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10.2 *Macrotermes natalensis* termite colonies in seasonally flooded savannas

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Abstract

In seasonally inundated landscapes of southern central Africa very large termite mounds of *Macrotermes natalensis* offer a refuge for flood-intolerant trees during the flood season. In the matrix landscape surrounding these islands the seasonally waterlogged and then anaerobic soil conditions and the browsing by megaherbivores during the dry season allow for grass and herbaceous vegetation only. During the rainy season each termitarium forms an isolated island which due to its relative dryness allows survival of the trees and the associated fauna. During the dry season the termites try to establish new colonies with new mounds. However, the successful formation of new termitaria islands seems to be a rare event. In this case study from Dundumwezi in the Kafue National Park, Zambia, we provide a description of the termitaria islands and their vegetation. Furthermore, we analyse spatial patterns of termite mound islands in the surroundings of Kafue National Park and Bangweulu Plains / Kasanka National Park based on remote sensing imagery. Our results confirm that competition among colonies of large termitaria in homogeneous habitats causes very regular spatial patterns.

Introduction

Vast areas of the Mopane woodlands of Angola and Zambia are seasonally inundated during the rainy season. The hot and dry southern valleys of the Luangwa and Zambezi Rivers of Zambia are dominated by Mopane and Munga woodlands (UNEP 2015). These open woodlands consisting of an overstory dominated by *Colophospermum mopane* are known to be periodically waterlogged (Krug 2017). The depth of water during peak times of the rain season (February–March) is mostly in the range of a few decimetres to half a meter.

Soil water availability is one of the major limiting factors to survival, growth, species composition and distribution of savanna tree and shrub species of southern Africa (Desanker 1995). Depending on the water uptake patterns, the physiological responses of the species in particular habitats, the inundation of areas determines the survival of particular species. Waterlogged soils inhibit survival of woody plants, mainly due to the lack of oxygen in the rhizosphere and perhaps additional toxic compounds generated in anaerobic soil redox systems. Only plants with specific adaptations like e.g. a well- developed aerenchym (many swamp reeds and herbs), aerial roots (certain mangroves) or thermo-osmotic gas transport (trees of the genus *Alnus*) are able to take up oxygen from the air and to survive in such anaerobic soils (Parolin et al. 2004, Jung et. al. 2008).

Within the southern African savannas such waterlogged soils usually carry grassy vegetation mainly composed of Poaceae and Cyperaceae, excluding woody growth forms. In Zambia these are often referred to as "Dambo".

In certain waterlogged clay soils, Mopane trees are able to grow. They often form vast natural woodlands which share various properties with the savanna-type seasonal floodplains like the Llanos, Pantanal or Chaco of Brazil.

A third vegetation landscape—widely distributed in Angola and Zambia—combines grassy and woody vegetation in a pattern which can adequately been described as a mosaic of elevated swamp islands which carry trees and that are surrounded by a matrix of predominantly grassy vegetation in the inundated plains. Similarly, in seasonal savanna wetlands in South America, termites build mounds that eventually become colonized by trees, e.g. *Curatella americana* in the Pantanal (Wantzen et al. 2016), forming regular patterns of seemingly equidistant mounds known as "campos de murundu" (Nunes da Cunha & Junk 2011, Renard et al. 2012).

Such African tree islands caused by termites have early been described. Dangerfield et al.

Figure 10.2.1: Studied termite mound islands in the seasonally inundated landscape 4.3 km north of Dundumwezi in Kafue NP. Image source Google Earth, Copyright 2021 Maxar Technology (Dundumwezi, 28.06.2012).

1998 mention termite-created islands in the Okavango Delta, that become the foci for biodiversity of woody plant species and the organisms associated with them. Mujinya et al. (2014) and Erens et al. (2015) provided further environmental and soil data. Mounds of *Macrotermes natalensis* can have the size of a house, up to 10 m high and 15 m diameter (Erens et al. 2015). In accordance to the large mass of minerals accumulated by the termites, Erens et al. (2015) provided radiocarbon age data of up to 2335 years for large termite mounds in the Miombo Woodland of Katanga, DR Congo.

Due to the size and due to the colour contrast between the dark trees on the termite mounds and lighter grassland between them, this vegetation mosaic is easily spotted in satellite and aerial images. Mujinya et al. (2014) showed the high spatial regularity of the termitaria, using satellite images.

Methods

Reconnaissance trips during the dry season confirmed that these woodland patches are large termite mounds. We could not find a detailed description of the morphology, vegetation and termites of these forest patches on termitaria islands. The *Macrotermes natalensis* (Haviland) termites were identified based on the morphological traits of large soldiers using the identification key of Ruelle (1970). Obviously, studies of inundated savanna vegetation during the wet season are hampered by numerous logistic problems and there are health risks. Therefore, we sampled only one inundated area during the wet season. It is located at the southwestern margin of the inundated landscape in the southern Kafue swamps, located near Dundumwezi, the southern entrance gate of the Kafue National Park.

We applied the standard methods for vegetation studies as described in Strohbach & Jürgens (2010). Most of the work had to be done by walking in shallow or deep water during the rainy season with frequent rains. The equipment had to be carried during the whole work day. Therefore, only light equipment was used. The topography was measured with folding yardsticks.

The Dundumwezi study area was explored two times. In 2000 Jürgens visited the area during the dry season. The more detailed records of the morphology, vegetation and fauna were carried out by the whole team during the peak of the vegetation period and flood season in March 2016. After some initial reconnaissance trips the team selected an area 4.3 km north of Dundumwezi. East of a forest track a rectangular area of roughly 100 m (west–east) x 200 m (north–south) containing six larger swamp island termitaria was studied (Fig. 10.2.1).

In three rectangular study areas of 1.11 km² and in one case 1 x 0.5 km, the spatial pattern of termitaria island landscape was studied using point pattern analysis (Diggle 1983). The pair-correlation function *g(r)* quantifies the organization of point-like objects in a two-dimensional space at multiple spatial scales using an increasing radius from a typical point. Pattern are compared to a null model of complete spatial randomness (CSR) or *g(r)* = 1). Deviations from CSR at certain distances can either show regularity (*g(r)* <1) indicating repulsion of objects or clumping or attraction of objects (*g(r)* >1). Regularity is often interpreted as a pattern that can result from competition between foraging animals while clumping is often observed for processes that start from a certain source like seeds falling from a tree. In order to produce sound results we calculated confidence envelopes for each pair correlation function by recalculating the pattern 999 times.

Results

While the topographical units (islands) 1 to 5 are simple mounds, island 6 is composed of three subunits named 6a, 6b, 6c. The majority of the topographical structures are not perfectly circular but have a longish shape with a maximum diameter in south-southwest-north-northeast direction. The size and selected soil properties are shown in Table 10.2.1. These measurements indicate that the termite mounds have a slightly higher pH and electrical conductivity than the surrounding grassy matrix. Soils of the termite mounds are neutral with pH generally between 6 and 7, while the matrix is slightly acidic with pH values ranging from 4.5 to 5.5. Conductivity on the mounds is surpassing 190 mS on all termite mounds while in the matrix it is always lower than 10 mS. Remarkable is the very high PO_4 content of the mounds, compared to the surrounding plains. Other soil nutrients such as potassium, magnesium or calcium do not show a clear difference between termite mound and surrounding matrix.

The organismic composition of each island was different. For example, there were 17 bush pig holes on island 4, 11 on island 5, one on island 1 and zero on all other islands. Matabele ants were seen only on island 1 and 5.

Table 10.2.1:
Basic properties and a few selected soil parameters of six termitaria islands near Dundumwezi (conductivity in μS, ion contents in ppm, texture classes:
Sg = coarse sand,
Sm = medium sand,
Sf = fine sand,
Ug = coarse silt,
Um = medium silt,
Uf = fine silt,
Tg = coarse clay,
Tm = medium clay,
Tf = fine clay)

Mound Nr	Type	Height	Diameter (max)	Compartment	pH	Cond.	Sg	Sm	Sf
1	simple	300	32	termite mound	6.63	233.00	0.53	7.85	33.05
1	simple			termite mound margin	5.80	209.00	0.51	14.12	39.80
1	simple			matrix nearby	5.54	28.10	0.00	15.82	42.10
1	simple			matrix distant	5.08	19.25	0.00	14.21	41.77
2	simple	310	34	termite mound	6.06	211.00	1.16	9.82	36.99
2	simple			matrix nearby	4.80	18.68	0.37	9.10	34.12
2	simple			matrix distant	4.50	16.78	0.00	15.14	38.96
3	simple	350	34	termite mound	7.32	219.00	1.37	8.36	32.35
3	simple			termite mound margin	5.45	35.30	1.22	19.40	40.00
3	simple			matrix nearby	4.68	17.92	2.30	20.56	34.07
4	simple	120	25	termite mound	5.82	193.20	0.90	11.35	37.99
5	simple	300	34	termite mound	6.98	317.00	2.42	11.82	33.02
6a	composed	70	7	termite mound	6.88	191.50	3.27	11.60	28.94
6b	composed	100	15	termite mound	6.93	234.00	0.35	10.99	39.87
6c	composed	260	28	termite mound	6.97	262.00	1.82	12.30	35.74

For the plant species composition see Table 10.2.2: In three out of six of the studied termite mounds Mopane trees (*Colophospermum mopane*) dominated the tree layer. In others, single individuals of Baobab (*Adansonia digitata*) or *Euphorbia ingens* stood out. Frequent but without dominating the termine mound tree vegetation were spinous trees such as *Acacia nigrescens* or *Ziziphus* spp. The shrublayer was characterised by species such as *Friesodielsia obovata, Rhus quartiniana* or *Combretum* species. Striking was the frequent occurrence of lianas such as *Carissa* sp., *Landolphia parvifolia* or *Cyphostemma* sp..

The woody vegetation showed the highest number of stems at the margin of the islands. Sometimes stems with a BHD >50 cm were also located at the top 33%: three on island 5, one on islands 2, 3 and 6a.

Also, in other regions of Zambia the pronounced dense woody vegetation at the margin of the termitaria island is found, sometimes with one or a few trees in the centre of the island (Fig. 10.2.8). In other regions the island is partially or completely used as agricultural field for cassava (*Manihot esculenta*) (Fig. 10.2.9).

The point patterns in all four rectangular study plots (Fig. 10.2.10) reveal strong regularity showing repulsion ($g(r)$ <1) between 30 and 70 m.

Table 10.2.2:
Woody vegetation of six termitaria islands near Dundumwezi. The shown figures are the total cover, i.e. the relative area of the ground surface covered by the respective species in a view from above.

Species	1	2	3	4	5	6
Colophospermum mopane	40		40	70		
Adansonia digitata					20	30
Acacia nigrescens	20			1	10	0.1
Friesodielsia obovata	30		10	5		5
Carissa sp.				15		
Grewia falcistipula				10		1
Acacia formosa			10	0.5		
Combretum sp.			10	0.5		
Euphorbia ingens	1		0.5			
Commiphora sp.		0.5			0.5	
Rhus quartiniana			0.1	0.5	0.2	0.5
Ziziphus macrophylla			5		0.5	1
Ziziphus mucronata	2					
Combretum molle	1					
Commiphora cf. *merckii*	1					
Dombeya burgessiae		0.1			1	
Ficus sycomorus		10				
Vangueriopsis longiflora		0.2		1		
Landolphia parvifolia		0.1				
Cyphostemma sp.				0.1		
Ficus sp.					3	5
Rhus sp.					0.1	

Ug	Um	Uf	Tg	Tm	Tf	Cl	$N0_2$	$N0_3$	$P0_4$	$S0_4$	Na	NH_4	K	Mg	Ca
32.02	16.21	7.77	2.56	0.01	0.00	5.12	1.31	0.00	47.01	0.42	1.32	0.00	0.57	1.38	3.27
27.64	11.50	4.93	1.50	0.00	0.00	6.53	1.76	0.00	33.01	0.00	0.00	0.80	1.60	0.18	4.05
23.26	12.19	5.46	1.17	0.00	0.00	7.29	0.00	1.03	16.45	0.34	1.81	0.00	1.50	1.17	3.47
22.52	13.51	6.41	1.60	0.00	0.00	1.81	0.00	1.41	15.77	0.00	0.76	0.00	1.11	1.20	3.55
29.35	14.27	6.69	1.73	0.00	0.00	4.94	0.00	2.25	27.23	0.00	1.78	0.00	1.04	1.22	3.58
29.35	17.13	7.41	2.52	0.01	0.00	2.47	0.00	1.12	16.67	0.00	1.11	0.00	0.22	0.85	3.44
23.54	14.01	6.48	1.87	0.00	0.00	0.00	0.00	0.00	6.11	0.00	1.83	0.00	1.43	0.20	4.03
32.15	16.32	7.04	2.36	0.05	0.00	7.10	0.74	1.40	52.27	214.47	0.98	0.00	0.04	1.23	3.42
23.78	9.67	4.95	0.97	0.00	0.00	5.46	0.26	1.09	29.32	0.00	1.81	0.00	1.12	0.74	3.96
21.57	12.77	6.88	1.85	0.00	0.00	0.75	0.00	0.95	2.46	0.00	3.03	0.00	0.92	3.10	7.26
29.53	13.21	5.55	1.46	0.00	0.00	7.43	1.32	0.00	0.00	246.60	0.00	0.00	1.41	0.18	4.20
27.19	14.94	7.77	2.83	0.00	0.00	5.93	1.02	0.00	47.30	0.00	1.67	0.83	1.26	0.18	4.54
26.79	16.77	9.40	3.21	0.02	0.00	25.46	1.99	0.00	48.72	0.00	1.72	0.80	0.73	0.20	3.94
29.22	12.09	5.80	1.69	0.00	0.00	14.65	0.00	0.00	22.82	0.00	1.69	0.00	1.37	0.13	4.07
28.12	13.56	6.60	1.86	0.00	0.00	0.00	0.00	0.00	7.21	0.00	1.67	0.80	1.38	0.16	3.98

Figure 10.2.2:
A profile through a *Macrotermes natalensis* termite mound east of Dundumwezi, caused by road works. Members of a student excursion with a 2 m folding rule illustrate the size.

Figure 10.2.3:
Macrotermes natalensis termite mound west of Dundumwezi. The student group is passing a grass plain with culms of Yellow thatching grass (*Hyperthelia dissoluta*) reaching over 2 m. The grassland is flooded by 15 cm deep water. Small termitaria islands can be seen in the background.

Figure 10.2.4:
Top of the studied termitaria island Nr. 1 north of Dundumwezi. Note the large and open ventilation tunnels.

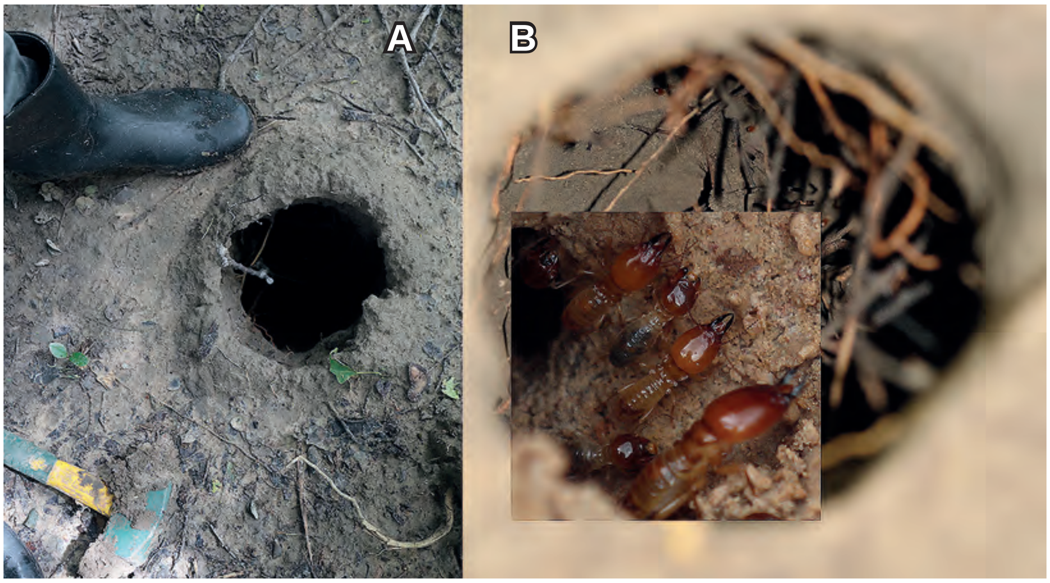

Figure 10.2.5 A and B: Top of the studied termitaria island Nr. 1 north of Dundumwezi. Open ventilation tunnels with rubber boots and a hammer for size comparison and *Macrotermes natalensis* termites at the wall of the ventilation tunnel.

Figure 10.2.6: Termitaria island north of Dundumwezi with mopane trees during the dry season. Note the pioneer formation of a new termite mound in the foreground.

Figure 10.2.7: Termitaria island north of Dundumwezi with *Euphorbia ingens* and *Colophospermum mopane* during the dry season.

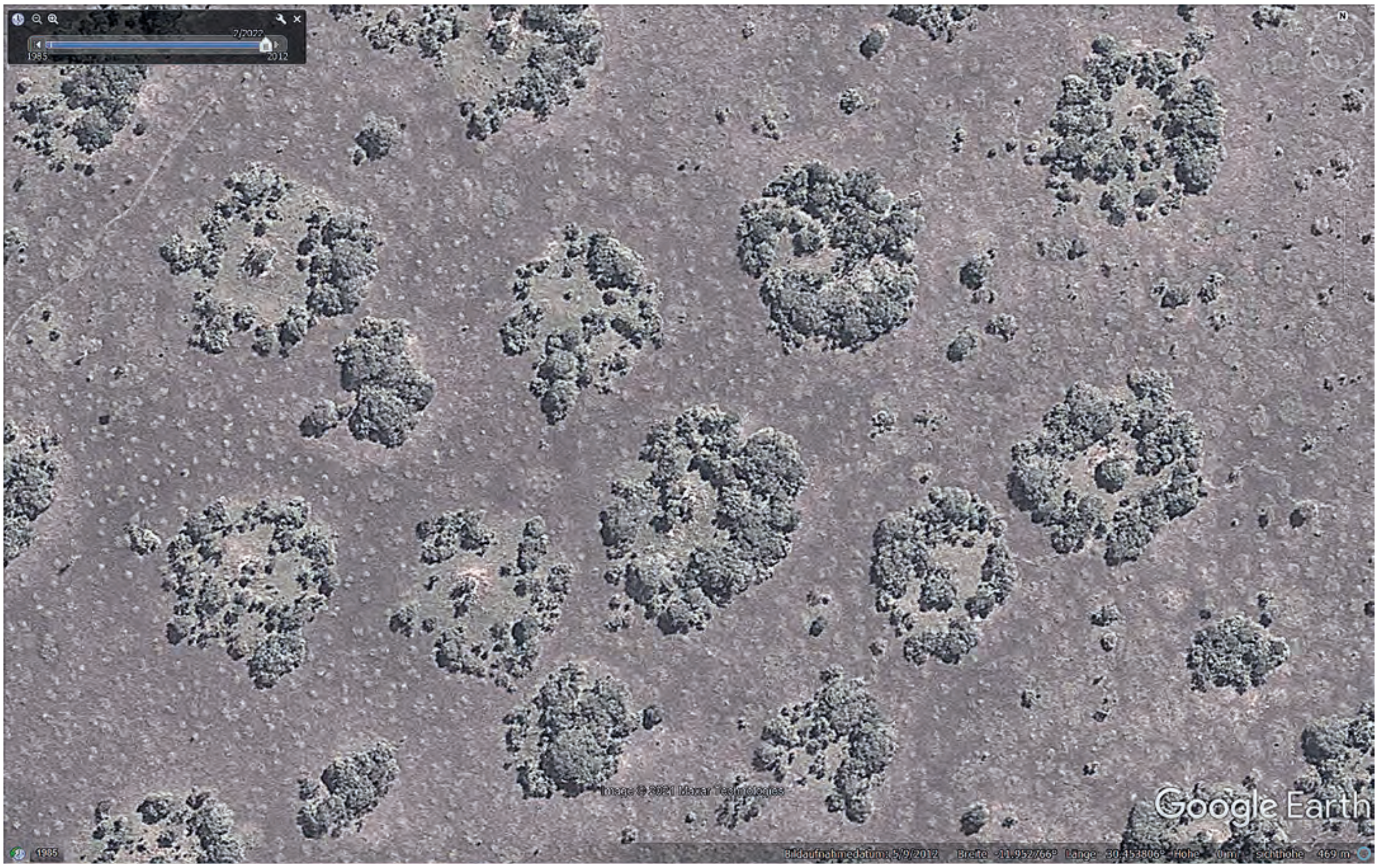

Figure 10.2.8:
Part of the study area Bangweulu/Kasanka 3. Note the regular spatial pattern of the termitaria islands, the pronounced woody vegetation at the margin and the frequent formation of one or a few woody plants in the island centre.

At higher distances the *g(r)* pattern was undulating around the null-model. The minimum distances between pairs of termitaria islands was between 20 and 70 m. Only for the fairy circles of the Namib Desert (Jürgens et al. 2013, Vlieghe et al. 2015) such high regularity was also found (Getzin et al. 2015). In fact, a high spatial regularity of the large termitaria was expected by the authors, due to the very homogeneous habitat in the vast, topographically even, flooded plains. Also, the homogeneity of the substrate of the flooded plains, sorted and deposited by water transport, may be at a similar degree as the homogeneity of the aeolian sands in vast sandy plains inhabited by fairy circles, sorted and deposited by wind.

Résumé

The here described very large termitaria in seasonally flooded woodlands merit a much higher profile and they should be studied in more detail with regard to their life history and environmental drivers. It may well be that the awareness of the tree-inhibiting conditions of seasonal floods turns earlier published results into the opposite interpretation. For example, the interpretation by Bonachela et al. (2015) of tree islands on termitaria as a product of the termites that can "enhance dryland´s resistance to and recovery from drought" should be re-visited in the light of the above described termitaria in seasonally flooded woodlands.

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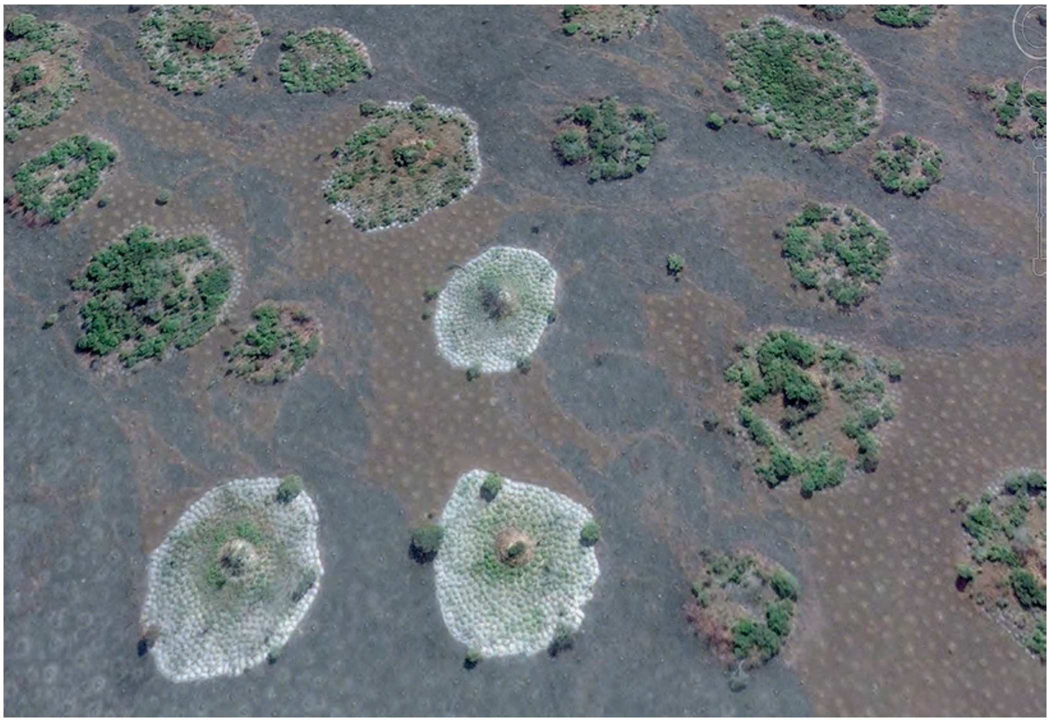

Figure 10.2.9: Termitaria islands south of Bangweulu used for agricultural plantations of cassava (*Manihot esculenta*).

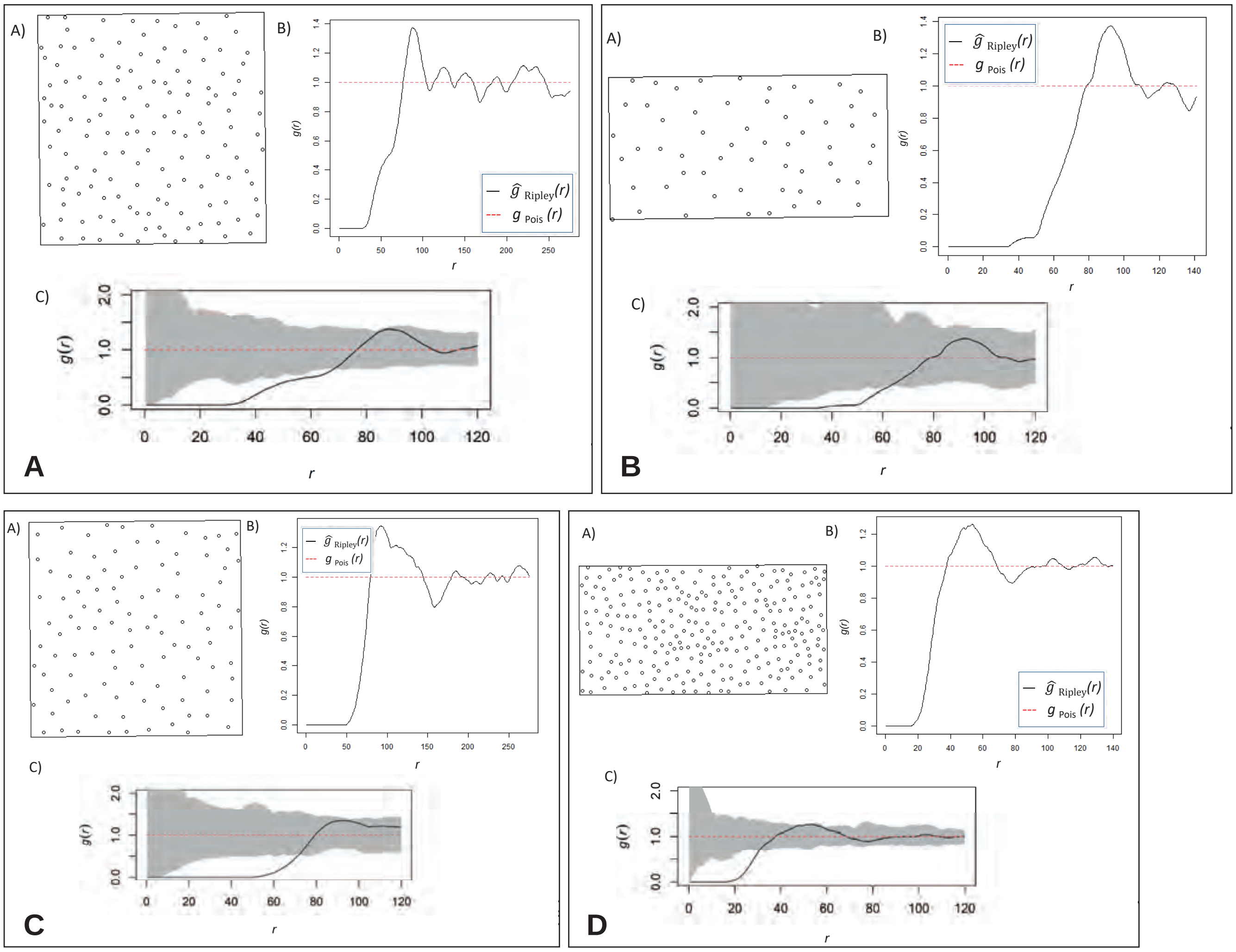

Figure 10.2.10 A, B, C, D: Pair Correlation Functions of some examples from termitaria island landscapes: A = Bangweulu/Kasanka 1 (-12.058, 30.133), B = Bangweulu/Kasanka 2 (-12.092, 30.283), C = Bangweulu/Kasanka 3 (-11.952, 30.453), D = Kafue (-16.701, 25.979).

References for Chapter 10.2

Adam, M., Mees, F., Bogaert, J., Vranken, I., Erens, H., Baert, G., Ngongo, M., Van Ranst, E. (2014) Spatial patterns and morphology of termite (Macrotermes falciger) mounds in the Upper Katanga, D.R. Congo. *Catena*, 114, 97-106.

Bonachela, J.A., Pringle, R.M., Sheffer, E., Coverdale, T.C., Guyton, J.A., Caylor, K.K., Levin, S.A., Tarnita, C.E. (2015) Termite mounds can increase the robustness of dryland ecosystems to climate change. *Science* 347, 651-655.

Dangerfield J M; McCarthy T S ; Ellery W N: 1998: The mound-building termite Macrotermes michaelsenii as an ecosystem engineer. *Journal of Tropical Ecology* 14: 507-520.

Diggle PJ (1983). Statistical analysis of spatial point patterns. Academic Press Inc

Desanker, P. V., Frost, P.G.H., Justice, C.O., & Scholes, R.J. 1995. The Miombo Network: Framework for a Terrestrial Transect Study of Land-Use and Land-Cover Change in the Miombo Ecosystems of Central Africa, *IGBP Report* 41. Stockholm, Sweden.

Erens H; Boudin M.; Mess F; Mujinya B B ; Baert G ; Van Strydonck M ; Boeckx P; Van Ranst E (2015) The age of large termite mounds – radiocarbon dating of Macrotermes falciger mounds of the Miombo woodland of Katanga, DR Kongo. *Palaeogeography, Palaeoclimatology Palaeoecology* 435: 265-271.

Getzin, S., Wiegand, K., Wiegand, T., Yizhaq, H., von Hardenberg, J., Meron, E. (2015). Adopting a spatially explicit perspective to study the mysterious fairy circles of Namibia. *Ecography*, 38(1), 1-11.

Jung, J., Lee, S.C. & Choi, HK. Anatomical patterns of aerenchyma in aquatic and wetland plants. *J. Plant Biol.* 51, 428–439 (2008). https://doi.org/10.1007/BF03036065Mujinya, B.B.,

Jürgens, N. (2013). The biological underpinnings of Namib Desert fairy circles. *Science*, 339(6127), 1618-1621.

Krug, J.H.A. Adaptation of Colophospermum mopane to extra-seasonal drought conditions: site-vegetation relations in dry-deciduous forests of Zambezi region (Namibia). *For. Ecosyst.* 4, 25 (2017). https://doi.org/10.1186/s40663-017-0112-0

Nunes da Cunha, C., and W. J. Junk. 2011. A preliminary classification of habitats of the Pantanal of Mato Grosso and Mato Grosso do Sul, and its relation to national and international wetland classification systems Pages 127-141 *in* W. J. Junk, C. J. da Silva, C. Nunes da Cunha, and K. M. Wantzen, editors. The Pantanal: Ecology, Biodiversity and Sustainble Management of a Large Neotropical Seasonal Wetland. Pensoft publishers Sofia-Moscow.

Parolin, P., O. De Simone, K. Haase, D. Waldhoff, S. Rottenberger, U. Kuhn, J. Kesselmeier, B. Kleiss, W. Schmidt, M. T. F. Piedade, and W. J. Junk. 2004. Central Amazonian Floodplain Forests: Tree adaptions in a Pulsing System. *The Botanical Review* **70**:357-380.

Renard, D., J. J. Birk, B. Glaser, J. Iriarte, G. Grisard, J. Karl, and D. McKey. 2012. Origin of mound-field landscapes: a multi-proxy approach combining contemporary vegetation, carbon stable isotopes and phytoliths. *Plant and Soil* **351**:337-353.

Ruelle, J. E. (1970) Revision of the termites of the genus Macrotermes from the Ethiopian region (Isoptera: Termitidae). *Bulletin of the British Museum Entomology*, 14, 363-444.

Strohbach, BJ & Jürgens, N. (2010) Towards a user-friendly vegetation map of Namibia: Ground truthing approach to vegetation mapping. In: Biodiversity in southern Africa: Patterns and processes at regional scale, 46-56.

Vlieghe, K., Picker, M., Ross-Gillespie, V., Erni, B. (2015). Herbivory by subterranean termite colonies and the development of fairy circles in SW Namibia. *Ecological Entomology*, 40(1), 42-49.

United Nations Environment Programme (UNEP) 2015, Benefits of Forest Ecosystems in Zambia and the role of REDD+ in a green economy transformation, UNON, Publishing Services Section, Nairobi. ISBN: 978-92-807-3452-2

Wantzen, K. M., M. R. Marchese, M. Marques, and L. Battirola. 2016. Invertebrates in Neotropical Floodplains. Pages 493-524 *in* D. Batzer and D. Boix, editors. Invertebrates in Freshwater Wetlands: An International Perspective on their Ecology. Springer, New York.