to test if the observed palm locations are distributed via a homogenous Poisson process [62]) by determining the expected and observed number of palms within the radius, r , of each palm within the sample plots. The transformed Ripley's K function, which was calculated using the Spatstat package [63] in the R statistical software package [64], was used to determine the spatial distribution of the total palms population with stems greater than or equal to 1 m in height [63]. After analyzing the total palm population with the transformed Ripley's K function, the palms were separated into adult (stem height greater than 3.5 m) and juvenile classes (stem height less than 3.5 m) [52,53]. The juvenile and adult populations were then analyzed using the Ripley's K function.

The three palm populations (total, juvenile, and adult), were analyzed in each of the six plots, yielding 18 different graphs of the transformed Ripley's K function. The null hypothesis for all 18 calculation sets was that the spatial distribution of the given population followed complete spatial randomness (*i.e.*, it follows a homogenous Poisson process). The alternative hypothesis was that patterns were either aggregated or dispersed (dispersed is sometimes described as uniform, regular or repulsed).

3. Results

A total of 363 palms were sampled in the six plots. The palms/ha, basal area, stand structure (juvenile: adult ratio), and the mean height varied considerably from plot

to plot (**Table 1**) [65]. Plot 1 had the largest number of juveniles (43), and Plot 2 has the smallest with 14 individuals. Plot 4 had the largest number of adults (51). Plots 3 and 6 had approximately 1:1 ratios of adults to juveniles (**Table 1**). Basal area and palm densities varied among the six plots (**Table 1**). Plot 4 has the highest basal area and palm densities, with 63% of the population represented by adult palms.

3.1. Total Palms Population

The theoretical (under the hypothesis of complete spatial randomness) and observed distribution of palms were generated using the transformed Ripley's K function and plotted for all palms. The transformed Ripley's K function, $L(r)$, was calculated for each radius, r , based on the observed data in each of the six plots. The transformed Ripley's K function allows assessment of patterns at different radii or local scales, ranging from 0 to 12 m within the 50 m \times 50 m plots. The calculation of $L(r)$ generates values of $L(r)$ for each radial distance, r , that are independent of one another and independent of palm density. Each graph shows a straight line passing through the origin that represents theoretical $L(r)$ if the distribution of palms was generated via a homogenous Poisson process (*i.e.*, they follow a complete spatial random pattern). Thirty-nine Monte Carlo simulations were calculated to generate confidence envelopes (shown in gray in the figures) with a significance level of $\alpha = 0.05$ [64,66]. When the observed $L(r)$ value is greater than the theoretical $L(r)$ and lies above of the gray 95% confidence envelope, the null hypothesis of complete spatial randomness is rejected, and the pattern is considered aggregated. When the observed $L(r)$ is less than the theoretical $L(r)$ and below the 95% confidence envelope, the null hypothesis of complete spatial randomness is again rejected, and the pattern is considered dispersed.

When Ripley's K function was calculated for palms with a stem height greater than 1 m, aggregation and spatial randomness were not consistent across all six plots. Both aggregated and spatially random distributions were found at various scales (*i.e.*, r values) in Plots 1, 2, 5, and

Table 1. Univariate statistics for palm populations on each plot.

Plot	Palms/ha	Basal Area* (m ² /ha)	Juvenile: Adult	Mean Height (m)
1	248	3.42	2.3:1.0	2.8
2	216	3.02	0.4:1.0	7.2
3	252	2.37	0.9:1.0	5.5
4	320	4.89	0.6:1.0	4.7
5	220	1.73	1.6:1.0	3.6
6	196	2.52	1.0:1.0	4.0

*Basal area does not include palms less than 1.5 m in height.

6 (Figures 1(a), (b), (e), and (f) respectively). Plots 3 and 4 had spatially random distributions at all scales (Figures 1(c), (d)). Plot 3 patterns fluctuated above and below the theoretical line for a spatially random distribution while Plot 4 exhibited random patterns with patterns of aggregation at all scales.

3.2. Juveniles and Adults

When the data set was separated by developmental classes, juveniles tended to aggregate while adults were more randomly distributed. This occurred in Plots 1 (Figures 2(a), 3(a)), 4 (Figures 2(d), 3(d)), and 5 (Figures 2(e), 3(e)). For Plots 3 (Figures 2(c), 3(c)) and 6 (Figures 2(f), 3(f)) both juveniles and adults were randomly distributed; however, the adults had lower $L(r)$ values than the juvenile populations for most scales. Plot 2 (Figures 2(b), 3(b)) was the exception with aggregated adult palms from 6 to 12 meters radius and aggregated juvenile palms when the radius was less than 9 meters; otherwise palms were randomly distributed. The juveniles of Plot 2 (Figure 3(b)) have higher $L(r)$ values than the adults from 2 to 12 m. Most adult aggregation in this plot was caused by two linear groups of palms.

In Plot 1 (Figure 3(a)) aggregation was observed among juveniles at distances from 2 m to 12 m and adults were randomly distributed at distances 0 to 12 m. This plot had the greatest number of juveniles and the lowest number of adults of all six plots (Table 1).

The same basic pattern, where juveniles were aggregated while adults were randomly distributed, was found in Plots 4 and 5 at distances 2 m to 10 m. In Plots 2, 3, and 6 some juveniles were randomly distributed and some adults were aggregated. In plot 2, adults were aggregated at 9 to 12 m (Figure 2(b)). Plot 3 juveniles had $L(r)$ values above theoretical random line at radii up to 6.5 meters, exhibiting random and aggregated patterns over the range (Figure 3(c)). The adults, on the other hand, had $L(r)$ values close to the expected values for a randomly distributed population. Plot 6 juveniles exhibited $L(r)$ values greater than expected $L(r)$ values at 1 to 12 m (Figure 3(f)).

The total palm population exhibited a spatially random distribution in three plots and an aggregated distribution in the other three plots (Figure 1). A consistent shift from aggregated juveniles to less aggregated adults was found among all six plots. The shift among juveniles and

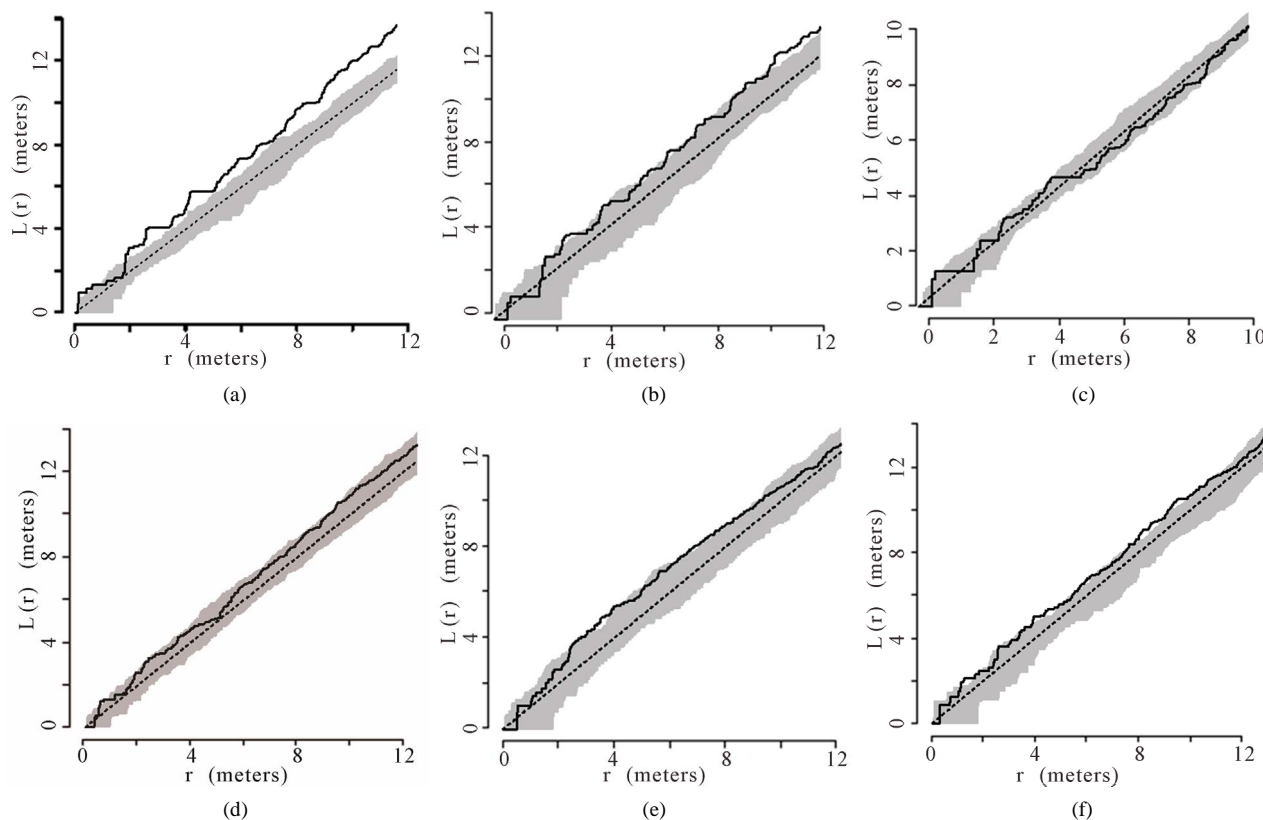


Figure 1. (a)-(f) for Plots 1 - 6 respectively. Transformed Ripley's K function, $L(r)$, with dashed line indicating theoretical complete spatial randomness and solid line indicating calculated $L(r)$ for all palm trees in each plot. Shaded area represents the 95% confidence envelope. When the calculated $L(r)$ is within the confidence envelope the palms are randomly distributed. When the calculated $L(r)$ is above the confidence envelope the palms are aggregated. When the calculated $L(r)$ is below the confidence envelope the palms are dispersed.

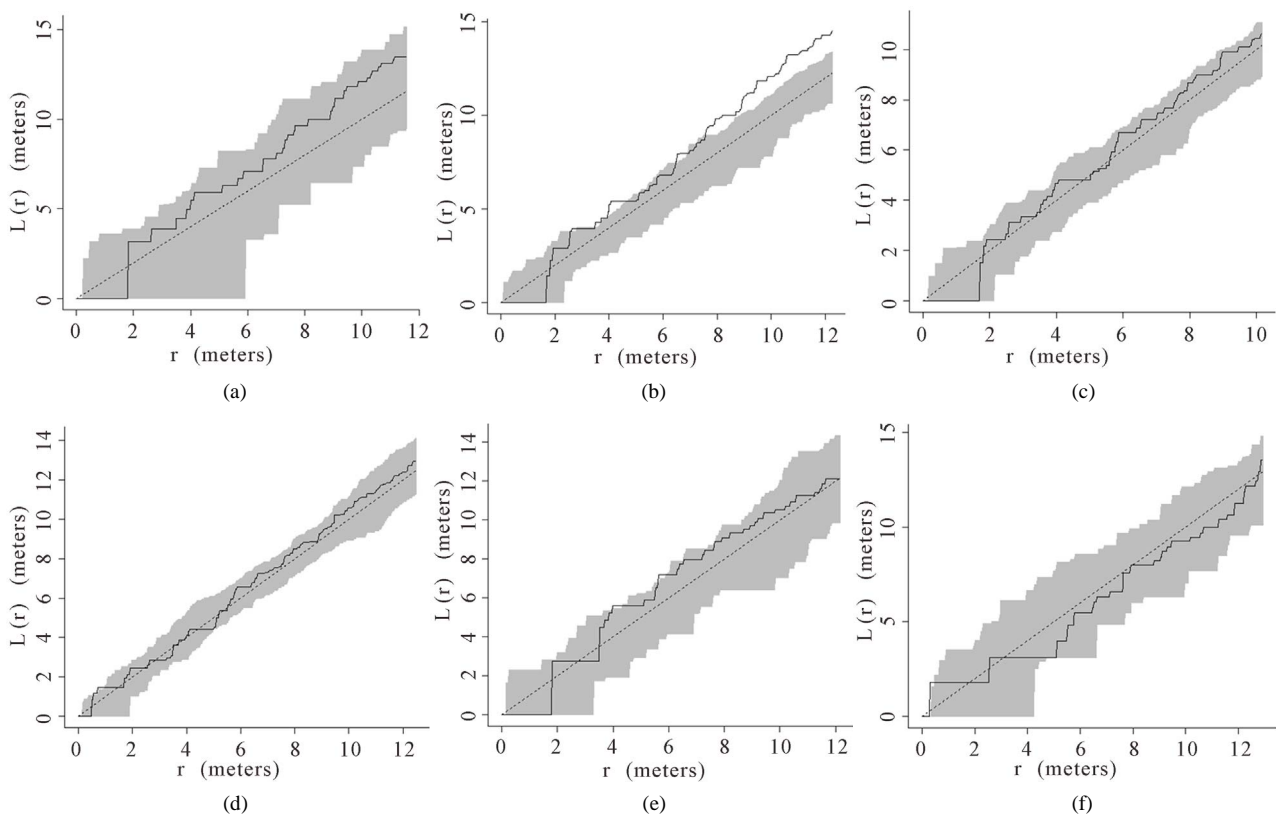


Figure 2. (a)-(f) for Plots 1 - 6 respectively. Transformed Ripley's K function, $L(r)$, with dashed line indicating theoretical complete spatial randomness and solid line indicating calculated $L(r)$ for adult palm trees in each plot. Shaded area represents the 95% confidence envelope. When the calculated $L(r)$ is within the confidence envelope the palms are randomly distributed. When the calculated $L(r)$ is above the confidence envelope the palms are aggregated. When the calculated $L(r)$ is below the confidence envelope the palms are dispersed.

adults populations was found despite differences in density, juvenile:adult ratios (**Table 1**) and the resulting structure among plots.

4. Discussion

Our comparison of total palms and then the palm population disaggregated into juvenile and adult populations indicates that aggregation patterns may change for different age cohorts within a stand. The shift from aggregated juvenile populations to less aggregated adult populations has also been found in other palm species, both in savanna and montane rain forests [1,26], in other tree species [13,20,23,25,67] and dominant shrubs [68]. However, other studies have used either adults [4,29] or different life stages but confounded by environmental heterogeneity [1] or the interaction with other species [13,29,32]. Pillay and Ward [34] also surveyed both juveniles and adults, although of woody semi-arid species, and found both juveniles and adults were aggregated. Our study avoided confounding aspects of topography and stand heterogeneity. Its location also contributed to an understanding of the Chaco, a relatively poorly studied and underappreciated environment.

Studies suggest that younger or juvenile plants tend to aggregate [6,32,34]. Aggregation within juvenile populations and random distribution among adults could be a product of intraspecific and inter-specific competition. As juveniles compete for resources with other young palms in small areas, higher rates of mortality may result. Water availability and soil nutrients can be important in driving spatial plant patterns [1,15,69]. Small scale juvenile aggregation could also reflect limited seed dispersal [1,13,21,25,26,28,70]. Wind patterns can determine the distance and direction of seed dispersal. Likewise, small rodents, bats, and birds distribute seeds at varying distances, altering spatial patterns [4,71]. As with other studies we find that aggregation varies with scale [5, 6,34].

5. Conclusions

Using the transformed Ripley's K function we observed a consistent pattern of aggregation in younger palms to a more spatially random pattern among adult palms. Our study site eliminated both competing dominant species and topographical variation as confounding elements in the study. The exploratory nature of the study did not

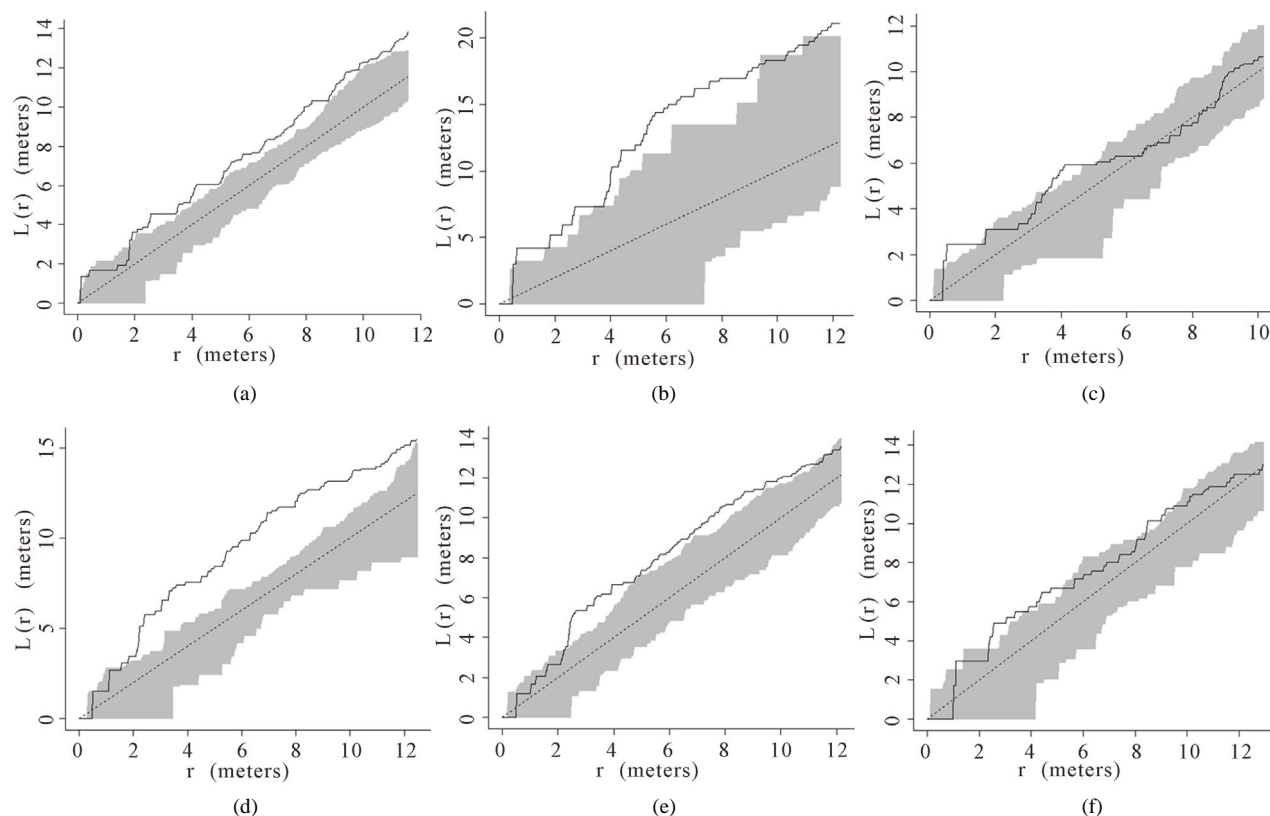


Figure 3. (a)-(f) for Plots 1 - 6 respectively. Transformed Ripley's K function, $L(r)$, with dashed line indicating theoretical complete spatial randomness and solid line indicating calculated $L(r)$ for juvenile palm trees in each plot. Shaded area represents the 95% confidence envelope. When the calculated $L(r)$ is within the confidence envelope the palms are randomly distributed. When the calculated $L(r)$ is above the confidence envelope the palms are aggregated. When the calculated $L(r)$ is below the confidence envelope the palms are dispersed.

allow us to determine underlying ecological drivers for the change in patterns. Future studies addressing the influence of fire, limited nutrient and water resources, and seed dispersal could help understand the mechanisms causing juveniles to aggregate and adults to be more randomly distributed. Long-term studies could lead to an understanding of palm savanna succession and how the plant communities are changing in response to fire and current climatic conditions.

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