Research Article

Spatial patterns of a savanna palm tree *Borassus aethiopum* and its temporal variability

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Abstract

The spatial distributions and associations of plant species in a stand can provide essential information about their dynamics. However, since tree spatial distribution and association depend on factors that operate at different scales, disentangling the effects of environmental heterogeneity and plant–plant interactions requires the choice of a suitable null model for spatial analysis. We analyzed the spatial distributions of the same savanna palm tree populations that were studied, the underlying hypothesis being that these distributions have changed in 20 years. To remove the effect of large-scale environmental heterogeneity, the inhomogeneous *L*-function under the heterogeneous Poisson null model was used. We showed: (i) unlike 20 years ago, adults had a regular distribution instead of an aggregated distribution in the grass savanna; (ii) although the spatial distribution of seedlings and juveniles was always aggregated, we observed a decrease in the size of the aggregates (intensities); (iii) except for juveniles, no other stages were associated with nutrient-rich patches, which was also different 20 years ago; (iv) we did not observe any particular difference in structure between two study sites, only that female palm trees were spatially associated with entire-leafed seedlings in the reserve while they were spatially independent in the rural area. Our study supports the hypothesis that the spatial distributions have partially changed, and that the management of spatial heterogeneity has improved and given more precision in the results.

Keywords spatial heterogeneity, palm trees, heterogeneous Poisson (HP) null model, spatial distribution, spatial association, Lamto reserve

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热带草原棕榈树的空间格局及其时间变异性

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摘要：物种的空间分布和关联可以提供林分的基本信息及动态。然而，由于树木的空间分布和关联依赖于不同尺度下的环境因子，要弄清环境异质性和植物间相互作用的影响，需要选择合适的空间模型进行分析。本研究分析了同一热带草原棕榈树的种群空间分布，并假设这些分布在20年内发生了变化。为了消除大规模环境异质性的影响，采用异质性泊松零模型下的非均质L-函数。研究结果发现：(i)与20年前不同，稀树草原地区的成年树种呈规则分布而非聚集分布；(ii)虽然幼苗和幼树的空间分布总是呈聚

集状，但聚集区域面积（强度）在减少；(iii)除幼树期，其它阶段均与富养斑块无关联，这也与20年前不同；(iv)没有两个研究地点在结构上有特别的差异，只是雌性棕榈树在空间上与保护区的整叶幼苗有关联，而在乡村，它们在空间上是相互独立的。我们的研究证明，空间分布发生了部分变化，同时对空间异质性的管理也更加完善，模拟结果也更精确。

关键词：空间异质性，棕榈树，异质性泊松零模型，空间分布，空间关联，Lamto保护区

Graphical Abstract
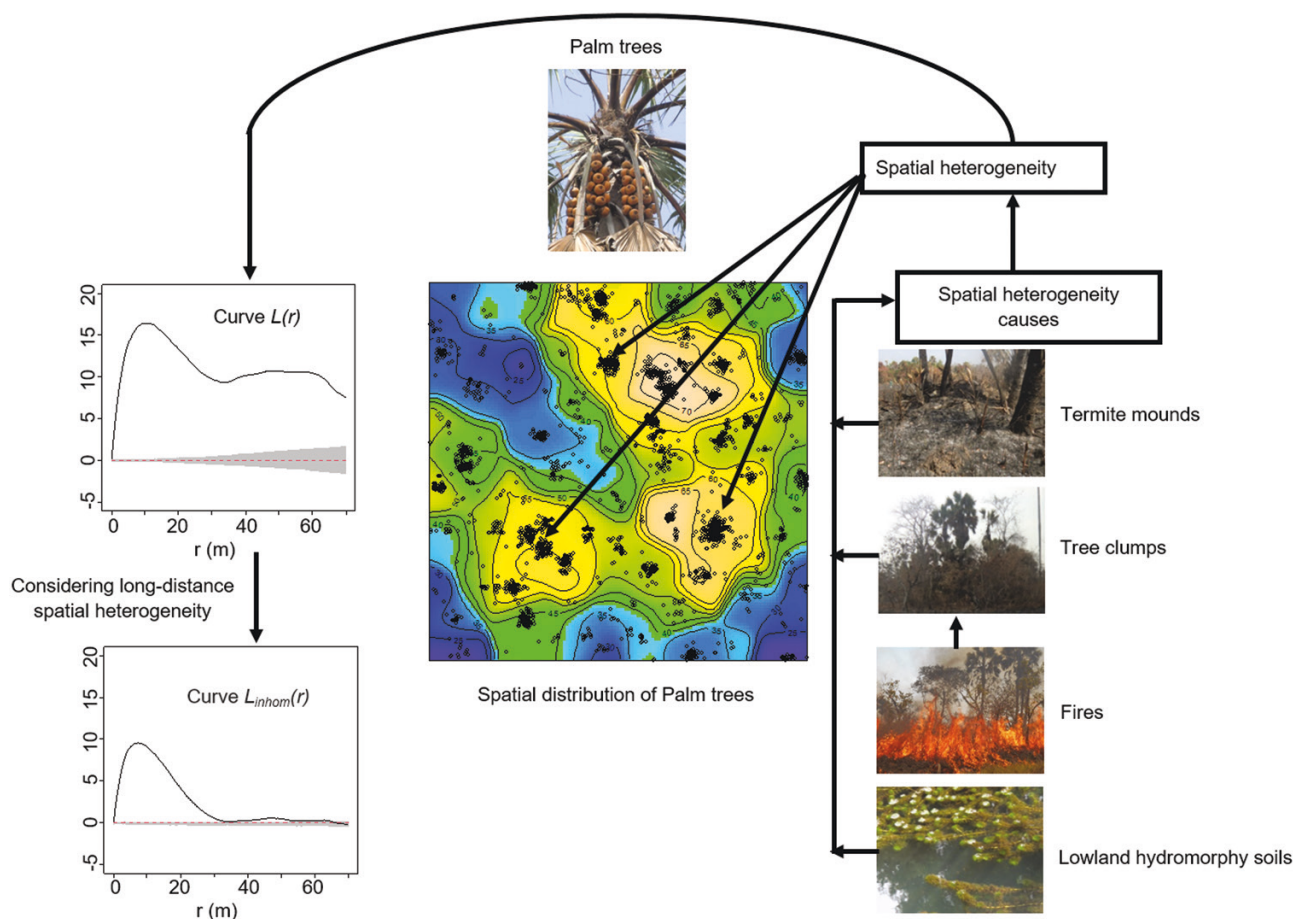
INTRODUCTION

Over the past two decades, the study of spatial patterns of plant populations has been recognized as essential to understand their demography, interactions between demography and environmental heterogeneity and interactions between plant individuals (Cheng *et al.* 2014; Wang *et al.* 2018). Indeed, these patterns of spatial distribution and association can significantly affect plant demography and, conversely, this demography impacts these spatial patterns (Barot and Gignoux 2003; Barot *et al.* 1999a).

Ecologists study the spatial patterns of plant populations at different life stages to deduce the underlying processes generating these patterns and to identify the scale at which these processes work for each stage (Cheng *et al.* 2014). Demographic processes can induce recognizable spatial structures. For example, competition between individuals tend to lead to regular distribution while the existence of favourable patches, where survival is high or poor dispersal abilities tend to lead to aggregated distributions. Conversely, the spatial structure of an ecosystem and the spatial distribution of the plants

play a key role in their dynamics and demographic processes at each stage of the life cycle. For example, the aggregation of young individuals due to their small size and their high densities may lead to intense competition between them, which would not be the case if they were randomly distributed and which is no longer the case at the adult stage because adult densities are much lower. Such spatial structures can be studied statistically using spatial analysis (Baddeley 2008).

To understand such complex feedbacks between demography and spatial patterns, we studied in the Lamto savanna (Ivory Coast) the *Borassus aethiopum*, a dioic and heliophile palm tree species growing naturally in many African savannas (Zongo *et al.* 2018). Our goal was twofold. We first wanted to deduce scenarios of links between demographic processes, spatial distribution and environmental heterogeneity using this palm tree as a model. We also wanted to compare our results to those of Barot *et al.* (1999a) who studied extensively the spatial distribution of the same species in the same savanna. This allowed us to test whether the spatial distributions of this palm tree have changed over time, such a temporal comparison of the spatial distributions of a plant species has almost never been achieved. The spatial distribution of palms may have changed because 20 years ago the population was not spatially balanced. In fact, it was close to demographic equilibrium (Barot *et al.* 2000), but this was not necessarily the case for its spatial distribution. For example, the high spatial aggregation of juveniles on termite mounds may have been due to the palm fruit dispersers, elephants and baboons, that disappeared in 1966 and 1969, respectively (Bourliere *et al.* 1974). The demographic parameters themselves (survival, fertility, etc.) may have changed due to climatic trends and changes in the intensity of the annual fire that burns the savanna in January. Fire is an important factor that strongly influences the structure and dynamics of savannas (Jung *et al.* 2010). In Guinean savannas, rainfall favours the production of a large biomass (Gignoux *et al.* 2006), resulting in more intense fires with higher flames that may reduce the recruitment of trees (N'Dri *et al.* 2018) and increase their mortality. The climatic series reveal a decrease in rainfall events, as well as an increase in temperatures and evaporation in Lamto (Bigot *et al.* 2004) and West Africa in general (Gemenne *et al.* 2017) in recent decades. This could have led to an increase or decrease in the survival of the palm trees.

To achieve these goals, as achieved by Barot *et al.* (1999a), we mapped all individual palm trees, whatever their stage, as well as the main sources of environmental heterogeneity, on 27.75 ha of savanna (including three plots within Lamto reserve and one plot outside). For palm trees, apart from other palm trees, the most influential sources of heterogeneity are trees and termite mounds. Both trees and mounds (Gignoux *et al.* 2006; Mordelet *et al.* 1996) are considered as nutrient-rich patches, whereas the soils of Lamto savanna are overall very nutrient-poor. As Barot *et al.* (1999a), we analysed extensively the spatial distribution of palm trees of all stages, as well as the spatial association between these stages, and between palm trees and sources of heterogeneity. While Barot *et al.* used Ripley's *K*-function (1981), we used its transformation *L*. This has the advantage of stabilizing the variance, therefore providing easier interpretation. More precisely, and unlike Barot *et al.* (1999a), we used the procedure (L_{inhom}) allowing to remove from the *L*-function, the effect of large-scale heterogeneity, such as environmental gradients at the scale of the mapped plot (Baddeley 2008). In turn, this should enable to better focus on the small-scale patterns (aggregates of individuals of a few metres, up to 10 m, in diameter, regular distributions with a distance of a few metres between individuals). We indeed want to emphasize patterns linked to demographic processes.

Barot *et al.* showed that juvenile palms and seedlings were aggregated while adults had a random distribution or were less aggregated. All stages of palm trees, except adult females, were spatially associated with nutrient-rich patches, but association distances increased with the stage of the life cycle. The seedlings were associated with females, while juveniles were not or were associated at longer distances. To guide the interpretation of our own spatial analyses, we hypothesize that: (i) The spatial distributions of palm tree in the Lamto reserve have changed since 1997. More, specifically, we hypothesize that disappearance of fruit dispersers for a longer period has led to a lower aggregation of juveniles in nutrient-rich patches. (ii) The spatial distributions and associations of palm tree in the Lamto reserve are different from those the outside reserve area. Anthropogenic disturbances prevent the aggregation of palm trees. (iii) The use of the heterogeneous Poisson (HP) model is an efficient strategy to detect small-scale spatial patterns and removing the effect of large-scale environmental heterogeneity allows to better emphasize small-scale spatial heterogeneity.

MATERIALS AND METHODS

Study site

The study was conducted in the Lamto reserve (central Ivory Coast, extending from 6°9′ N to 6°13′ N, and from −5°15′ W to −4°57′ W) and in a rural area next to the reserve. With an area of 2617 ha, the Lamto reserve is located at 160 km northwest of Abidjan, in the extreme south of the 'V Baoulé' (advanced area of the savannah in the rainforest). The climate is humid and intertropical (Le Roux 2006). The monthly rainfall ranged from 25.1 to 202.5 mm over the 20 years preceding our field work. The average annually rainfall was about 1222.3 mm over the past two decades with an average annually temperature of 28.50 °C. Three different savanna types can be distinguished according to their tree cover (Gautier 1990). (i) The grass savanna (GS) dominated by the perennial grass *Loudetia simplex* (Nees) C. E. Hubbard (tree cover 7%). It is characterized by hydromorphic sandy soils, which are saturated with water and with a low tree cover (lower than 7%). These soils inhibit the recruitment of trees and palm trees, except on termite mounds and a few metres around the termite mounds. In this type of savanna, temporary ponds appear during the rainy season. (ii) The tree savanna (TS) dominated by the grasses *Hyparrhenia diplanda* and *Andropogon* sp. It is characterized by an intermediate tree cover (between 7% and 62%). (iii) Savanna woodland (SW) are characterized by high tree cover (higher than 62%). These savannas have lower fire intensities, due to reduced grass biomass and fuel load under trees (N'Dri *et al.* 2014). Overall, more than 90% of the tree community is made up of four species: *Bridelia ferruginea*, *Crossopteryx febrifuga*, *Cussonia barteri* and *Piliostigma thonningii* (Menaut and César 1979). The higher trees are about 20 m high. But all facies are dominated by the palm trees (*Borassus aethiopum*), that are the tallest plants in these savannas (Barot *et al.* 1999a). Many termite mounds, ranging in diameter from 0.5 to 5 m, are dispersed in all types of savanna (Abbadie *et al.* 1992). These mounds are not aboveground termitaria *per se* but have been rather built by the cumulative activities of different termite species building both aboveground and belowground nests (Konaté *et al.* 1999). Fire occurs every year and burns only the grass layer and young trees below 2 m high (Barot *et al.* 1999a; N'Dri *et al.* 2014).

The species studied, *B. aethiopum* is a common dioecious palm common in many African savannas.

Four main life stages were distinguished (Barot *et al.* 2000): entire-leafed seedlings (P1) have one or two elongated entire leaves, slit-leafed seedlings (P2) have one or two leaves that are slit a few times, juveniles (J) that bear fan-shaped leaves but do not reproduce, and adults (A) (Fig. 1).

Data collection

Four plots were chosen across three different savanna types, including three plots in the Lamto reserve and one plot in a rural area not far from the reserve. Within the reserve two former plots (SW and GS) of Barot *et al.* (1999a) were chosen and enlarged. The three plots of the reserve consist of: (i) a 300 m × 300 m plot of SW; (ii) a 300 m × 250 m plot of TS (TS1) and (iii) a 250 m × 300 m plot of GS. The 250 m × 150 m rural area plot was set in a TS (TS2). All palm trees, trees and termite mounds were mapped (Fig. 2) in 2016. Cartesian coordinates (*x, y*) within 50 m × 50 m quadrats were measured using the distance from each mapped element to two different stakes materializing the quadrat. These distances were measured using a laser rangefinder GLM 250 VF Bosch Professional. The four plots had different palm densities (Table 1).

Spatial distribution analysis

For a spatial distribution of points, the analog of the average or expected value of a random variable is the intensity of a point process (the average density of points). In general, the intensity of a point process varies from place to place because ecological processes are highly dependent on the local environment (soil, topography, etc). Therefore, the study of intensity should be one of the first steps in analysing a point model before studying interaction between points (Baddeley 2008). This heterogeneity (intensity) was assessed using the density map and the *L*-function across the complete spatial randomness (CSR) (Pélissier and Goreaud 2001). The intensity study (preliminary results) confirmed that the palm distribution was heterogeneous at a scale of approximately 60 m in most plots (Supplementary Fig. S1). To avoid misinterpretation of results due to the heterogeneity environmental we used the $K(r)$-function for inhomogeneous point patterns (Baddeley *et al.* 2000) across the HP null model, $K_{inhom}(r)$, i.e. based on local estimates of the intensity. We computed the intensity function $\lambda(x, y)$ non-parametrically, applying the Epanechnikov kernel estimators (Wiegand *et al.* 2007) using a 20 m radius for seedling and juvenile palms and 50 m radius
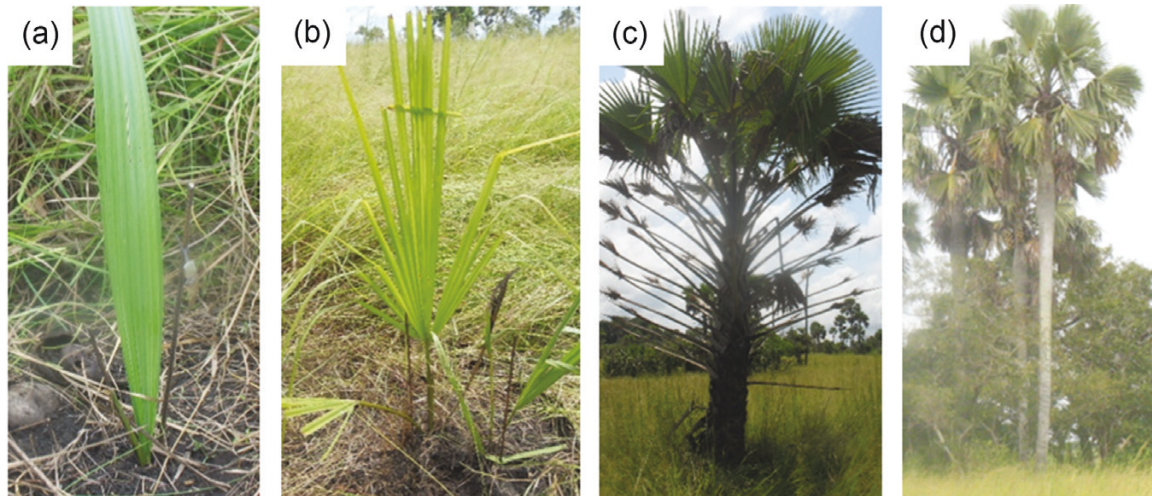
Figure 1: The four development stages of *Borassus aethiopum* Mart. (**a**) Entire-leafed seedlings, (**b**) slit-leafed seedlings, (**c**) juveniles and (**d**) adults.

for adult palms for the moving window estimator (Supplementary Fig. S1).

Spatial distribution of a single point type

The spatial distribution analysis was carried out using the L_{inhom} function (Besag and Diggle 1977). This function is an analogue of K_{inhom} of Ripley's $K(r)$ function (Ripley 1981). Ripley's $K(r)$ function is defined as the observed number of points within distance r of an arbitrary point divided by the intensity λ where λ is the intensity of the pattern in the study area (Ripley 1981). The $K(r)$ function is defined as:

$$K(r) = \frac{1}{A} \sum_{i=1}^{n} \sum_{j \neq i} \frac{w_{ij}}{\lambda^2} I(d_{ij} < r)$$

In this function, A denotes the area of the plot, λ is tree density, w_{ij} is an edge-correction term, d_{ij} represents the distance between two points and I is an index function where $I = 1$, if $d_{ij} \leq r$, and $I = 0$ otherwise (Ripley 1981). Tree density, λ, is the parameter to be estimated in this model. The estimator of the $L_{\text{inhom}}(r)$ function is:

$$L_{\text{inhom}}(r) = \sqrt{\frac{K_{\text{inhom}}(r)}{\pi}} - r$$

The $L_{\text{inhom}}(r)$ function is generally preferred to the $K_{\text{inhom}}(r)$ function because it has the advantage of stabilizing the variance, providing easier interpretation (Ripley 1981). In fact, under the heterogeneous null hypothesis, $L_{\text{inhom}}(r) = 0$; values of $L_{\text{inhom}}(r) < 0$ indicate that there are fewer neighbours at distance r from an arbitrary point in the spatial distribution than under the null hypothesis, so

that the distribution tends to be regular; values of $L_{\text{inhom}}(r) > 0$ indicate that there are more neighbours at distance r from an arbitrary point in the spatial distribution than under the null hypothesis, so that the distribution tends to be aggregated.

Spatial association between two point types

The intertype $K_{1.2}(r)$ function is a bivariate extension of Ripley's $K(r)$ function. While Ripley's $K(r)$ function characterizes the spatial structure of a univariate pattern at various scales, the intertype $K_{1.2}(r)$ function characterizes the spatial structure of a bivariate pattern, and more precisely the spatial relationship between two types of points located in the same study area. The intertype $K_{1.2}(r)$ function is defined so that $\lambda_2 K_{1.2}(r)$ is the observed number of type 2 points in a circle of radius r centred on an arbitrary type 1 point of the pattern. Symmetrically, we can define an intertype $K_{2.1}(r)$ function so that $\lambda_1 K_{2.1}(r)$ is the expected number of type 1 points in a circle of radius r centred on an arbitrary type 2 point. The intensity parameters λ_1 and λ_2 correspond to the observed numbers of type 1 and type 2 points per unit area, respectively. In order to interpret the observed values of $K_{1.2}(r)$ or $L_{1.2}(r)$, the null hypothesis of independence was used (Diggle 1983; Goreaud and Pélissier 2003; Wiegand and Moloney 2004). The null hypothesis of independence was used because the two types of points correspond to two populations whose specific spatial pattern can a priori be the result of different processes (for instance plants of various species or individuals of different cohorts), then the observed absence
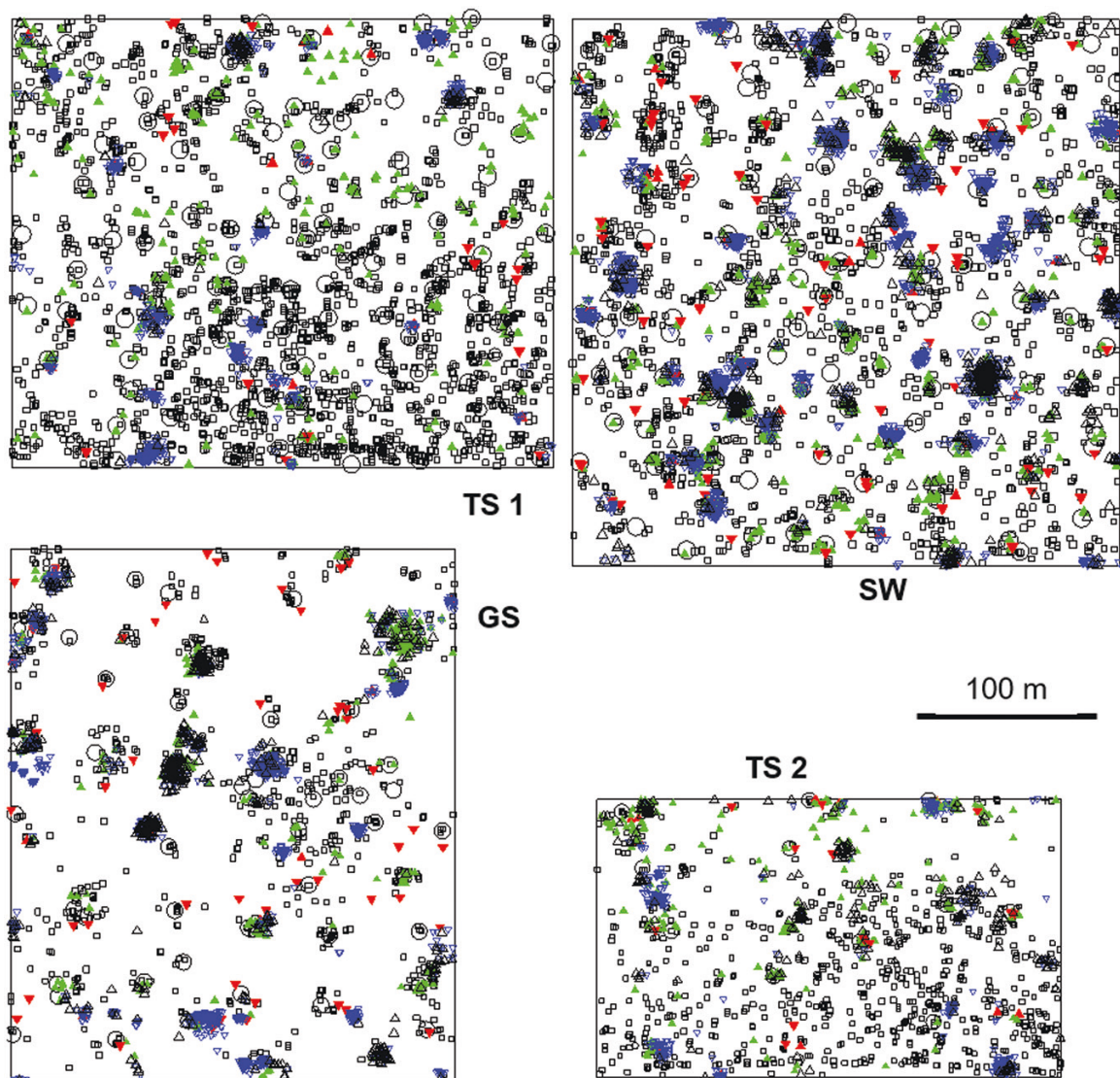
Mounds are classified according to their radius : ∘○◯ (1-3 m, 3-5 m, > 5 m, respectively) ; ▫, all trees. Palm trees are classified as follows : ▽, entire-leafed seedlings ; △, slit-leafed seedlings ; ▲, juveniles ; ▼, males ; ▲, females.

Figure 2: Maps of the four plots: GS, SW, TS1 (reserve), TS2 (rural area).

Table 1: Densities (number of individuals ha⁻¹) of the various mapped elements

Plots[a]	Area (ha)	Entire-leafed seedlings	Slit-leafed seedlings	Juveniles	Adults	All palm	Trees	Termite mounds
TS1	7.5	127.5	14	29.3	5.6	176.4	263.7	14.5
TS2	3.75	96.3	54.9	50.4	6.1	207.7	192.8	4.0
SW	9	302.8	76.1	49.6	13.4	440.6	203.5	6.9
GS	7.5	198.1	66.5	31.2	9.2	305.1	88.3	16.3

[a]Lamto reserve: TS1, SW and GS; rural area: TS2.

of interaction between the two types of points corresponds to an absence of interaction between the two populations. The estimator of the $L_{inhom1.2}(r)$ function is:

$$L_{inhom1.2}(r) = \sqrt{\frac{K_{inhom1.2}(r)}{\pi}} - r$$

Under the null hypothesis of independence of the two point distributions, $L_{inhom1.2}(r) = 0$. Values of $L_{inhom1.2}(r) > 0$ indicate that there are on average more type 2 points at distance r from type 1 points than would be observed under the independence assumption, indicating a positive spatial association (or spatial attraction) between the two types of points. Conversely, values of $L_{inhom1.2}(r) < 0$ indicate a repulsion effect (a negative spatial association) between the two point types up to distance r.

The 95% confidence envelopes were computed from 999 Monte Carlo simulations (Wiegand and Moloney 2004).

RESULTS

Density of sampled items

A total of 8355 palm trees were mapped (Table 1), with an average density of 301 individuals ha⁻¹. The number of individuals per stage was: 5496 entire-leafed seedlings (P1); 1515 slit-leafed seedlings (P2); 1089 juveniles (J) and 255 adults (A) including 102 females and 153 males. A total of 4885 trees were sampled: 788 individuals between 0 and 1 m tall, 698 individuals between 1 and 2 m tall and 3399 individuals over 2 m high. Finally, 298 termite mounds were mapped. The density of palm trees and termite mounds was higher in the reserve (307.4 individuals ha⁻¹ and 12.5 mounds ha⁻¹, respectively), than in the rural area (207.7 individuals ha⁻¹ and 4 mounds ha⁻¹, respectively). However, tree density was lower in the reserve plots (185.1 individuals ha⁻¹) than in the rural area plot (192.8 individuals ha⁻¹).

Spatial distributions

Spatial distributions of palm trees

For all spatial distribution analyses, the $L_{inhom}(r)$ function and the corresponding density maps were displayed in Fig. 3; Supplementary Fig. S2. Statistical results are summed up in Table 2. The entire-leafed (P1) and slit-leafed (P2) seedlings of the four plots had an aggregated spatial distribution over most of the analysis distances. Their $L_{inhom}(r)$ curve showed

marked positive peaks at around 10 m indicating that the average radius of these aggregates was about 10 m (Fig. 3; Supplementary Fig. S2). However, for plot TS1, the negative values, under the confidence envelope, highlighted the regularity of the spacing of the aggregates of slit-leafed seedlings at large distances (50 m, Fig. 3). Juvenile individuals (J) had an aggregate spatial distribution in all plots. This aggregate spatial distribution of juveniles extended to scales of (0–46, 0–42, 0–40 and 0–25 m), respectively, for plots (TS1, SW, GS and TS2, Fig. 3; Supplementary Fig. S2). Their $L_{inhom}(r)$ curve showed marked positive peaks at around 10 and 8 m, respectively (the reserve and rural area plots). Adult palms showed random spatial distributions in plot TS1, SW and TS2 while they had a regular spatial distribution in the GS plot (Fig. 3, Supplementary Fig. S2; Table 2). Female and male palms had a random spatial distribution regardless of the plot (Table 2).

Spatial distribution of trees and termite mounds

Analyses revealed an aggregate spatial distribution of trees. This spatial distribution was aggregated over all analysis distances for TS2 plot. However, the observed curve got outside the envelope between 0–25, 0–33 and 0–35 m for the TS1, SW and GS plots, respectively (Fig. 4; Table 2). Termite mounds had a regular spatial distribution in all plots but the GS plot, where their distribution was random. However, the average distance between two direct neighbouring termite mounds was about 20, 30 and 35 m for TS1, SW and TS2 plots, respectively (Fig. 4; Table 2).

Spatial association between point types
Spatial association between palm tree stages

Entire-leafed seedlings showed positive spatial associations (attraction) with slit-leafed seedlings and females from 0 to 20 m in all plots except the TS2 where they showed no spatial association with females at any distances (Supplementary Fig. S3). Entire-leafed seedlings also showed a lack of spatial association with males in the four plots but their bivariate curve $L_{inhom1.2}(r)$ got slightly below the confidence envelope at small scales (0–4 m) in the TS1 and TS2 plots (Supplementary Fig. S3). Entire-leafed seedlings showed positive spatial associations (attraction) with juveniles in the SW and GS plots although they showed no spatial association with them in the TS1 and TS2 (Supplementary Fig. S3; Table 3). The bivariate function $L_{inhom1.2}(r)$ revealed a positive spatial association (attraction) between slit-leafed seedlings and juveniles at 17–20, 0–33
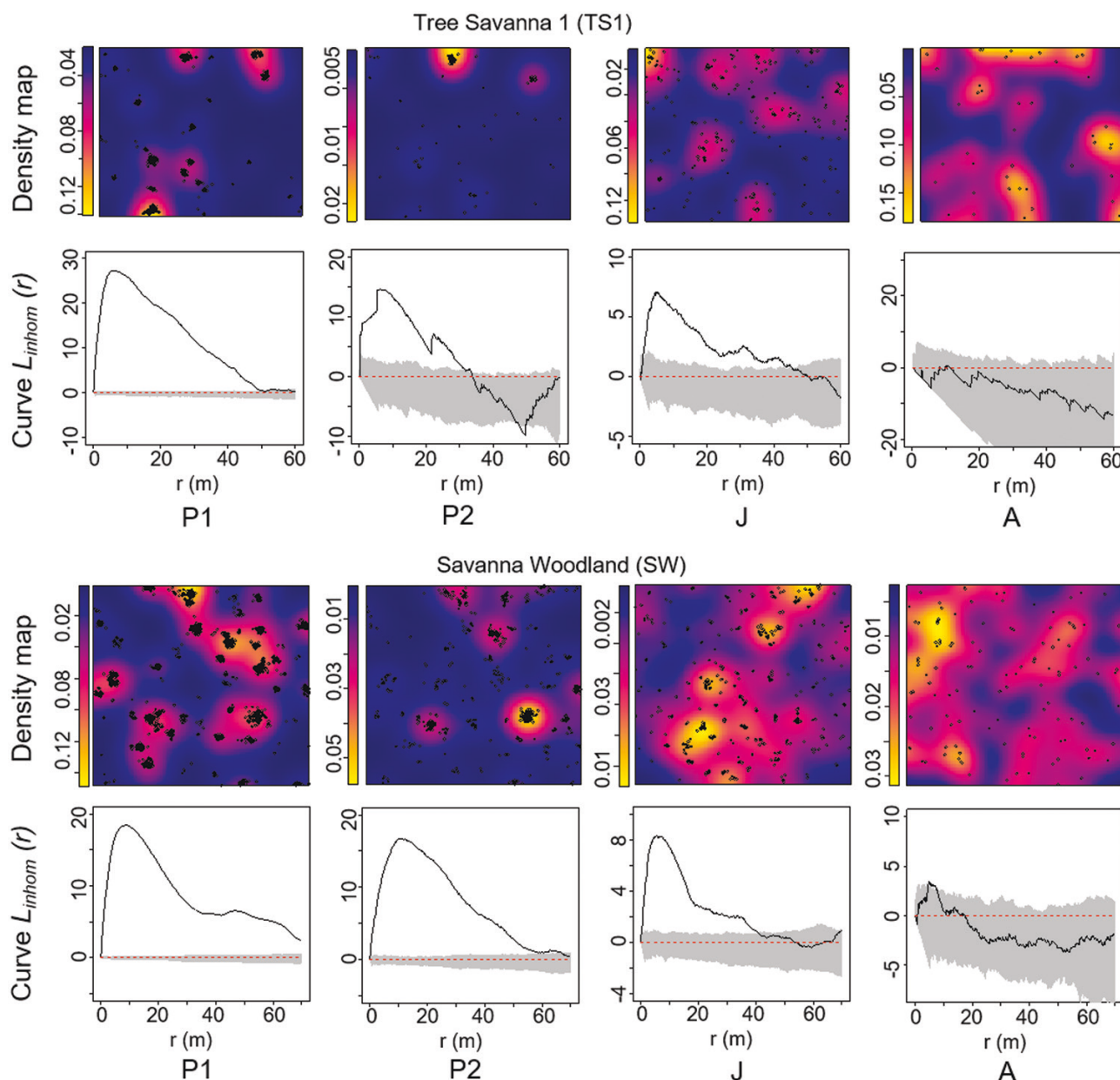
Figure 3: Spatial distribution of palm trees in the TS1 and SW plots: density map and $L_{inhom}(r)$ depending on the development stages. P1, entire-leafed seedlings; P2, slit-leafed seedlings; J, juveniles; A, adults. The grey part indicates the 95% confidence limit envelops generated by Monte Carlo simulations. The solid black line represents the observed value and the red dotted lines are theoretical values under the random distribution hypothesis.

and 0–24 m for TS1, SW and GS plots, respectively, while it showed no spatial association with juveniles in the TS2 plot (Supplementary Fig. S4). Slit-leafed seedlings also showed no spatial association with adult (Table 3). However, their bivariate curve $L_{inhom1.2}(r)$ was slightly on the positive side of the confidence envelope at small scales (Supplementary Fig. S4; Table 3). Juveniles showed no spatial association with females and males in all plots but SW where they showed a positive spatial association (attraction) with males (Supplementary

Fig. S4; Table 3). Females showed negative spatial association (repulsion) with males in the SW plot while there was no spatial association between them in the TS1 and GS plots (Table 3).

Spatial association between palm trees and trees

Trees were spatially independent from all stages of palm trees grouped together in all plots except in the GS plot where they exhibited a positive spatial association (attraction) (4–10 m) with palm trees (Fig. 5). Entire- and slit-leafed seedlings were

Table 2: Results of spatial distribution analyses ($L_{inhom}(r)$) in the different plots

Stages	TS1		TS2		SW		GS	
	N	$L_{inhom}(r)$	N	$L_{inhom}(r)$	N	$L_{inhom}(r)$	N	$L_{inhom}(r)$
Spatial analysis of the stages of palm trees								
Entire-leafed seedlings	956	a***	361	a***	2726	a***	1486	a***
Slit-leafed seedlings	105	a***	206	a***	685	a***	499	a***
Juveniles	220	a***	189	a***	433	a***	234	a***
Females	22	n	11	n	54	n	20	n
Males	20	n	12	n	67	n	49	n
All adult palm trees	42	n	23	n	121	n	69	r*
Spatial analysis of termite mounds								
Termite mounds	109	r***	15	r**	122	r***	52	n
Spatial analysis of trees								
Trees	1978	a***	723	a***	1526	a***	658	a***

Probabilities test based on 999 Monte Carlo simulations: $0.001 < P \leq 0.010$ (***); $0.010 < P \leq 0.025$ (**); $0.025 < P \leq 0.05$ (*); $P > 0.05$ (n). In case of significant deviation from the random spatial distribution: a, aggregated spatial distribution; r, regular spatial distribution.

independent from trees in all four plots except in the GS plot where slit-leafed seedlings exhibited a positive spatial association (attraction) with trees (Supplementary Fig. S5; Table 4). Trees were spatially associated with adult and juvenile palms at the scales of 5–18, 0–13 and 7–10, 0–20 m in the SW and GS plots, respectively, while they were independent from these stages in the TS1 and TS2 plots (Fig. 5; Table 4).

Spatial association between palm trees with termite mounds

Termite mounds showed a positive spatial association (attraction) with all stages of palm trees grouped together in the SW and GS plots. However, they showed a lack of spatial association with palm trees in the TS1 and TS2 plots (Fig. 5). Termite mounds were positively associated (attraction) with slit-leafed and adult palms in the SW plot, while they were negatively associated (repulsion) with these stages in the GS plot (Supplementary Fig. S6; Table 4). Juveniles showed positive spatial associations with mounds at the scales of 0–12, 0–15, 0–18 and 10–30 m in the TS1, SW, GS and TS2 plots, respectively (Fig. 5; Table 4).

Trees and the termite mounds were spatially associated in the three plots of the Reserve, while they were spatially independent from each other in the rural area (Fig. 5; Table 4).

DISCUSSION

Comparison with the spatial patterns 20 years back

Our new results show that trees have an aggregate distribution regardless of the savanna type. Termite mounds are regularly distributed in the TS and SW while randomly distributed in the GS. In addition, trees and termite mounds are spatially associated. The most likely hypothesis to explain tree aggregation for the Lamto savanna is that under the canopy of a tree, due to shade, grass biomass is so low that fire intensity decreases (Gignoux *et al.* 2006), and therefore causes a decrease in young trees mortality (Hochberg *et al.* 1994). The regular distribution of termite mounds could be due to competition between termite colonies (Korb 2003). The regular distribution of termite mounds in SW that we observed instead of the random distribution 20 years ago could be due to the large size of our plot (9 *vs.* 2.25 ha) and the high number of our samples (122 *vs.* 18).

The positive spatial associations of trees and termite mounds may be due to the fact that termite mounds could lead to tree protection from fire (Sileshi *et al.* 2010) and water clogging (Léonard and Rajot 2001) and that they are nutrient-rich patches (Abbadie *et al.* 1992). The data collected in Lamto (Konaté *et al.* 1999; Turner *et al.* 2006) suggest that termite mounds may protect plants against excesses of water and results from South African
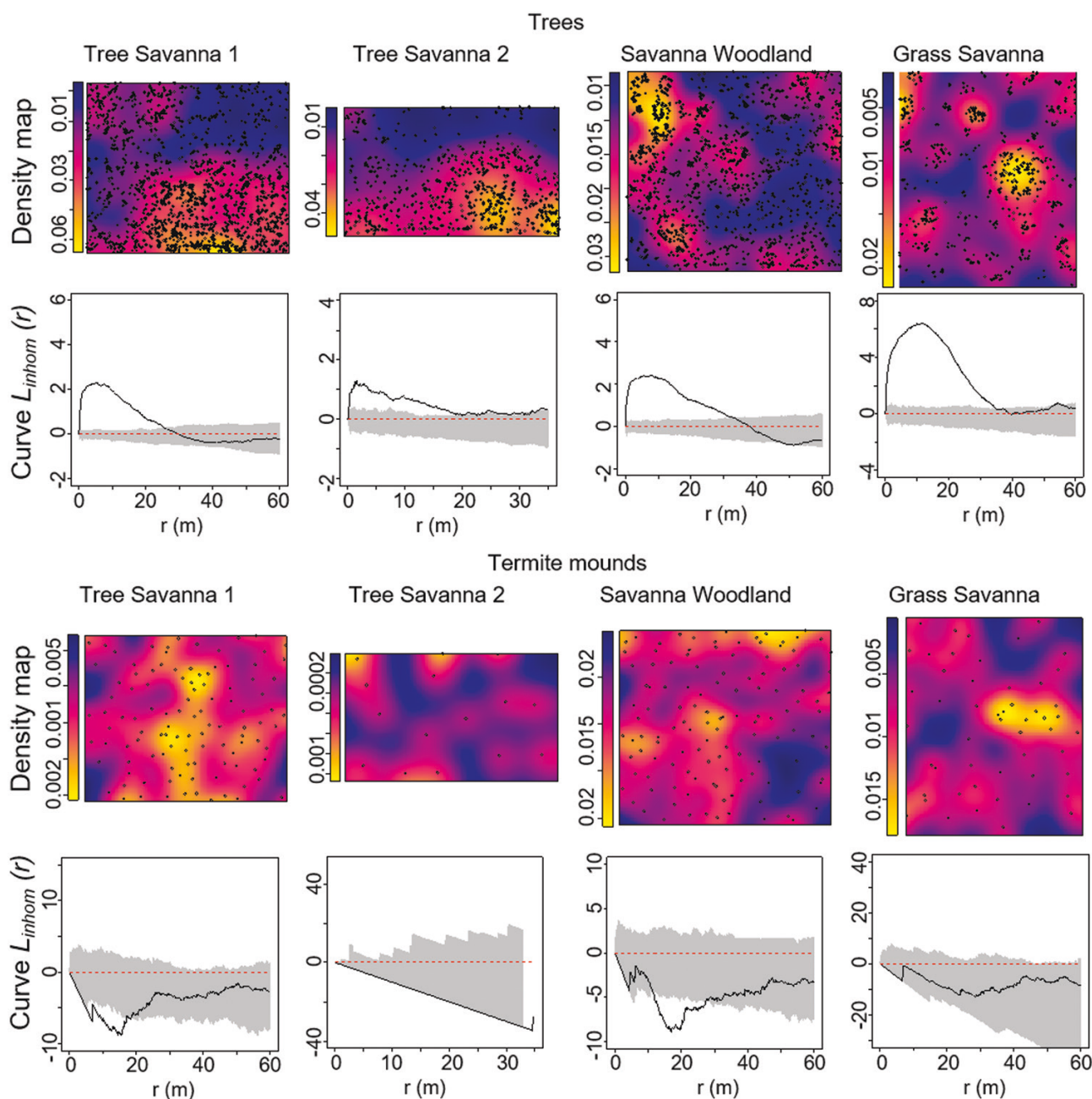
Figure 4: Spatial distribution of the trees and termite mounds of the four plots: density map and $L_{\text{inhom}}(r)$. The grey part indicates the 95% confidence limit envelops generated by Monte Carlo simulations. The solid black line represents the observed value and the red dotted lines are theoretical values under the random distribution hypothesis.

savannas confirm that termite mounds may have a positive effect on tree growth (Groen *et al.* 2008).

The spatial distribution of entire- and slit-leafed seedlings and juveniles had not changed. It is still aggregated. However, we observed a decrease in the intensities of the aggregations. This is thought to be due to the poor dispersal of the seeds of the *B. aethiopum* species. Indeed, *B. aethiopum* is a barochore species with very heavy fruits (0.5–1.5 kg) falling at the feet of females (Barot *et al.* 1999a). Such an aggregation

of plant individuals is indeed common, particularly in their early development stages (Salas *et al.* 2006; Wang *et al.* 2018). The aggregation of young palms could also be explained by the absence of elephants and baboons that have disappeared about 1966 years ago, since these animals were known to be highly dispersive.

As Barot *et al.* (1999a) we found in the SW and in the TSs that adult palms have a random distribution whereas, the distribution of adult palms had changed

Table 3: Results of analyses of the spatial association between palm stages ($L_{inhom1.2}(r)$) in the different plots

Spatial associations	TS1 $L_{inhom1.2}(r)$	TS2 $L_{inhom1.2}(r)$	SW $L_{inhom1.2}(r)$	GS $L_{inhom1.2}(r)$
Spatial association between palm stages				
Entire-leafed × Slit-leafed	A**	A***	A***	A***
Entire-leafed × Juveniles	n	n	A*	A*
Entire-leafed × Females	A***	n	A***	A**
Entire-leafed × Males	n	n	n	n
Entire-leafed × All adults	A***	n	A***	A***
Slit-leafed × Juveniles	A**	n	A***	A***
Slit-leafed × Females	n	n	n	n
Slit-leafed × Males	n	n	n	n
Slit-leafed × All adults	n	n	n	n
Juveniles × Females	n	n	n	n
Juveniles × Males	n	n	A**	n
Juveniles × All adults	n	A*	A***	n
Females × Males	n	—	R**	n

Probabilities test based on 999 Monte Carlo simulations: $0.001 < P \leq 0.010$ (***); $0.010 < P \leq 0.025$ (**); $0.025 < P \leq 0.05$ (*); $P > 0.05$ (n); —, insufficient data. In case of significant deviation from the spatial independence: A, positive spatial association; R, negative spatial association.

in the GS. We observed a regular spatial distribution instead of the aggregated spatial distribution observed 20 years ago. The emergence of random or regular distributions from the aggregated distribution of seedlings and juveniles may be due to competition between individuals that leads to locally density-dependent 'self-thinning' mortality (Getzin *et al.* 2006). Indeed, adult palms need more resources than juveniles, and they have e.g. been shown to explore the soil extensively (Mordelet *et al.* 1997). This locally density-dependent process causes distributions to become random and sometimes regular by switching from juveniles to adults (Zhu *et al.* 2010).

In this context, the observation of the regular distribution of adult palms in GS (while Barot *et al.* found an aggregated distribution) may be due to such self-thinning but may also be due to the fact that we have now used a HP process (Baddeley *et al.* 2000), unlike Barot *et al.* (1999a). The F, G and K functions used by Barot *et al.* (1999a) are defined and estimated assuming that the point process is homogeneous and are not adapted if the process is not (Pélissier and Goreaud 2001; Wiegand and Moloney 2004). These functions are often not very instructive for univariate spatial distributions

(Velázquez *et al.* 2016) because the effects of large-scale heterogeneity (first-order) introduce a systematic bias in the K-function, at both large and small scales (Wiegand and Moloney 2004). Thus, the aggregated distribution found 20 years ago in the GS, may well be due to large-scale spatial heterogeneity (first-order) rather than to small-scale processes (second-order) (Bailey and Gatrell 1995), which could lead to a misinterpretation of the spatial structure (Pélissier and Goreaud 2001; Velázquez *et al.* 2016).

We found that juveniles are spatially associated with nutrient-rich patches (mounds and trees) in all three savanna types like 20 years ago. This may be explained by the positive effect of termite mounds on juveniles (Barot and Gignoux 2003). Slit-leafed seedlings are negatively associated (repulsion) to these patches in GS. In addition, adult palms have different spatial associations with termite mounds depending on the type of savanna: independence in TS, attraction in SW and repulsion in GS. These results are different from those of 20 years ago, which showed that all stage palm trees were spatially associated with nutrient-rich patches except adult females. Overall, our results also suggest that the
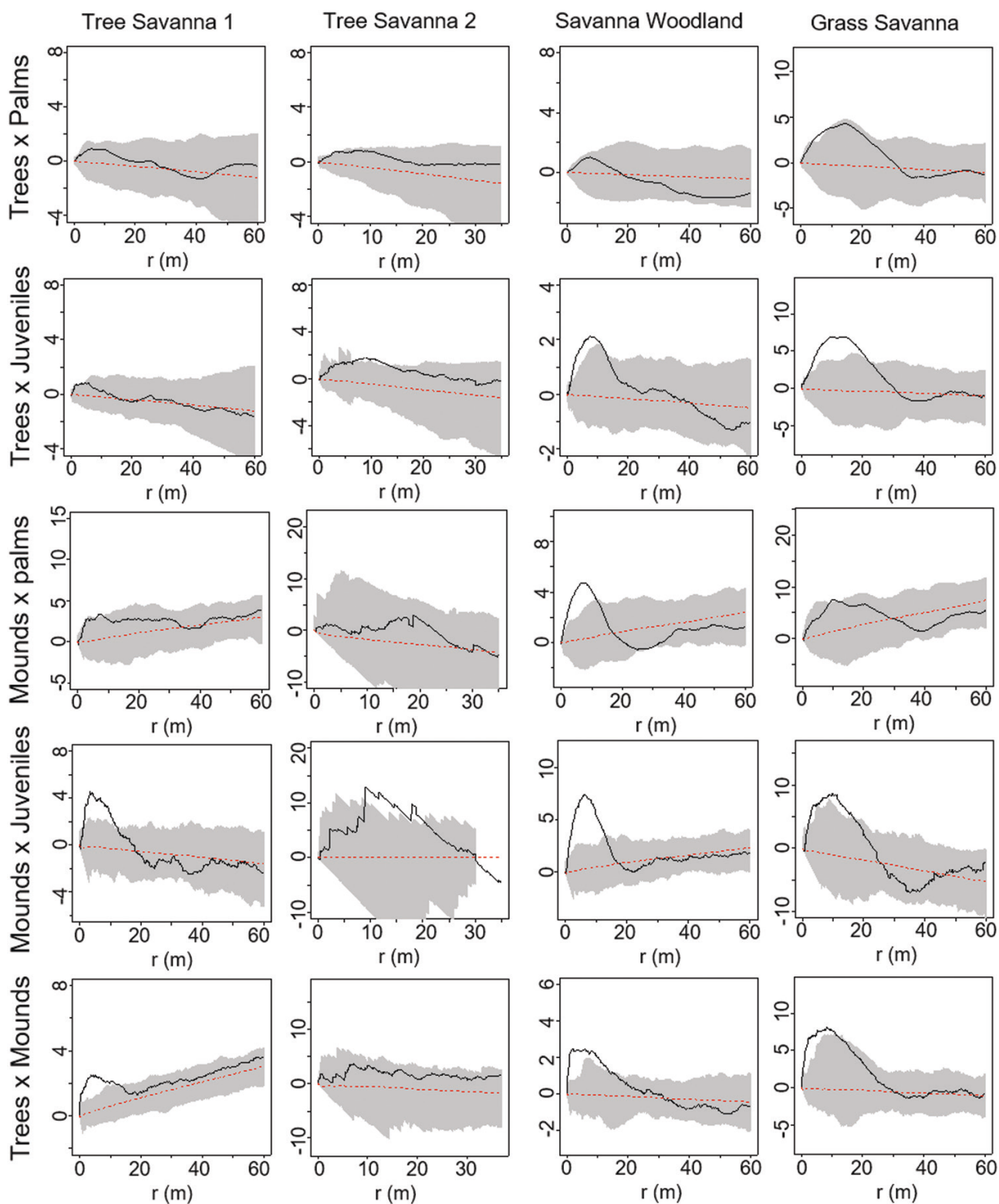
Figure 5: Spatial association analyses based on the function $L_{\text{inhom1.2}}(r)$. From top to bottom, between trees, termite mounds, juveniles and all palm trees of the four plots. The grey part indicates the 95% confidence limit envelops generated by Monte Carlo simulations. The solid black line represents the $L_{\text{inhom1.2}}(r)$ function for the observed distribution and the red dotted lines are the values of the function when the two types of point are spatially independent.

Table 4: Results of analyses of the spatial association ($L_{\text{inhom1.2}}(r)$) between palm stages and trees/termite mounds; between females/males; and between mounds and trees in the four plots

	TS1	TS2	SW	GS
Spatial associations	$L_{\text{inhom1.2}}(r)$	$L_{\text{inhom1.2}}(r)$	$L_{\text{inhom1.2}}(r)$	$L_{\text{inhom1.2}}(r)$
Spatial associations between palm trees, trees and termite mounds				
All palm trees × Trees	n	n	n	A***
All palm trees × Mounds	n	n	A***	A***
Trees × Mounds	A***	n	A***	A***
Spatial association of palm stages with trees and mounds				
Entire-leafed seedlings × Trees	n	n	n	n
Slit-leafed seedlings × Trees	n	n	n	A***
Juveniles × Trees	n	n	A***	A***
All adults × Trees	n	n	A***	A***
Entire-leafed seedlings × Mounds	n	n	A***	n
Slit-leafed seedlings × Mounds	n	n	A***	R*
Juveniles × Mounds	A***	A**	A***	A***
All adults × Mounds	n	—	A***	R***
Spatial association based on the sex of palm trees with trees and mounds				
Females palms × Trees	n	n	A*	n
Females palms × Mounds	n	—	A***	n
Males palms × Trees	n	n	A*	A***
Males palms × Mounds	n	—	A***	n

Test probabilities based on 999 Monte Carlo simulations: $0.001 < P \leq 0.010$ (***); $0.010 < P \leq 0.025$ (**); $0.025 < P \leq 0.05$ (*); $P > 0.05$ (n); —, insufficient data. In case of significant deviation from the spatial independence: A, positive spatial association; R, negative spatial association.

population of *B. aethiopum* have reached a spatial equilibrium, and that the underlying demographic mechanisms based on locally negative (competition) and positive interactions (effect of nutrient-rich patches) have partially changed.

Comparison between the reserve and the rural area

Overall, we found the same spatial distributions and associations within and outside Lamto reserve. However, trees are positively associated with termite mounds in the reserve while they are spatially independent in the rural area. Juvenile palms are spatially associated with slit-leafed seedlings in the reserve while they are spatially independent in the rural area. These results could be due to the dispersal over longer distances by livestock or humans outside

the reserve. Such an influence of livestock and humans was proved by the falling or disappearance of many stakes used to label individual palm trees (for a non-published demographic study) only outside the reserve.

Female palm trees are spatially associated with entire-leafed seedlings in the reserve while they are spatially independent in the rural area. This could partially be due to the dispersal of fruits by humans and cattle (see above). To do so, their sap is extracted from the terminal bud till the death of the palm tree. The non-association of seedlings with females could also be explained by the collection of fruits by rural populations. According to Zongo *et al.* (2018), rural populations collect ripe fruits *of B. aethiopum* to let them germinate in order to eat the young shoots later on.

Large-scale spatial heterogeneity

Large-scale spatial heterogeneity is a characteristic of most natural ecosystems i.e. difficult to handle analytically, particularly in the absence of knowledge about the exogenous factors responsible for this heterogeneity (Pélissier and Goreaud 2001). Moravie and Robert (2003) comment that both biotic and abiotic heterogeneous effects act to further confuse the links between spatial distributions and processes. Since spatial distributions of plant individuals depend on factors operating at different scales, the choice of the null model for spatial distributions analysis can significantly influence the results. While classical methods of analysing spatial point distributions generally require the assumption of homogeneity, the HP process null model is used to study spatial structure at a finer scale while removing the influence of large-scale heterogeneity. This null model led to results different from those of Barot et al. (1999a). For example, according to HP, the spatial distribution of trees was less aggregated than under the null model of CSR, in all types of plots. This is probably due to the fact that, besides the small-scale spatial aggregation of trees in tree clumps, tree density is also varying at the scale of the mapped plot (several tens of metres).

What could be the causes of such a large-scale spatial heterogeneity in terrestrial ecosystems? Heterogeneity may result from exogenous factors, i.e. external to the biological community studied. For example, soil properties, water availability and topography influence plant growth, population densities and, therefore, affect vegetation dynamics and vegetation spatial structure (Barot and Gignoux 2004; Wiegand et al. 2007). Heterogeneity may also result from endogenous factors, i.e. linked to the functioning of plant communities (Abbadie et al. 1992): plant demography determines the spatial distribution of plant individuals and these individuals in turn modify their environment. In the case of Lamto savanna, differences between the results of the homogeneous and HP processes confirm that the vegetation is structured both at the plot scale (from 50 to 100 m) and at a finer scale (about 10 m). Though we cannot prove it at this stage, the large-scale structure is likely due to the topography (there are slopes from SWs on the plateaux towards TSs, and GSs growing near riparian forests) and the existence of lowland hydromorphic soils impeding tree growth (in GS). Complex feedbacks between tree density, grass biomass, fire intensity and fire propagation could also lead to large areas with higher tree survival and create large-scale heterogeneity (besides the creation of

tree clumps). Shedding new lights on the thus subject would require mapping very large plots (2 km × 2 km) or studying the vegetation and the topography using remote sensing.

In turn, small-scale spatial heterogeneity is created by tree clumps that are created and maintained by differences in grass biomass and fire intensity (Sileshi et al. 2010). Finally, due to the inputs of tree litter (both leaves and roots) (Jacobs et al. 2018), the decrease in nutrients and organic matter losses due to the decrease in fire intensity (Ando et al. 2014), and the concentration of mineral nutrients due to root foraging by trees outside tree clump below nitrification inhibiting grasses (Konaré et al. 2019, 2021), tree clumps are turned into nutrient-rich patches (Mordelet et al. 1997).

CONCLUSIONS

The use of new spatial analysis methods allowed the results to be refined by eliminating the effect of long-distance spatial heterogeneity. The results show that the distribution of palms has somewhat changed: (i) in the grassy savannah, adult palms have a regular distribution instead of an aggregated distribution 20 years ago; (ii) although the spatial distribution of seedlings and juveniles is still aggregated, we observed a decrease in the size of the aggregates (intensities); (iii) with the exception of juveniles, no other stages are associated with nutrient-rich patches, which also differed 20 years ago. However, the trees are still aggregated and associated with termite mounds.

The comparative study between the reserve and the rural area showed great similarities in the spatial distribution in the two zones. Nevertheless, differences were noted: (i) female palm trees are spatially associated with entire-leafed seedlings in the reserve while they are spatially independent in the rural area; (ii) trees are positively associated with termite mounds in the reserve while they are spatially independent in the rural area. These differences are likely due to perturbations by humans and cattle outside the reserve.

In general, our results (2020) within and outside Lamto reserve showed that the spatial structure of the palm population is still not stable. The tree community is rather stable over time but this stability should be verified through the spatial distribution of each tree species. This paves the way for more studies documenting changes in the spatial structure of plant populations in time.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: Univariate analysis of the spatial distribution of palm trees and comparison between Ripley's $L(r)$ and $L_{\text{inhom}}(r)$ function of the four plots: density map and $L_{\text{inhom}}(r)$.

Figure S2: Spatial distribution of palm trees in the GS and TS2 plots: density map and $L_{\text{inhom}}(r)$ depending on the development stages.

Figure S3: From top to bottom, $L_{\text{inhom1.2}}(r)$ function between entire-leafed seedlings (P1) and the other stages (Slit-leafed seedlings (P2); Juveniles; Females; Males) of the four plots.

Figure S4: From top to bottom, $L_{\text{inhom1.2}}(r)$ function between slit-leafed seedlings (P2) and the other stages (Juvenile; Female; Males) and between the stage Juvenile and Female and Male of the four plots.

Figure S5: From top to bottom, $L_{\text{inhom1.2}}(r)$ function between trees and (entire-leafed seedlings (P1); slit-leafed seedlings (P2); Juveniles; Females; Males) of the four plots.

Figure S6: From top to bottom, $L_{\text{inhom1.2}}(r)$ function between mounds and (entire-leafed seedlings (P1); slit-leafed seedlings (P2); Juveniles; Females; Males) of the four plots; DI : Not enough individuals.

Authors' Contributions

A.S.T., S.B. and K.I.K. conceived the study and performed data collection. A.S.T. analysed achieved the statistical analyses and wrote the first version of the manuscript. Prof. S.B. and J.G. improved the writing of the manuscript. All the authors discussed the results and commented on the manuscript and gave final approval for publication.

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