Macrotermes termite mounds influence the spatial pattern of tree species in two African rainforest sites, in northern Congo. But were they really forests in the past?

Benoit Penel, Vincent Freycon, Eric Marcon, Vivien Rossi, Guillaume Cornu, Fabrice Bénédet, Éric Forni, Sylvie Gourlet-Fleury

HAL Id: hal-03669972
https://hal.inrae.fr/hal-03669972v1

Submitted on 22 Jun 2022

Research Article

CAMBRIDGE
UNIVERSITY PRESS

Macrotermes termite mounds influence the spatial pattern of tree species in two African rainforest sites, in northern Congo. But were they really forests in the past?

Benoit Penel[1,2,3], Vincent Freycon[2,3], Éric Marcon[4], Vivien Rossi[3,5,6], Guillaume Cornu[2,3], Fabrice Bénédet[2,3], Éric Forni[3,7] and Sylvie Gourlet-Fleury[2,3]

[1]Aix Marseille Univ, IMBE, Institut Méditerranéen Biodiversité & Ecologie, Marseille, Aix-en-Provence, France; [2]CIRAD, UPR Forêts et Sociétés, F-34398, Montpellier, France; [3]Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France; [4]AgroParisTech, UMR Amap, Univ Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France; [5]Plant Systematic and Ecology Laboratory (LaBosystE), Department of Biology, Higher Teachs' Training College, University of Yanoudé I, PO Box 047, Yaoundé, Cameroon; [6]RU Forests and Societies, CIRAD, Yaoundé, Cameroon and [7]CIRAD, UPR Forêts et Sociétés BP 1352, Brazzaville, République du Congo

Abstract

Termite mounds have been poorly studied in tropical rainforest in contrast to those of savannahs where they create fertility hotspots and influence the spatial pattern of vegetation. An inventory of termite mounds and of 15 tree species with a diameter at breast height ≥ 10 cm was carried out in two 800-ha blocks, in two rainforest sites located in northern Congo. We used inhomogeneous and intertype K functions to study the spatial pattern of termite mounds and of tree species around mounds, respectively. We found that mounds in Loundoungou were over-dispersed within a radius of less than 70 m, while those in Mokabi were randomly spaced. Tree species within a 20-m radius around a mound were aggregated towards the mound, e.g. *Entandrophragma cylindricum*, randomly distributed, or even repulsed by the mound. The specific responses also differed in the two sites. These results suggest that (i) the mounds in Loundoungou were created by savannah termite species 3,000-2,000 years BP during the Late Holocene Rainforest Crisis and (ii) the mounds in Mokabi are characteristic of forest mounds. The impact of termite mounds on the spatial pattern of tree species is thus site-dependent, and these differences might be due to species seed dispersal strategies and to soil calcium concentrations.

Introduction

Termites are arthropods that belong to the Blattodea clade (Evangelista *et al.* 2019) and are mainly found in tropical and subtropical regions (Eggleton *et al.* 1994). They are known to be soil engineers: namely, the fungus-growing termites of the genus *Macrotermes* (Mueller & Gerardo 2002) build giant termite mounds (Jones *et al.* 1994; Lavelle *et al.* 1997; Dangerfield *et al.* 1998).

In savannahs, giant termites mounds are known to be fertility hotspots, which are particularly favourable areas for plant recruitment, development, and survival (Dangerfield *et al.* 1998; Traoré *et al.* 2008; Moe *et al.* 2009; Sileshi *et al.* 2010; Muvengwi *et al.* 2016). Indeed, tree density on and close to termite mounds is higher than in the surrounding savannah (Loveridge & Moe 2004; Moe *et al.* 2009; Davies *et al.* 2014, 2016; Muvengwi *et al.* 2016). The soil conditions created by termite mounds are also sufficiently fertile to enable the recruitment and development of new tree species that have higher water and nutrient requirements than the original savannah tree community (Joseph *et al.* 2013; Davies *et al.* 2016), thereby increasing local diversity (Loveridge & Moe 2004; Moe *et al.* 2009; Erpenbach *et al.* 2013; Muvengwi *et al.* 2016). Trees in the vicinity of termite mounds are also taller (Levick 2010), larger (Pringle *et al.* 2010), and have both better growth rates (Holt & Lepage 2000; Groen *et al.* 2008) and reproductive success (Brody *et al.* 2010) than elsewhere.

Giant termite mounds are over-dispersed (evenly spaced) at scales below 60–100 m (Pomeroy 2005; Pringle *et al.* 2010; Davies *et al.* 2014; Pringle & Tarnita 2017). This spatial pattern results from competition for resources between termite colonies (Pringle *et al.* 2010; Pringle & Tarnita 2017) and, as a consequence, maximizes the impact of termite mounds on the environment.

The impact of termite mounds and their spatial pattern is well documented in savannahs, but not in tropical rainforests even though giant termite mounds have been observed in tropical forests throughout Africa (Guillot 1981; Lanfranchi & Schwartz 1990; Boulvert 1995a), in
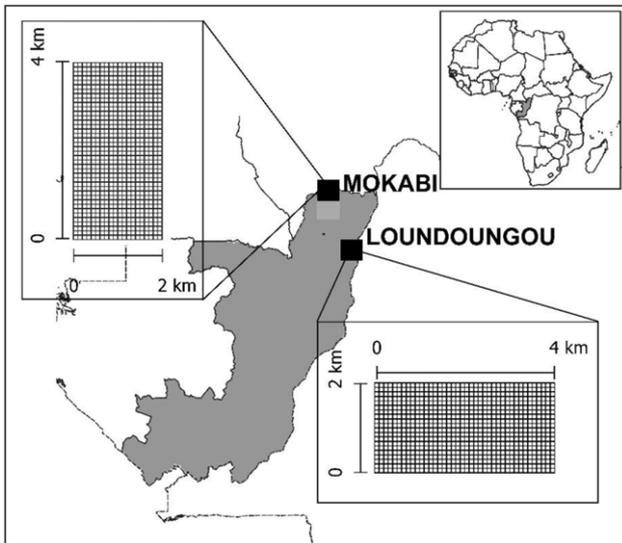
Figure 1. Location of the two 800-ha blocks in the Loundoungou and Mokabi study sites in the Republic of Congo.

South America (Martin *et al.* 2018), and Asia (Beaudrot *et al.* 2011). So far, Beaudrot *et al.* (2011) were the only authors who studied responses (biodiversity and tree density) of a tropical rainforest in Malaysia to a local increase in fertility produced by termite mounds. However, their conclusions were drawn from a very small sample of termite mounds ($n = 8$). The objectives of the present study were consequently to investigate the spatial pattern of termite mounds in two rainforest sites in northern Congo and their effects on tree spatial pattern. As litter resources are more abundant in forest than in savannahs and as termite mounds tend to favour species with higher nutrient requirements we predicted that in both sites: (i) termite mounds are randomly distributed at the local scale (< 100 m) unlike in savannahs and (ii) the influence of termite mound distance on tree density is species dependent.

Materials and methods

Study sites

The study was carried out in the northern part of the Republic of Congo, at two sites located 90 km apart, Loundoungou (2˚20'N, 17˚32'E, in the CIB-Olam concession) and Mokabi (3˚19'N, 16˚76'E, in the Rougier Mokabi SA concession). In both sites, study blocks were rectangular areas covering 800 ha (2 km x 4 km) (Figure 1). The mean annual temperature at both sites is 25℃, while the mean annual precipitation is around 1,600 mm in Loundoungou (Loubota Panzou *et al.* 2018) and 1,400 mm in Mokabi (Mokabi station located 3˚16'N, 16˚44'E, calculated over the period 2018–2020). Loundoungou site has an Am climate type, and Mokabi site has an Aw climate type according to the Köppen-Geiger classification (Peel *et al.* 2007).

The Loundoungou site is located in a transition area between the Carnot sandstone plateau and the alluvial deposits of the Congolese basin, while the Mokabi site is located right on the plateau (Boulvert 1995a). Soils in Loundoungou and Mokabi are mainly sandy clay loam and acid. Further details on the characteristics of the reference soil profiles for both sites are provided in Appendix 1.

The Loundoungou site is located in a semi-deciduous forest, dominated by medium wood density tree species, while the Mokabi site is located in an evergreen semi-deciduous forest, dominated by high wood density species (Réjou-Méchain *et al.* 2021). Respectively, 240 and 230 tree species were identified in four 9-ha plots located in the two sites, including 192 shared species, but which abundance varies according to the site. Tree densities ranged from 346.8 ± 5.8 tree.ha^{-1} at Loundoungou to 426.8 ± 3.6 tree.ha^{-1} at Mokabi (Forni *et al.* 2019).

Giant epigeous termite mounds, in which *Macrotermes amplus* Sjöstedt (formerly known as *M. muelleri*, see Krishna *et al.* 2013, pp. 1023–1024) (Roisin, pers. comm) was found, were observed in both sites. However, their architecture differs between the sites. In Loundoungou, all the termite mounds have a central cone and a wide peripheral dome certainly resulting from erosion of the central cone (Aloni 1975), with a radius of 9.9 ± 3.3 m and a height of 4.1 ± 1.5 m (Freycon *et al.* 2018). In Mokabi, termite mounds have a central cone and a narrow peripheral dome, with a radius of around 1 m and a height of between 2 and 3 m (Freycon 2014), which is generally reported for this species (Grassé & Noirot 1951; Weidner 1961). A mean density of 2.2 termite mound.ha^{-1} was observed at Loundoungou and 2.1 termite mound.ha^{-1} at Mokabi (Freycon 2014).

Survey design

An inventory of several tree species of commercial interest, with a diameter at breast height (DBH) ≥10 cm, was conducted in Loundoungou between 18 April 2013, and 25 January 2015, and in Mokabi between 20 August 2013, and 24 August 2014 [Appendix 2]. Among the 94,308 trees inventoried, we selected 32,384 trees in Loundoungou and 42,737 in Mokabi belonging to 15 species, which are quite abundant in both sites: *Amphimas pterocarpoides*; *Autranella congolensis*; *Diospyros crassiflora*; *Entandrophragma angolense*; *Entandrophragma candollei*; *Entandrophragma cylindricum*; *Entandrophragma utile*; *Erythrophleum suaveolens*; *Greenwayodendron suaveolens*; *Manilkara mabokeensis*; *Nesogordonia kabingaensis*; *Pterocarpus soyauxii*; *Pycnanthus angolensis*; *Staudtia kamerunensis;* and *Tessmannia africana*. The complete nomenclature is listed in Appendix 2.

During the inventory, 1,786 termite mounds were mapped in Loundoungou and 1,705 in Mokabi.

Statistical analysis

Different techniques are used to study the spatial pattern of points in a system, including the widely used Ripley's K function (Ripley 1977), a second-order statistic that uses all inter-point distances to provide information on the spatial pattern of the points. Ripley's K function assumes that the studied system is homogeneous and isotropic. Because in our study, the density of termite mounds was heterogeneous (Figure 2) and varied significantly with elevation (GLM Poisson; *P value* < 0.001; pseudo r^2 =0.0315 and 0.109; respectively, in Loundoungou and Mokabi) we used Baddeley's Kinhom-function (Baddeley *et al.* 2000). This function, which generalises Ripley's K-function, is operational when the assumption of homogeneity is not respected. We also performed a $K(r)/\pi * r^2$ normalisation of the output of the Kinhom-function as documented in Marcon and Puech (2017). The reference value of the K and Kinhom-function is 1 whatever the distance r if the points are independently distributed. If the observed K or
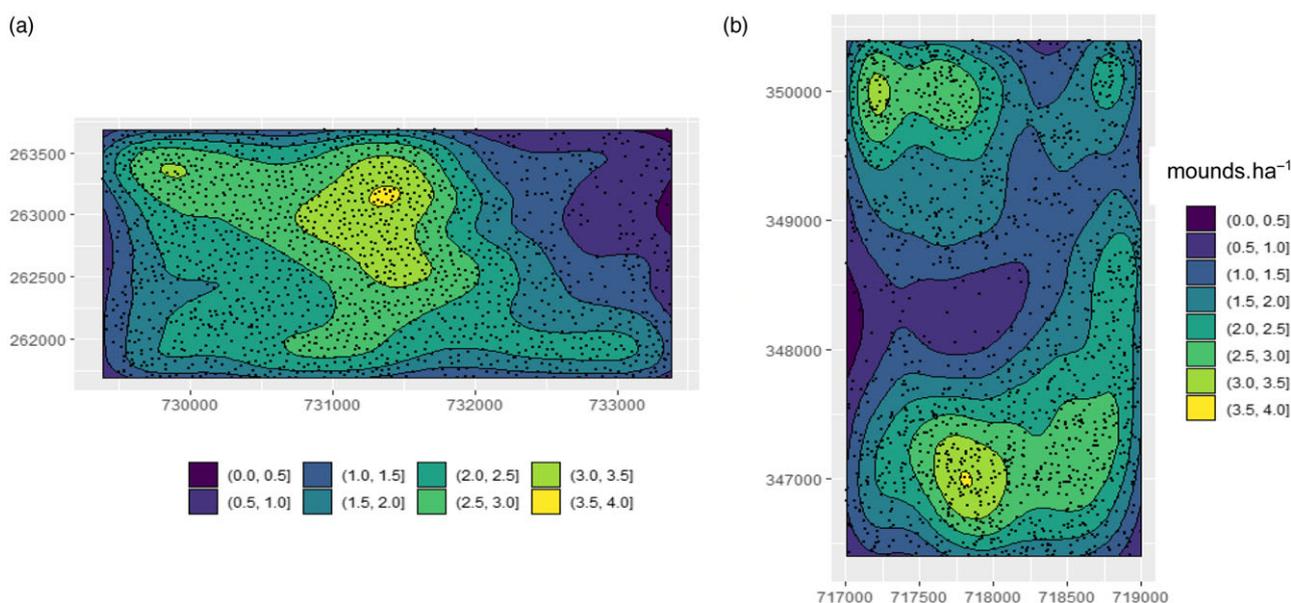
Figure 2. Local heterogeneous density of termite mounds (mounds.ha^{-1}) within the 800-hectare Loundoungou (a) and Mokabi (b) sites, $n = 1,786$ and $n = 1,705$, respectively. The density plots were generated with a two-dimensional Kernel Density estimator implemented in ggplot2 3.3.5. The x and y axes are in metres in the EPSG: 32633 – WGS 84/UTM 33N projected coordinate system. The black dots indicate the locations of the termite mounds studied. The contour lines and colour gradients in the background correspond to the local density of termite mounds in the study sites and range from [0, 0.5] mounds.ha^{-1} in purple to [3.5, 4.0] mounds.ha^{-1} in yellow.

Kinhom-function value is < 1, the points are over-dispersed, if it is > 1, the points are aggregated.

In both Loundoungou and Mokabi, we tested the randomness of the spatial pattern of the termite mounds using a Monte Carlo scheme with the transformed Kinhom-function (Davies *et al.* 2014). We compared the transformed Kinhom-function values based on the data with a 95% confidence interval of transformed Kinhom-function values in 999 simulations. Each simulation was generated from the same number of mounds as in the real data, then the stimulated mounds were randomly located in the area with respect to spatial heterogeneity.

For each of the 15 selected species, we studied the impact of termite mounds on tree density using a bivariate spatial pattern analysis based on the intertype K function (Lotwick & Silverman 1982). The intertype K function enables analysis of tree density relative to distance from a termite mound. We used the same transformation as for the Kinhom-function for the intertype K function outputs. If the transformed intertype K function value produced with the data obtained from sampling is < 1, the trees are repulsed from the termite mounds, while when it is > 1, the trees are aggregated with termite mounds. Then, we tested the randomness of the tree patterns relative to termite mounds using a Monte Carlo scheme with the transformed intertype K function (Davies *et al.* 2014). We compared the transformed Kinhom-function values on the data with the 95% confidence interval of transformed intertype K function values in 999 simulations: the locations of trees were shifted according to a torus translation test respecting their relative distances, while the locations of the termite mounds remained unchanged.

To compare the results obtained at Loundoungou and Mokabi, we previously randomly sampled the same number of trees of each species studied in each site 20 times [Appendix 2]. The 20 sub-samples of each species were used for the intertype K function. We then compared the results obtained with the intertype K function between the 20 iterations to check if a specific selection produced distinct patterns. Once this complexity had been checked and discarded, the comparison between sites was possible.

Edge effect corrections were already implemented in the Kinhom and Intertype K function. All the statistical analyses were conducted in R v. 4.0.3 (R Development Core Team). The envelop function from spatstat 1.64-1 (Baddeley *et al.* 2015) was used to produce Kinhom function and the 95% confidence interval associated. The KEnvelopp function from dbmss 2.7-4 (Marcon *et al.* 2015) was used to produce the intertype K function and the 95% confidence interval associated.

Results

Spatial patterns of the termite mounds

In Loundoungou, the Kinhom-function showed a significantly over-dispersed spatial pattern of the mounds within a radius of less than 70 m, whereas beyond 70 m, they displayed an aggregated spatial pattern (Figure 3a). In Mokabi, the function showed a random pattern of mounds within a radius of less than 40 m, whereas beyond 40 m, they displayed a significantly aggregated spatial pattern (Figure 3b). Moreover, in Loundoungou, the Kinhom-function displayed a flat curve around 1.1 for r between 100 to 1,000 m, while the one of Mokabi displayed a curve with a peak up to 1.2 around $r = 100$ m (Figure 3). The results from the Kinhom-function highlighted the less marked heterogeneity of termite mound density at Loundoungou than at Mokabi as shown in Figure 2.

Spatial patterns of species around termite mounds

Different species spatial patterns were observed around the termite mounds: half is aggregative and half is random. In Loundoungou, species with an aggregative spatial pattern tended to be aggregated
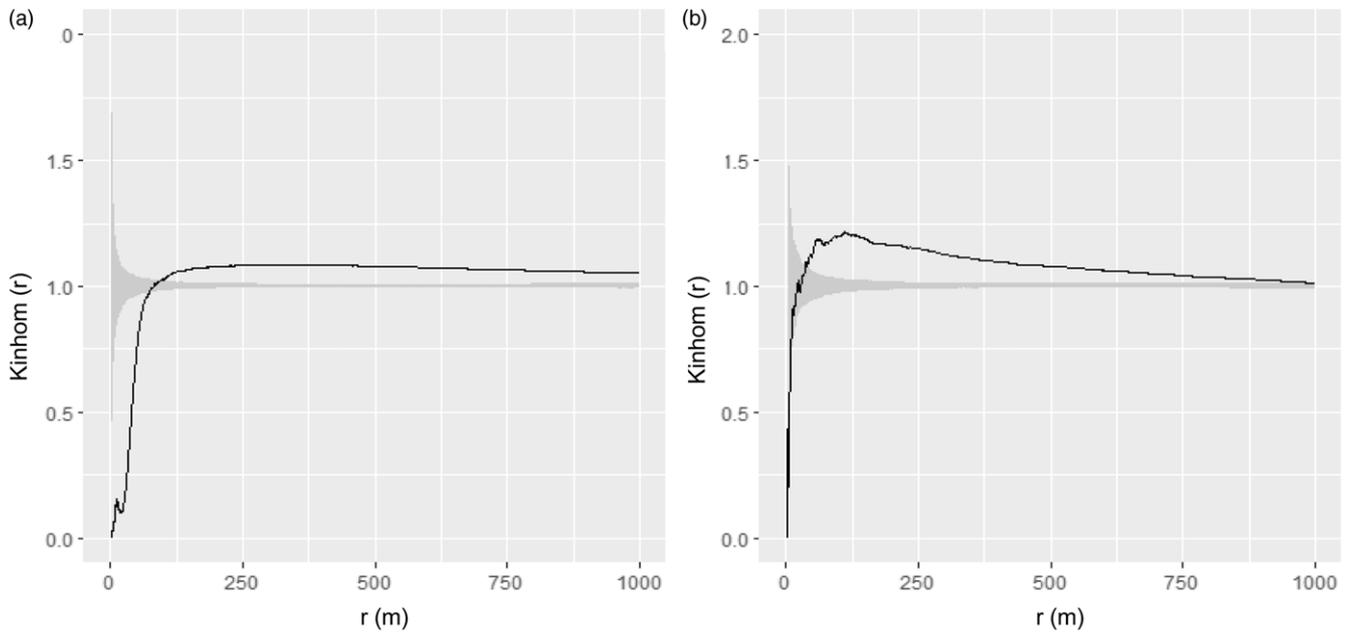
Figure 3. Graphs of the Baddeley's Kinhom-function for termite mounds in Loundoungou n= 1,786 (a) and Mokabi *n* = 1,705 (b). Kinhom values (previously transformed) are plotted against distance (r) in m. The grey intervals represent 95% confidence intervals for statistical testing of the null hypothesis run with 999 Monte Carlo simulations. The black line represents observed termite mound distribution. Values below the grey interval indicate over-dispersion (even spacing), while values above indicate clustering.

within a 20 m radius from the centre of termite mounds, while in Mokabi, they tended to be aggregated within a variable radius ranging from 5 to 20 m (Figures 4 and 5).

Eight out of the 15 species displayed similar spatial patterns around termite mounds in both Loundoungou and Mokabi: *D. crassiflora, E. candollei, N. kabingaensis, A. pterocarpoides, A. congolensis, P. soyauxii, E. cylindricum,* and *E. angolense* (Figure 4). Among these eight species, *D. crassiflora, E. candollei, A. pterocarpoides,* and *P. soyauxii* displayed a random pattern while *N. kabingaensis, A. congolensis, E. cylindricum,* and *E. angolense* displayed an aggregated spatial pattern. The density of these species around termite mounds was thus higher than in the surrounding environment. In both sites, *A. congolensis* displayed the strongest aggregated spatial pattern around termite mounds with an aggregation up to 12 and 25 times greater than a random pattern in Loundoungou and Mokabi, respectively.

Surprisingly, seven species displayed different spatial patterns around the termite mounds depending on the site (Figure 5). *Manilkara mabokeensis, E. utile* and *E. suaveolens* displayed a random spatial pattern around the mounds in Loundoungou, whereas they appeared to be aggregated in Mokabi. The spatial patterns of *P. angolensis* were the reverse. *Staudtia kamerunensis* and *G. suaveolens* displayed, respectively, an aggregated and a random spatial pattern around the mounds in Loundoungou, while they displayed a repulsion spatial pattern in a circle with a radius of 3–5 m around the mounds in Mokabi. Both species are very abundant in Mokabi (resp 15.2 and 18.1 trees.ha^{-1}), but their tree density was expected to be reduced to half around the mounds. *Tessmannia africana* was the only species that displayed a repulsion spatial pattern around termite mounds in Loundoungou, while it was randomly distributed in Mokabi. *Tessmannia africana* tree density was reduced up to 20 m away from the termite mounds in Loundoungou, and the reduction in density was in the order of 50% in the first 10 m.

Discussion

An over-dispersed spatial pattern in Loundoungou probably inherited from a past savannah

Our first hypothesis was that termite mounds are randomly distributed at local scale, within a radius of less than 100 m. This hypothesis was invalidated in Loundoungou where termite mounds are over-dispersed but confirmed in Mokabi where termite mounds are randomly distributed. Contrasting results in Loundoungou and Mokabi suggest two different past histories.

First, the over-dispersed spatial pattern in Loundoungou resembles the patterns found in savannahs by Pomeroy (2005); Levick *et al.* (2010); Pringle *et al.* (2010); Davies *et al.* (2014); Pringle & Tarnita (2017); Martin *et al.* (2018). As this spatial pattern usually results from competition between termite colonies for resources (Pringle *et al.* 2010; Pringle & Tarnita 2017), in Loundoungou, it could be a heritage from the past related to competition between savannah colonies. The architecture and size of *M. amplus* mounds in Loundoungou are also similar to those observed in savannahs (Boulvert 1995b; Pullan 1979). For instance, termite mounds in Loundoungou exhibit a conical architecture. This structure is typical of savannah termite mounds and reflects the strategy of savannah colonies to deal with high solar radiation and wind load (Fagundes *et al.* 2021). Termite mounds in Loundoungou had a size up to 15 m in radius and 6.4 m high, comparable to the one described in Pullan (1979), i.e. a termite mound up to 15 m in radius and 10 m high. The spatial pattern, the architecture and the size of the mounds in Loundoungou thus suggest that they are old savannah termite mounds. Indeed, termite mounds undergo colonization–abandonment–recolonization processes that allow some of them to increase in size over time (Dangerfield *et al.* 1998) and slow erosion dynamics (Lepage 1984); which could explain the difference in height. A few mounds may persist for centuries or even millennia. Erens *et al.* (2015)
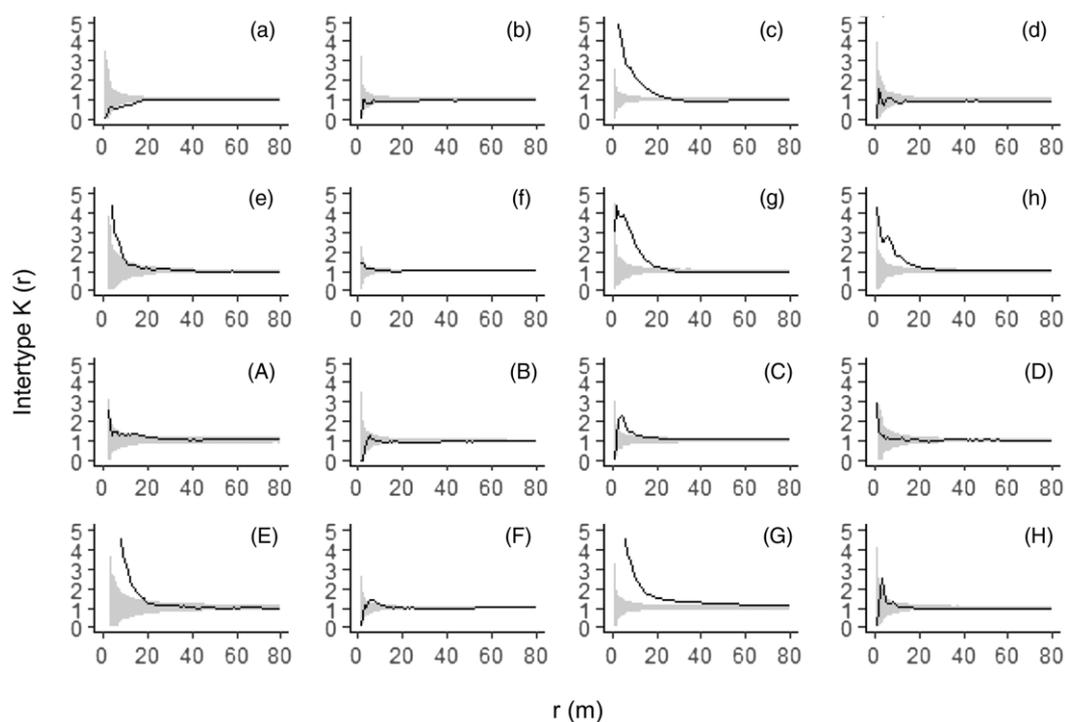
Figure 4. Graphs of intertype K – function analysis of Diospyros crassiflora (a/A), Entandrophragma candollei (b/B), Nesogordonia kabingaensis (c/C), Amphimas pterocarpoides (d/D), Autranella congolensis (e/E), Pterocapus soyauxii (f/F), Entandrophragma cylindricum (g/G) and Entandrophragma angolense (h/H) trees around termite mounds in Loundoungou (lowercase letters) and Mokabi (capital letters). Intertype K values (previously transformed) are plotted against distance (r) in metres. The grey intervals represent 95% confidence intervals for statistical testing of the null hypothesis run with 999 Monte Carlo simulations. The black line represents observed tree distribution. Values below the grey intervals indicate repulsion of trees around termite mounds. Values above the grey intervals indicate tree aggregation around the termite mounds.
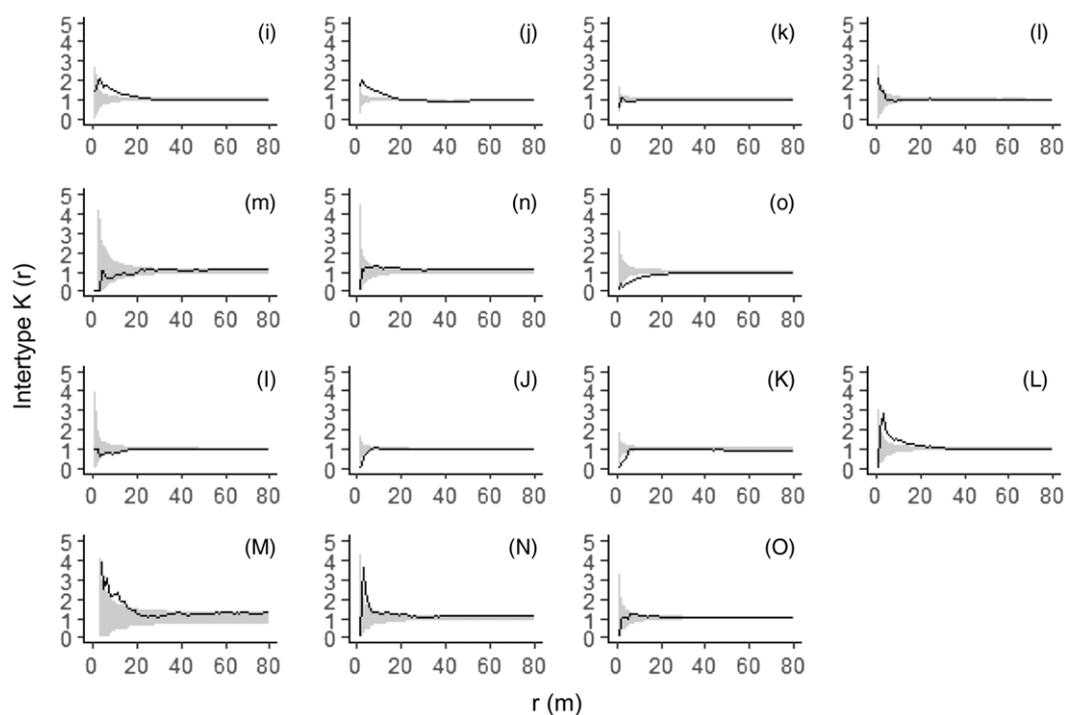
Figure 5. Graphs of intertype K – function analysis of *Pycnanthus angolensis* (i/I), *Staudtia kamerunensis* (j/J), *Greenwayodendron suaveolens* (k/K), *Manilkara mabokeensis* (l/L), *Entandrophragma utile* (m/M), *Erythrophleum suaveolens* (n/N) and *Tessmania africana* (o/O) trees around termite mounds in Loundoungou (lowercase letters) and Mokabi (capital letters). Intertype K values (previously transformed) are plotted against distance (r) in metres. The grey intervals represent 95% confidence intervals for statistical testing of the null hypothesis run with 999 Monte Carlo simulations. The *black* line represents observed tree distribution. Values below the grey intervals indicate repulsion of trees around termite mounds. Values above the grey intervals indicate tree aggregation around the termite mounds.

estimated the age of a *Macrotermes falciger* mound, similar in size to those observed in Loundoungou, to be 2,300 years old. This hypothesis of old savannah mounds was already put forward by Lanfranchi & Schwartz (1990) in northern Congo, at a location 180 km from Loundoungou. This hypothesis is also consistent with the Late Holocene Rainforest Crisis (LHRC) in Central Africa 3000-2000 years BP, during which the rainforests regressed while the savannahs spread, resulting in a forest-savannah mosaic. The origins of LHRC and of the forest-savannah mosaics are still the

subject of heated debate leading to two visions of the replacement of forest by savannah, one being the result of a paleoclimatic change (Bostoen *et al.* 2015; Clist *et al.* 2018; Giresse *et al.* 2018; Maley *et al.* 2018; Giresse *et al.* 2020) and the other a past marked by human activity (Bayon *et al.* 2012; Garcin *et al.* 2018). However, recently some authors have shown flexibility in their statements and have put forward less clear-cut hypotheses. Adeleye *et al.* (2021) and Bayon *et al.* (2019) claim that paleoclimatic change was the main factor of the LHRC, but that anthropogenic impact

cannot be excluded from the scenario since it is very difficult to quantify. In our study, evidence of past human occupation, such as shards of pottery, scorias, and charcoal, was found in Loundoungou (Freycon *et al.* 2018), consistent with the presence of old savannah termite mounds. However, this does not invalidate a potential role for paleoclimatic change.

Second, the random spatial pattern of termite mounds in Mokabi does not match that of Loundoungou, nor that of savannah mounds (Pomeroy 2005; Levick *et al.* 2010; Pringle *et al.* 2010; Davies *et al.* 2014; Pringle & Tarnita 2017; Martin *et al.* 2018). These termite mounds are therefore probably not the result of the activity of ancient savannah termites, but of forest termites. Indeed, the termite mounds of Mokabi are randomly distributed at local scale, which could be linked to the lack of competition between forest termite colonies in a context of more abundant litter resources (e.g. 6.1 t.ha^{-1}.y^{-1} produced in a primary rainforest in Congo, see Loumeto 2003 pp. 1241) than in savannahs (e.g. 2.3 t.ha^{-1} of leaf litter and 1.3 t.ha^{-1} of wood litter produced annually in a Nigerian savannah, see Collins 1977, pp. 169,167). The architecture of these mounds can be described as a vertical dome similar to the one expected for shaded termite mounds (Fagundes *et al.* 2021). The termite mounds are also smaller, with a radius of approximately 1 m and a height of 2–3 m, which is generally described for *Macrotermes amplus* (Grassé & Noirot 1951; Weidner 1961). Our observations thus suggest that savannahs never existed in Mokabi even if the site is located in the area where the paleoclimatic change associated with LHRC occurred. These observations are consistent with those reported in the study by Bremond *et al.* (2017) carried out in the "Sangha River Interval" region, close to Mokabi. Indeed, based on phytolith and soil carbon isotope composition analyses, the occurrence of the LHRC is questioned in this region. In our study, two explanations are possible: (1) the drier paleoclimatic climate change did not lead to a forest crisis because the trees were probably deep-rooted. Indeed, Freycon *et al.* (2015) still found roots at a depth of 5 m in similar soils derived from the weathering of Carnot sandstone at a distance of around 100 km from Mokabi. Deep roots probably enabled trees to access a large soil water reserve and hence to withstand drought episodes and (2) no evidence of human presence has been found in Mokabi, which could be explained by the scarcity of watercourses in this area.

Our results contribute to the assumption that the origin of the LHRC is probably a combination of climate change and human impacts (Bayon *et al.* 2019; Adeleye *et al.* 2021). Both these conditions were met in Loundoungou where savannah termite mounds can still be observed but not in Mokabi where forest termite mounds are present. Savannahs did not extend everywhere in this region.

An alternative hypothesis to explain the differences in spatial pattern and the architecture of termite mounds between the two study sites would be a difference in the age of these mounds between sites. Indeed, young and small termite mounds do not lead to an over-dispersed spatial pattern in comparison to old and large ones that lead to intercolony competition (Korb & Linsenmair 2001; Grohmann *et al.* 2010). In Loundoungou, termite mounds would be large and over-dispersed because they are old, while in Mokabi they would be small and randomly dispersed because they are young. However, we lack information on the age of the termite mounds studied to confirm or refute this hypothesis. It would be interesting to test the spatial pattern of termites mounds in other tropical forest areas where they have been observed (Guillot 1981; Lanfranchi & Schwartz 1990; Boulvert 1995a, b; Beaudrot *et al.*

2011) as well as taking into account their age to compare our results.

Species spatial patterns are influenced by termite mounds within a radius of 20 metres

Regarding our second hypothesis, we predicted that the influence of termite mound distance on tree density would be species dependent. This hypothesis was confirmed. Density of *N. kabingaensis*, *A. congolensis*, *E. cylindricum* and *E. angolense* was greater within a radius of 20 m around the termite mounds in both sites, while density of *D. crassiflora*, *E. candollei*, *A. pterocarpoides*, and *P. soyauxii* was independent from the distance to the termite mounds. Our results are similar to those found by Davies *et al.* (2016) in a southern African savannah. These authors showed that certain (riparian) species are aggregated around termite mounds, while other savannah species are not. However, in our study, aggregated species are not incoming species as reported by Davies *et al.* (2016), but forest native species (African Plant Database 2021).

Our results suggest that the local increase in tree density recorded for *N. kabingaensis*, *A. congolensis*, *E. cylindricum,* and *E. angolense* around mounds is linked to a local increase in the recruitment of these species. Indeed, giant termite mounds in savannahs are known to be fertility hotspots (Dangerfield *et al.* 1998; Traoré *et al.* 2008; Moe *et al.* 2009; Sileshi *et al.* 2010; Muvengwi *et al.* 2016) which increase both growth rates (Holt & Lepage 2000; Groen *et al.* 2008) and reproductive success (Brody *et al.* 2010). The stimulation of these two processes coupled with the seed dispersal strategy of these species, i.e. large winged or barochorus seeds (Dike & Aguguom 2010; Bénédet *et al.* 2013; Eckebil *et al.* 2017; Nuñez *et al.* 2019) dropped near the seed trees, probably explains the significant number of progeny observed in the vicinity of the seed tree. On the other hand, the absence of a local increase in tree density recorded for *D. crassiflora*, *E. candollei*, *A. pterocarpoides,* and *P. soyauxii* is hypothesised to be linked to (i) lack of stimulation of growth and reproduction processes by mounds and/or (ii) a long-distance seed dispersal strategy, i.e. endozoochory (Deblauwe 2021) or long-distance abiotic dispersion (Dike & Aguguom 2010; Nuñez *et al.* 2019; Yakusu *et al.* 2021).

The suggested impact of termite mounds on the growth and reproduction processes, and the impact on the spatial pattern of trees probably result from termite-induced changes in the physical and chemical soil properties, such as a local increase in calcium (Ca) concentration. This increase in Ca concentration was found in Loundoungou (Lenz 2018) and suspected at Mokabi. *Entandrophragma cylindricum*, which was aggregated within a 20 m radius around termite mounds, has been reported to be associated with high concentrations of Ca in the soil (Hall *et al.* 2004). The highest density of *E. cylindricum* observed around mounds could therefore be linked to a local increase in the Ca concentration. On the other hand, *E. candollei,* which we described as randomly distributed around the mounds, has low Ca requirements according to Hall *et al.* (2004). This low affinity for Ca could explain its random pattern in the two sites, despite a short-distance seed dispersal strategy (Yakusu *et al.* 2021) and the increase in Ca fertility produced by the termite mounds.

In seven of the species we studied, tree responses differed in the two sites. We are unable to explain the different patterns observed in the two study sites based on soil characteristics. This observation illustrates the limitations of our study. To go further and to better understand our results, we need to study more forest sites with a spatial pattern of termite mounds. Another limitation of our study

is that our data do not distinguish between active or abandoned mounds, which influences the fertility hotspot created by termites (Lenz 2018) and hence the pattern of vegetation. The lack of this information means we were unable to take their temporal dynamics into consideration. To overcome this limitation, it would be necessary to carry out systematic inventories of large forest termite mounds during logging inventories conducted by timber concessions as well as in forest research plots.

References

Adeleye MA, Connor SE and Haberle SG (2021) A quantitative synthesis of Holocene vegetation change in Nigeria (Western Africa). *The Holocene* **31**, 1681–1689.

African Plant Database (2021) Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria. Version 3.4.0. http://africanplantdatabase.ch.

Aloni J (1975) Le sol et l'évolution morphologique des termitières géantes du Haut-Shaba (Rép. Zaïre). *Pédologie* **25**, 25–39.

Baddeley AJ, Møller J and Waagepetersen R (2000) Non- and semi-parametric estimation of interaction in inhomogeneous point patterns. *Statistica Neerlandica* **54**, 329–350.

Baddeley A, Rubak A and Turner R (2015) *Spatial Point Patterns: Methodology and Applications with R*. London: Chapman and Hall/CRC Press.

Bayon G, Dennielou B, Etoubleau J, Ponzevera E, Toucanne S and Bermell S (2012) Intensifying weathering and land use in iron age Central Africa. *Science* **335**, 1219–1222.

Bayon G, Schefuss E, Dupont L, Borges AV, Dennielou B, Lambert T, Mollenhauer G, Monin L, Ponzevera E, Skonieczny C and André L (2019) The roles of climate and human land-use in the late Holocene rainforest crisis of Central Africa. *Earth and Planetary Science Letters* **505**, 30–41.

Beaudrot L, Du Y, Rahman Kassim A, Rejmánek M and Harrison RD (2011) Do epigeal termite mounds increase the diversity of plant habitats in a tropical rain forest in peninsular Malaysia? *PLoS ONE* **6**, e19777.

Bénédet F, Doucet JL, Fayolle A, Gillet JF, Gourlet-Fleury S and Vincke D (2013) CoForTraits, African plant traits information database v.1.0, https://doi.org/10.18167/DVN1/Y2BIZK.

Bostoen K, Clist B, Doumenge C, Grollemund R, Hombert JM, Koni Muluwa J and Maley J (2015) Middle to late Holocene paleoclimatic change and the early Bantu expansion in the rain forests of western Central Africa. *Current Anthropology* **56**, 354–384.

Boulvert Y (1995a) *Étude géomorphologique de la République Centrafricaine: Carte à 1: 1 000 000 en Deux Feuilles Ouest et Est*. Paris: Institut de Recherche Pour le Développement.

Boulvert Y (1995b) Répartition en Centrafrique et exigences écologiques des trois principales espèces de termitières géantes, cathédrales ou champignons. *Cahiers géologiques* **125**, 1501–1509.

Bremond L, Bodin SC, Bentaleb I, Favier C and Canal S (2017) Past tree cover of the Congo Basin recovered by phytoliths and δ13C along soil profiles. *Quaternary International* **434**, 91–101.

Brody AK, Palmer TM, Fox-Dobbs K and Doak DF (2010) Termites, vertebrate herbivores, and the fruiting success of *Acacia drepanolobium*, *Ecology* **91**, 399–407.

Clist B, Bostoen K, De Maret P, Eggert MKH, Höhn A, Mbida Mindzié C, Neumannd K and Seidensticker D (2018) Did human activity really trigger the late Holocene rainforest crisis in Central Africa? *Proceedings of the National Academy of Sciences of the USA* **115**, E4733–E4734.

Collins NM (1977) Vegetation and litter production in Southern Guinea savanna, Nigeria. *Oecologia* **28**, 163–175.

Dangerfield JM, Mccarthy TS and Ellery WN (1998) The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology* **14**, 507–520.

Davies AB, Baldeck CA and Asner GP (2016) Termite mounds alter the spatial distribution of African savanna tree species. *Journal of Biogeography* **43**, 301–313.

Davies AB, Levick SR, Asner GP, Robertson MP, Van Rensburg BJ and Parr CL (2014) Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. *Ecography* **37**, 852–862.

Deblauwe V (2021) Life history, uses, trade and management of *Diospyros crassiflora Hiern*, the ebony tree of the Central African forests: a state of knowledge. *Forest Ecology and Management* **481**, 118655.

Dike MC and Aguguom AC (2010) Fruits/seeds weights, flight patterns and dispersal distances of some Nigerian rainforest tree species. *Journal of Agricultural and Biological Science* **5**, 56–60.

Eckebil PPT, Verheggen F, Doucet J-L, Malaisse F, Daïnou K, Cerutti PO and Vermeulen C (2017) *Entandrophragma cylindricum (Sprague)* Sprague (Meliaceae), une espèce ligneuse concurrentielle en Afrique centrale (synthèse bibliographique). *Biotechnology, Agronomy, Society Environment* **21**, 80–97.

Eggleton P, Williams PH and Gaston KJ (1994) Explaining global termite diversity: productivity or history? *Biodiversity and Conservation* **3**, 318–330.

Erens H, Boudin M, Mees F, Mujinya BB, Baert G, Strydonck MV, Boeckx P and Van Ranst E (2015) The age of large termite mounds—radiocarbon dating of *Macrotermes falciger* mounds of the Miombo woodland of Katanga, DR Congo. *Palaeogeography, Palaeoclimatology, Palaeoecology* **435**, 265–271.

Erpenbach BR, Wittig T and Hahn K (2013) Termite-mound vegetation along a climatic gradient. *Journal of Tropical Ecology* **29**, 11–23.

Evangelista DA, Wipfler B, Béthoux O, Donath A, Fujita M, Kohli MK, Legendre F, Liu S, Machida R, Misof B, Peters RS, Podsiadlowski L, Rust J, Schuette K, Tollenaar W, Ware JL, Wappler T, Zhou X, Meusemann K and Simon S (2019) An integrative phylogenomic approach illuminates the evolutionary history of cockroaches and termites (Blattodea). *Proceedings of the Royal Society B: Biological Sciences* **286**, 20182076.

Fagundes TM, Ordonez JC and Yaghoobian N (2021) The role of mound functions and local environment in the diversity of termite mound structures. *Journal of Theoretical Biology* **527**, 110823.

Fayolle A, Picard N, Doucet J-L, Swaine M, Bayol N, Bénédet F and Gourlet-Fleury S (2014) A new insight in the structure, composition and functioning of central African moist forests. *Forest Ecology and Management* **329**, 195–205.

Forni E, Rossi V, Gillet J-F, Bénédet F, Cornu G, Freycon V, Zombo I, Mazengue M, Alberny E, Mayinga M, Istace V and Gourlet-Fleury S (2019) Dispositifs permanents de nouvelle génération pour le suivi de la dynamique forestière en Afrique centrale: bilan en République du Congo. *Bois et Forêts des Tropiques* **341**, 55–70.

Freycon V (2014) *Caractérisation des Sols de Loundoungou et de Mokabi (Congo) (Rapport de Mission DynAfFor)*. Montpellier: Cirad.

Freycon V, Wonkam C, Fayolle A, Laclau JP, Lucot E, Jourdan C, Cornu G and Gourlet-Fleury S (2015) Tree roots can penetrate deeply in African semi-deciduous rain forests: evidence from two common soil types. *Journal of Tropical Ecology* **31**, 13–23.

Freycon V, Roisin Y, Bousserrhine N, Forni E and Gourlet-Fleury S (2018) *Caractérisation des Termitières de Loundoungou et de Mokabi (Congo). Préparation de Stages sur les Relations Termitières-Sols. (Rapport de Mission DynAfFor)*. Montpellier: Cirad.

Garcin Y, Deschamps P, Ménot G, De Saulieu G, Schefuß E, Sebag D, Dupont LM, Oslisly R, Brademann B, Mbusnum KG, Onana JM,

Ako AA, Epp LS, Tjallingii R, Strecker MR, Brauer A and Sachse D (2018) Early anthropogenic impact on Western Central African rainforests 2,600 years ago. *Proceedings of the National Academy of Sciences* **115**, 3261–3266.

Giresse P, Maley J and Chepstow-Lusty A (2020) Understanding the 2500 year BP rainforest crisis in West and Central Africa in the framework of the late Holocene: pluridisciplinary analysis and multiarchive reconstruction. *Global and Planetary Change* **192**, 103257.

Giresse P, Maley J, Doumenge C, Philippon N, Mahé G, Chepstow-Lusty A, Aleman J, Lokonda M and Elenga H (2018) Paleoclimatic changes are the most probable causes of the rainforest crises 2,600 years ago in Central Africa. Proceedings of the National Academy of Sciences 115, E6672–E6673.

Grassé P-P and Noirot C (1951) Nouvelle recherches sur la biologie de divers termites champignonnistes (Macrotermitinae). *Annales des Sciences Naturelles, Zoologie (11e série)* **13**, 291–342

Groen TA, Van Langevelde F, Van de Vijver CADM, Govender N and Prins HHT (2008) Soil clay content and fire frequency affect clustering in trees in South African savannas. *Journal of Tropical Ecology* **24**, 269–279.

Grohmann C, Oldeland J, Stoyan D and Linsenmair KE (2010) Multi-scale pattern analysis of a mound-building termite species. *Insectes Sociaux* **57**, 477–486.

Guillot B (1981) Rendements de la cacaoculture et formations végétables: essai d'écologie pratique des forêts de la Sangha (Congo) et du sud-est du Cameroun. *Orstom Sciences Humaines XVIII*, 63–106.

Hall JS, McKenna JJ, Ashton PMS and Gregoire TG (2004) Habitat characterizations underestimate the role of edaphic factors controlling the distribution of *Entandrophragma*. *Ecology* **85**, 2171–2183.

Holt JA and Lepage M (2000) *Termites and soils properties*. In Abe T, Bignell DE and Higashi M (eds), *Termites: Evolution, Sociality, Symbioses, Ecology*. Dordrecht: Springer Netherlands, pp. 389–408.

Jones CG, Lawton JH and Shachak M (1994) Organisms as ecosystem engineers. *Oikos* **69**, 373–386.

Joseph S, Seymour CL, Cumming GS, Cumming DHM and Mahlangu Z (2013) Termite mounds as islands: woody plant assemblages relative to termitarium size and soil properties. *Journal of Vegetation Science* **24**, 702–711.

Krishna K, Grimaldi DA and Krishna V (2013) Treatise on the isoptera of the World. 4. Termitidae (Part One). *Bulletin of the American Museum of Natural History* **377**, 975–1494.

Korb J and Linsenmair KE (2001) The causes of spatial patterning of mounds of a fungus-cultivating termite: results from nearest-neighbour analysis and ecological studies. *Oecologia* **127**, 324–333.

Lanfranchi R and Schwartz D (1990) *Evolution des paysages de la Sangha (R.P. du Congo) au Pléistocène supérieur : bilan des observations archéologiques, géomorphologiques, pédologiques et paléobiologiques*. In Lanfranchi R and Schwartz D (eds), *Paysages Quaternaires de l'Afrique Centrale Atlantique*. Paris: Orstom, pp. 248–259.

Lavelle P, Bignell D, Lepage M, Wolters V, Roger PA, Ineson P, Heal OW and Dhillion S (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology* **33**, 159–193.

Lenz S (2018) *Influence des Termites Macrotermes Amplus Sur les Propriétés Physico- Chimiques des Termitières et des Sols Environnants Dans un Écosystème Forestier, République du Congo. (Rapport de Mission Stage)*. Montpellier: Cirad.

Lepage M (1984) Distribution, density and evolution of M*acrotermes bellicosus* nests (Isoptera: Macrotermitinae) in the North-East of Ivory Coast. *Journal of Animal Ecology* **53**, 107–117.

Levick SR (2010) The spatial extent of termite influences on herbivore browsing in an African savanna. *Biological Conservation* **143**, 2462–2467.

Levick SR, Asner GP, Chadwick OA, Khomo LM, Rogers KH, Hartshorn AS, Kennedy-Bowdoin T and Knapp DE (2010) Regional insight into savanna hydrogeomorphology from termite mounds. *Nature Communications* **1**, 65.

Lotwick HW and Silverman BW (1982) Methods for analysing spatial processes of several types of points. *Journal of the Royal Statistical Society. Series B (Methodological)* **44**, 406–413.

Loubota Panzou GZ, Fayolle A, Feldpausch TR, Ligot G, Doucet J-L, Forni E, Zombo I, Mazengue M, Loumeto JN and Gourlet-Fleury S (2018) What controls local-scale aboveground biomass variation in central Africa? Testing structural, composition and architectural attributes. *Forest Ecology and Management* **429**, 570–578.

Loumeto JJ (2003) *Litterfall and nutriment return in tropical rainforest in the Chaillu area (southwest Congo)*. In Tiezzi E, Brebbia CA and Uso JL (eds), *Ecosystems and Sustainable Development*. Brazzaville: Witpress, pp. 1238–1249.

Loveridge JP and Moe SR (2004) Termitaria as browsing hotspots for African megaherbivores in miombo woodland. *Journal of Tropical Ecology* **20**, 337–343.

Maley J, Doumenge C, Giresse P, Mahé G, Philippon N, Hubau W, Lokonda MO, Tshibamba JM and Chepstow-Lusty A (2018) Late Holocene forest contraction and fragmentation in central Africa. *Quaternary Research* **89**, 43–59.

Marcon E and Puech F (2017) A typology of distance-based measures of spatial concentration. *Regional Science and Urban Economics* **62**, 56–67.

Marcon E, Traissac S, Puech F and Lang G (2015) Tools to characterize point patterns: dbmss for R. *Journal of Statistical Software* **67**, 1–15.

Martin SJ, Funch RR, Hanson PR and Yoo E-H (2018) A vast 4,000-year-old spatial pattern of termite mounds. *Current Biology* **28**, R1292–R1293.

Moe SR, Mobæk R and Narmo AK (2009) Mound building termites contribute to savanna vegetation heterogeneity. *Plant Ecology* **202**, 31–40.

Mueller UG and Gerardo N (2002) Fungus-farming insects: multiple origins and diverse evolutionary histories. *Proceedings of the National Academy of Sciences of the United States of America* **99**, 15247–15249.

Muvengwi J, Ndagurwa HGT, Nyenda T and Mbiba M (2016) Nutrient dynamics and plant assemblages of *Macrotermes falciger* mounds in a savanna ecosystem. *Acta Oecologica* **76**, 13–21.

Nuñez CL, Clark JS, Clark CJ and Poulsen JR (2019) Low-intensity logging and hunting have long-term effects on seed dispersal but not fecundity in Afrotropical forests. *Aob Plants* **10**, ply074.

Peel MC, Finlayson BL and McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* **12**, 1633–1644.

Pomeroy D (2005) Dispersion and activity patterns of three populations of large termite mounds in Kenya. *Journal of East African Natural History* **94**, 319–341.

Pringle RM, Doak DF, Brody AK, Jocqué R and Palmer TM (2010) Spatial pattern enhances ecosystem functioning in an African savanna. *PLoS Biology* **8**, e1000377.

Pringle RM and Tarnita CE (2017) Spatial self-organization of ecosystems: integrating multiples mechanisms of regular-pattern formation. *Annual Review of Entomology* **62**, 359–377.

Pullan RA (1979) Termite hills in Africa: their characteristics and evolution. *Catena* **6**, 267–291.

Réjou-Méchain M, Mortier F, Bastin JF, Cornu G, Barbuer N, Bayol N, Bénédet F, Bry X, Dauby G, Deblauwe V, Doucet JL, Doumenge C, Fayolle A, Garcia C, Kibambe Lubamba JP, Loumeto JJ, Ngomanda A, Ploton P, Sonké B, Trottier C, Vimal R, Yongo O, Pélissier R and Gourlet-Fleuty S (2021) Unveiling African rainforest composition and vulnerability to global change. *Nature* **593**, 90–94.

Ripley BD (1977) Modelling spatial patterns. *Journal of the Royal Statistical Society. Series B (Methodological)* **39**, 172–212.

Sileshi GW, Arshad MA, Konaté S and Nkunika POY (2010) Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns. *Journal of Vegetation Science* **21**, 923–937.

Traoré S, Tigabu M, Ouédraogo SJ, Boussim JI, Guinko S and Lepage MG (2008) *Macrotermes* mounds as sites for tree regeneration in a Sudanian woodland (Burkina Faso). *Plant Ecology* **198**, 285–295.

Weidner H (1961) Beiträge zur Kenntnis der Termiten Angolas, hauptsächlich auf Grund der Sammlungen und Beobachtungen von A. de Barros Machado (2. Beitrag). *Publicações Culturais da Companhia de Diamantes de Angola* **54**, 13–77.

Yakusu EK, Monthe FS, Bourland N, Hardy OJ, Louppe D, Lokanda FBM, Hubau W, Kahindo Muhongya JM, Van Den Bulcke J, Van Acker J, Beeckman H (2021) *Entandrophragma*: taxonomy and ecology of a genus of African tree species with economic importance. *Biotechnologie, Agronomie, Société et Environnement* **25**, 140–153.