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Elephant-induced damage drives spatial isolation of the dioecious palm *Borassus aethiopum* Mart. (Arecaceae) in the Pendjari National Park, Benin

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Abstract

Spatial patterns (SP) of treefall by elephants is known to be clustered across landscapes as a result of food selection and group foraging. Yet, few studies have explicitly elucidated how elephant pressure (EP) alters SP and tree-to-tree distance of tree species especially for dioecious plant species, at stand scale. Using the pair-correlation function and distance to the nearest neighbour on spatial data from five plots of 1–1.5 ha, this article compared SP of damaged and undamaged individuals and tree-to-tree distance of the dioecious palm *Borassus aethiopum* Mart. in stands of low versus high EP in the Pendjari National Park. We tested the hypothesis that high EP would modify SP and results into isolated adults. Nested ANOVAs were used to compare distances. The overall SP of individuals did not vary, but distance among living adults was twofold extended in stands of high EP. The Janzen–Connell escape hypothesis is supported by our data for ungrazed saplings. The study concluded that increasing EP reduces density and induces spatial isolation of adults that may increase pollination failure and threat persistence of *B. aethiopum*.

Key words: Benin, *Borassus aethiopum* Mart., damages, *Loxodonta africana* Blumenbach, pair-correlation function, spatial pattern

Résumé

Il est connu que la structure spatiale (SS) de l'abattage des arbres par les éléphants est agglomérée á l'échelle du paysage du fait de leur comportement alimentaire sélectif et en groupe. Mais peu d'études ont explicité comment la pression exercée par les éléphants (PE) altère la SS et la distance d'arbre à arbre selon les espèces, spécialement chez les espèces dioïques, à l'échelle du peuplement. En utilisant la fonction de corrélation par paire et la distance par rapport au voisin le plus proche pour des données spatiales tirées de cinq placeaux de 1 à 1,5 ha, cet article a comparé la SS d'individus endommagés et intacts et la distance d'arbre à arbre pour le palmier dioïque *Borassus aethiopum* Mart. dans des peuplements de faible *vs* forte PE dans le Parc National de la Pendjari. Nous avons testé l'hypothèse selon laquelle une forte PE modifierait la SS et aboutirait à l'isolement spatial des individus adultes. Nous avons utilisé des ANOVA modèles hiérarchisés pour comparer les distances. En général la SS des individus ne variait pas mais la distance entre adultes vivants était deux fois plus grande dans des peuplements où la PE est élevée. L'hypothèse d'échappement de Janzen-Connell est confortée par nos données pour les jeunes palmiers intacts. L'étude a conclu qu'une PE croissante réduit la densité et induit un isolement spatial des adultes qui peut augmenter l'échec de la pollinisation et menacer la survie de *B. aethiopum*.

Introduction

Elucidating how species are spatially organized [spatial patterns (SP)] offers opportunity to understand the ecological processes that drive their coexistence (Law *et al.*, 2009; Martínez *et al.*, 2013; Li *et al.*, 2014). Spatial arrangement of trees is determinant in pollination success with potential consequences on seeds and seedlings

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production, especially for dioecious species (Berry, 2006; Gouwakinnou *et al.*, 2011). In dioecious species particularly, factors such as sex ratio and the distance between males and females determine the probability of successful pollination (Berry, 2006). However, some disturbances (e.g. fires, anthropogenic activities, introduction of invasive species, megaherbivores' damages) may occur and alter the original SP and thus the underlying processes (Chu, Wang & Zhang, 2014; Riginos *et al.*, 2015). From a demography perspective, these disturbances may induce growth, stability or decline of the populations (Schmidt *et al.*, 2011).

In ecosystems where plant species co-occur with megaherbivores such as elephants, alteration of trees SP may be frequent. Indeed, several studies have reported that elephants cause substantial disturbances in trees stands and may induce local extirpation of some much appreciated food species (O'Connor, Goodman & Clegg, 2007) despite their widely acknowledged ecological importance in biodiversity conservation (Blake *et al.*, 2009; Campos-Arceiz & Blake, 2011; Yessoufou *et al.*, 2013).

Elephant–plant–environment interactions have long been the focus of research. The current body of knowledge provides relatively comprehensive information on SP of intensity of elephant damage in relation to watering points (Loarie, Aarde & Pimm, 2009a), greenness of vegetation/landscape (Loarie, Aarde & Pimm, 2009b; Valeix *et al.*, 2011), life-history stages (Levick & Asner, 2013; Kassa *et al.*, 2014), soil types and plant nutrient content (Holdo, 2003; Shrader *et al.*, 2012), and management systems (Loarie, Aarde & Pimm, 2009a). Yet, fine-scale impact of elephant pressure (i.e. how does elephant pressure alter SP of tree species especially dioecious plant species at stand scale?) has so far been poorly elucidated. Understanding how SP of trees has been modified by increasing elephant pressure may improve current knowledge on plant–animal interactions particularly with regard to processes shaping biodiversity patterns and driving local extinction of plant species. Indeed, alteration of SP that leads to an increase in distances between reproductive males and females may result in pollination failure, hindering reproductive process and gene flow (Somanathan & Borges, 2000).

Recent investigations on SP of treefall by elephants at landscape scale show a significant clustering pattern (Levick & Asner, 2013) which has been attributed to group foraging behaviours of elephants, and their selective choice for preferential food (Calenge *et al.*, 2002). Examining SP of treefall at finer scale (i.e. at stand scale) is also crucial to understand how the demography of a species especially a dioecious species may be affected.

This study is a part of a research project examining interactions between elephants and the dioecious palm species, *Borassus aethiopum* Mart. in the Pendjari National Park (PNP) in Benin (west Africa) by the first author. Previous observations revealed adult uprooting as the major damage of elephant to *B. aethiopum*, and based on density of this damage, stands were categorized into stands of high and low elephant pressure (EP) (ongoing work by Salako K.V. in the PNP). It was also observed that saplings were the most grazed individuals and EP had no significant effect on adults' sex ratio. Here, we aim to assess how EP affects SP and tree-to-tree distance of *B. aethiopum* individuals. Earlier study on SP of *B. aethiopum* showed an aggregated spatial distribution of juveniles, saplings and seedlings, while adults have a random pattern or were more loosely aggregated (Barot, Gignoux & Menaut, 1999). Seedlings were associated with female adults because of the low dispersal distance of the heavy fruits (Barot, Gignoux & Menaut, 1999).

Based on the evidence that increasing EP would result in low densities of adult *B. aethiopum*, we predicted that high EP would affect SP of *B. aethiopum* and result into increased distance among adult individuals especially between males and females. In plant–animal interactions, distance of offspring to mother trees has been identified as a key factor for escaping herbivores' damages (Janzen, 1975; Wahungu *et al.*, 2009). This hypothesis known as the Janzen–Connell escape hypothesis predicts that predators (elephants here) would concentrate their foraging activities near mother trees where seed input is the highest (Janzen, 1975). As such, offspring standing far from mother trees will likely escape damages and successfully recruit. We would then expect grazed saplings to be closer to adult female trees than ungrazed saplings are.

Material and methods

Study system

The study took place in the Pendjari National Park (PNP, 10°30′–11°30′N & 0°50′–2°00′E, Fig. 1), a protected area that covers ~2660 km² and provides one of the few remaining refugia for elephants in west Africa (Bouché *et al.*, 2011). The PNP is located in northern Benin (West Africa) in the semi-arid zone with one rainy season (April/May–October) and one dry season (November–March).

The mean total annual rainfall is ~1000 mm, and the mean annual daily temperature is 27°C. The vegetation is made up of a mosaic of shrubs, trees, woodland savannahs and grasslands (Sokpon *et al.*, 2008). The PNP is mainly watered by the Pendjari River, 300 km long, which is surrounded by several natural ponds (Fig. 1) which attracts a variety of animals, including elephants particularly during the dry season.

Borassus aethiopum is a common dioecious palm species in west African humid savannahs (Barot *et al.*, 2000) that provides important food resources for elephants (Giffard, 1967). It occurs in marshy areas and along water courses (Azihou *et al.*, 2013). In the PNP, stands of *B. aethiopum* of 100–300 m width connected by small linear patches are found along the Pendjari River (Azihou, 2013) and close to natural ponds. Four main successive life-history stages are distinguishable in *B. aethiopum*: seedlings bearing only entire leaves or slit leaves, saplings which have fan-shaped leaves but not stemmed, juveniles which have fan-shaped leaves but stemmed, and adults (reproductive), stemmed and with the same fan-shaped leaves as juveniles (Barot *et al.*, 2000).

In the PNP, population of elephant has slightly increased from 826 individuals in 1985–1991 to 869 individuals in 2005–2010 (Bouché *et al.*, 2011). However, high annual fluctuations have been found in their abundance, possibly as a result of migration from bordering reserves (Tehou, 2002). Elephants are now found everywhere in the PNP (P.A.P.E., 2013; Kassa *et al.*, 2014) with Porga, Arly and Konkombri having the highest density (Bouche *et al.*, 2004; Tehou *et al.*, 2012; P.A.P.E., 2013).

Sampling and data collection

An ongoing work on elephant damage to *B. aethiopum* by the first author in the PNP revealed that leaves of saplings

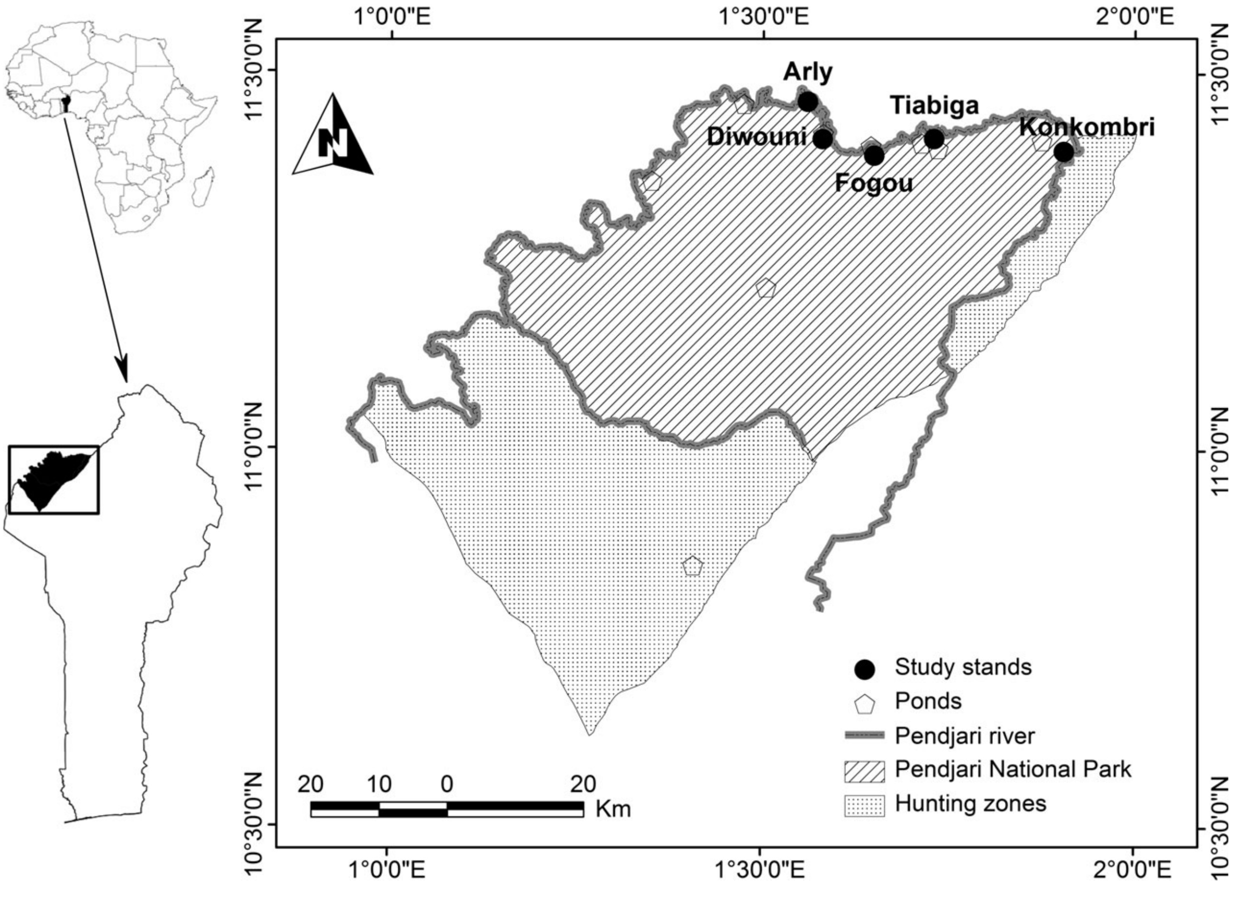

Fig 1 Study area showing the Pendjari River, the ponds and the study stands

and juveniles are grazed while the most harmful damage, that is uprooting, occurs only in adults. Stands at Diwouni and Tiabiga (Fig. 1) were subject to low EP (~35 uprooted adult trees.ha^{-1}), while stands at Arly, Fogou and Konkombri (Fig. 1) were subject to high EP (~120 uprooted adult trees.ha^{-1}).

The SP of *B. aethiopum* stands was studied in five plots of different sizes distributed in the five stands (Table 1, Fig. 1). Plots were selected so as close as possible to the overall pattern of each stand (Table 1). In each plot, all adults, juveniles and saplings (damaged and undamaged) of *B. aethiopum* were mapped. Starting from a reference tree, the mapping process consisted of measuring distance, azimuth and slope to the successive and nearest neighbours' trees using a laser-distance meter, a compass and a clinometer, respectively. Seedlings were too numerous and were not mapped. Juveniles were practically absent (see Table 1) and were not considered in the analyses.

Statistical analyses

Arpent 1.3.d. software (Lejeune, 2001) was used to convert distance, azimuth and slope data in x and y coordinates. Fine-scale SP of trees can be studied with the pair-correlation function (see Benot *et al.*, 2013). The global pair-correlation function g for a point process of two types of stimuli i and j (referred to *B. aethiopum* life stages, with or without elephant-caused damages, see first column of Table 1) is (Baddeley & Turner, 2005) as follows:

$$g_{i,j}(r) = \frac{K'_{i,j}(r)}{2\pi r}$$

where $K'_{i,j}(r)$ is the derivative of the Ripley's K function $K_{i,j}(r)$ (Ripley, 1981) of the point process at distance r.

This function was used to determine whether the distribution of each mapped stimulus was random, aggregated or regular; whether the relationship between two stimuli suggests spatial association, repulsion or independence; and the spatial scale at which these patterns occurred (Stoyan & Stoyan, 1994).

When only one stimulus is concerned, the analysis is univariate and for two stimuli, the analysis is bivariate. The significance of any observed pattern that deviates from the distribution expected under the null model (complete spatial randomness for univariate SP or spatial independence for bivariate SP) was assessed by comparing the observed distribution function to the confidence envelope generated by 500 Monte Carlo simulations of the null model (Diggle, 2003). When $g(r)$ was for a given scale r outside the simulation envelopes ($\neq 1$), the null hypothesis was rejected at this scale. For a univariate point pattern, $g(r) = 1$ indicates randomness, while $g(r) > 1$ and $g(r) < 1$ indicate clumping and regularity, respectively. For a bivariate point pattern, $g_{i,j}(r) = 1$ indicates a spatial independence whereas $g_{i,j}(r) > 1$ and $g_{i,j}(r) < 1$ indicate a positive association (attraction) and a negative association (repulsion), respectively. Spatial analyses were carried out in the package *spatstat* (Baddeley & Turner, 2005) of the statistical software R 3.0.3 (R Core Team, 2014).

Table 1 Number of the various mapped individuals in each stand (plot). Diwoumi, Tiabiga, Arly, Fogou and Konkombri are the names of the sites where the measurements took place

	Low pressure		High pressure		
Mapped individuals (stimuli)	Diwouni 100 × 120 m²	Tiabiga 100 × 120 m²	Arly 100 × 150 m²	Fogou 100 × 130 m²	Konkombri 100 × 100 m²
Saplings ungrazed	5	3	1	10	11
Saplings grazed	56	101	164	203	197
Juveniles ungrazed	1	0	0	0	0
Juveniles grazed	0	0	0	0	2
Saplings–Juveniles dead	2	2	7	9	17
Adults female	98	99	23	21	22
Adults male	115	106	39	25	18
Adults-uprooted	46	39	155	138	116
Other trees	12	16	57	28	8
Total	335	366	446	434	391

Statistical significance was set to 5%. Functions *nndist* and *nncross* of the package *spatstat* were used to compute the distance *d* from each point to its nearest neighbour for univariate and bivariate point pattern analyses, respectively. These distances allow analysing spacing between individuals of the same or different types. Nested ANOVA models were used to test whether EP and stands affect *d*. To test the Janzen–Connell escape hypothesis, distance of ungrazed saplings to female adults was compared to distance of grazed saplings to female adults using two samples *t*-test.

Results

Univariate SP

Undamaged individuals. Results of the univariate SP analyses are summarized in Table 2. Very few ungrazed saplings were found in stands of low EP, that is Tiabiga and Diwouni, and thus did not permit to build a SP. Conversely, in stands of high EP where they were relatively abundant, ungrazed saplings were aggregated in clumps of 3-6 m radius, except Konkombri where they were randomly distributed (Fig. 2-Ia, Table 2). In all stands except Fogou where clumps of 2–6 m radius were found, undamaged adult palms, irrespective of sex, had a random pattern (Table 2). Adult males and females also had a random pattern in all plots (Fig. 2-Ib, Table 2).

Overall SP did not vary much with EP. However, looking at the distance among individuals (Table 2), we found that EP significantly affects distance to nearest neighbour (P-value = 0.000, Table 3). Undamaged adults were less distant in stands of low EP as compared to stands with high EP (about 1.5-fold); 9.67 ± 0.23 m versus 14.41 ± 0.95 m, 13.60 ± 0.44 m versus 21.17 ± 1.71 m, 15.28 ± 0.50 m versus 22.05 ± 1.78 m for adults irrespective of sex, male and female, respectively (Table 2).

Damaged individuals. Uprooted adults had an aggregated pattern in stands of low EP and a random pattern in stands of high EP (Fig. 2-IIa), except Arly where 5 m radius clumps were found (Table 2). For all r values, grazed saplings were aggregated while dead saplings and juveniles had random pattern irrespective of the EP and the stands (Fig. 2-IIb, Table 2). Combining ungrazed and grazed individuals, saplings showed an aggregated pattern irrespective of stands. Conversely, combined adults (uprooted + live) showed an aggregated pattern in stands of low EP but random pattern in stands of high EP (Table 2).

Except for uprooted adults, the overall SP did not vary much with EP. However, level of EP significantly affected distance to nearest neighbour (P-value < 0.05, Table 3) except for combined adults (uprooted + live) (P-value = 0.054, Table 3). Uprooted adults and grazed saplings were distant in stands of low EP but close in stands of high EP; 10.16 ± 0.38 m versus 8.82 ± 0.31 m and 9.01 ± 0.34 m versus 4.36 ± 0.17 m, respectively (Table 2). Comparing distance among combined uprooted and live adult trees (reflecting original SP) to the distance among only live adults (reflecting situation after uprooting by elephants), it came out that high EP has significantly increased distance among live adult trees (t-value = 14.30, df = 1234, P-value = 0.000); from 6.98 ± 0.12 m to 9.67 ± 0.23 m (about 1.5-fold increase) and from 7.33 ± 0.20 m to 14.41 ± 0.95 m (about twofold increase), in stands of low and high EP, respectively (Table 2). There was, however, no significant effect of stands on distances among trees for a given EP (P-value > 0.05, Table 3).

Bivariate SP

Undamaged individuals. Males were either associated with or independent from females in both stands of low and high EP (Table 2). Ungrazed saplings were always spatially independent from live adults, males and females (Fig. 2-Ic & Table 2). Adult males and females were significantly (P-value < 0.05, Table 3) and two times more distant in stands of high EP (11.61 ± 1.27 m) than in stands of low EP (5.62 ± 0.31 m). Ungrazed saplings were significantly (P-value < 0.05, Table 3) distant two times far from adults in stands of low EP (60.02 ± 2.89 m to 62.71 ± 2.24 m) than they were in stands of high EP (32.95 ± 3.24 m to 38.92 ± 2.86 m) (Table 2).

Damaged individuals. Grazed saplings and dead saplings and juveniles were all spatially independent from uprooted adults (Fig. 2-IIc & Table 2). But grazed saplings were found significantly (P-value = 0.019, Table 3) closer to uprooted adults in stands of low EP (7.88 ± 0.41 m) than in stands of high EP (10.60 ± 0.73 m; Table 2). The reverse was true for dead saplings and juveniles (P-value = 0.000, Table 3), 36.10 ± 1.17 m and 19.81 ± 0.94 m for low and high EP, respectively.

Table 2 Results of the univariate and bivariate analyses of the spatial patterns of individuals of *B. aethiopum* in five stands in the PNP

Items, life stages and damages	Spatial patterns (r in m) [1]					d_{ii}/d_{ij} [2] (m)	
	Tiabiga	Diwouni	Arly	Fogou	Konkombri	Low pressure	High pressure
Undamaged – Univariate analyses							
Adults (Males + Females)	n	n	n	a (2-6)	n	9.67 ± 0.23^{b}	14.41 ± 0.95^{a}
Males		n	n	n	n	13.60 ± 0.44^{b}	21.17 ± 1.71^{a}
Females	n	n	n	n	n	15.28 ± 0.50^{b}	22.05 ± 1.78^{a}
Saplings ungrazed	NA	NA	a (0–6)	a (0–3)	n	–	23.17 ± 4.55
Damaged - Univariate analyses							
Adults-uprooted (burned + not burned)	a	a	a (0–5)	n	n	10.16 ± 0.38^{a}	8.82 ± 0.31^{b}
All adults (uprooted + live)	a	a	n	n	n	6.98 ± 0.12^{a}	7.33 ± 0.20^{a}
Saplings grazed	a	a	a	a	a	9.01 ± 0.34^{a}	4.36 ± 0.17^{b}
All saplings (grazed + ungrazed)	a	a	a	a	a	9.27 ± 0.39^{a}	4.49 ± 0.17^{b}
(Saplings + Juveniles) dead	NA	NA	n	n	n	–	25.07 ± 2.82
Undamaged ($i \times j$) - Bivariate analyses							
Females × Males	n	n	n	n	n	5.62 ± 0.31^{b}	11.61 ± 1.27^{a}
Males × Ungrazed saplings	NA	NA	n	n	n	62.71 ± 2.24^{a}	32.95 ± 3.24^{b}
Females × Ungrazed saplings	NA	NA	n	n	n	60.02 ± 2.89^{a}	38.92 ± 2.86^{b}
Adults × Ungrazed saplings	NA	NA	n	n	n	61.53 ± 1.78^{a}	36.03 ± 2.16^{b}
Damaged (i×j) - Bivariate analyses							
Adults-uprooted × Grazed saplings	n	n	n	n	n	7.88 ± 0.41^{b}	10.60 ± 0.73^{a}
Adults-uprooted × (Saplings + Juveniles) dead	NA	NA	n	n	n	36.10 ± 1.17^{a}	19.81 ± 0.94^{b}
Undamaged – *Damaged* (i×j) - Bivariate analyses							
Males × Adults-uprooted	n	n	n	n	n	6.97 ± 0.37^{a}	6.14 ± 0.50^{a}
Males × Grazed saplings	n	n	n	n	n	8.64 ± 0.60^{b}	16.76 ± 2.60^{a}
Males × (Saplings + Juveniles) dead	NA	NA	n	n	n	41.15 ± 1.44^{a}	28.66 ± 2.46^{b}
Females × Adults-uprooted	n	n	n	n	n	6.00 ± 0.31^{a}	7.17 ± 0.62^{a}
Females × Grazed saplings	n	n	n	n	n	7.81 ± 0.60^{b}	12.48 ± 2.18^{a}
Females × (Saplings + Juveniles) dead	NA	NA	n	n	n	43.20 ± 1.82^{a}	28.11 ± 2.71^{b}
Adults × Adults-uprooted	n	n	n	n	n	6.54 ± 0.25^{a}	6.67 ± 0.40^{a}
Adults × Grazed saplings	n	n	n	n	n	8.27 ± 0.43^{b}	14.56 ± 1.70^{a}
Adults × (Saplings + Juveniles) dead	NA	NA	n	n	n	42.05 ± 1.14^{a}	28.38 ± 1.82^{b}
Ungrazed saplings × Adults-uprooted	NA	NA	n	n	n	3.66	6.94 ± 0.73
Ungrazed saplings × Grazed saplings	NA	NA	n	n	n	13.17 ± 2.05^{b}	17.04 ± 2.81^{a}
Ungrazed saplings × (Saplings + Juveniles) dead	NA	NA	n	n	n	45.88	18.19 ± 2.23

[1] a, aggregated pattern (at distance *r*); A, spatial association; r, regular pattern; R, repulsion; n, no pattern [random pattern or independence]; NA, not applicable.

[2] d, distance to nearest neighbour: In the same line, values with different letters are significantly different (SNK test, $\alpha = 5\%$) for d_{ii}/d_{ij}.

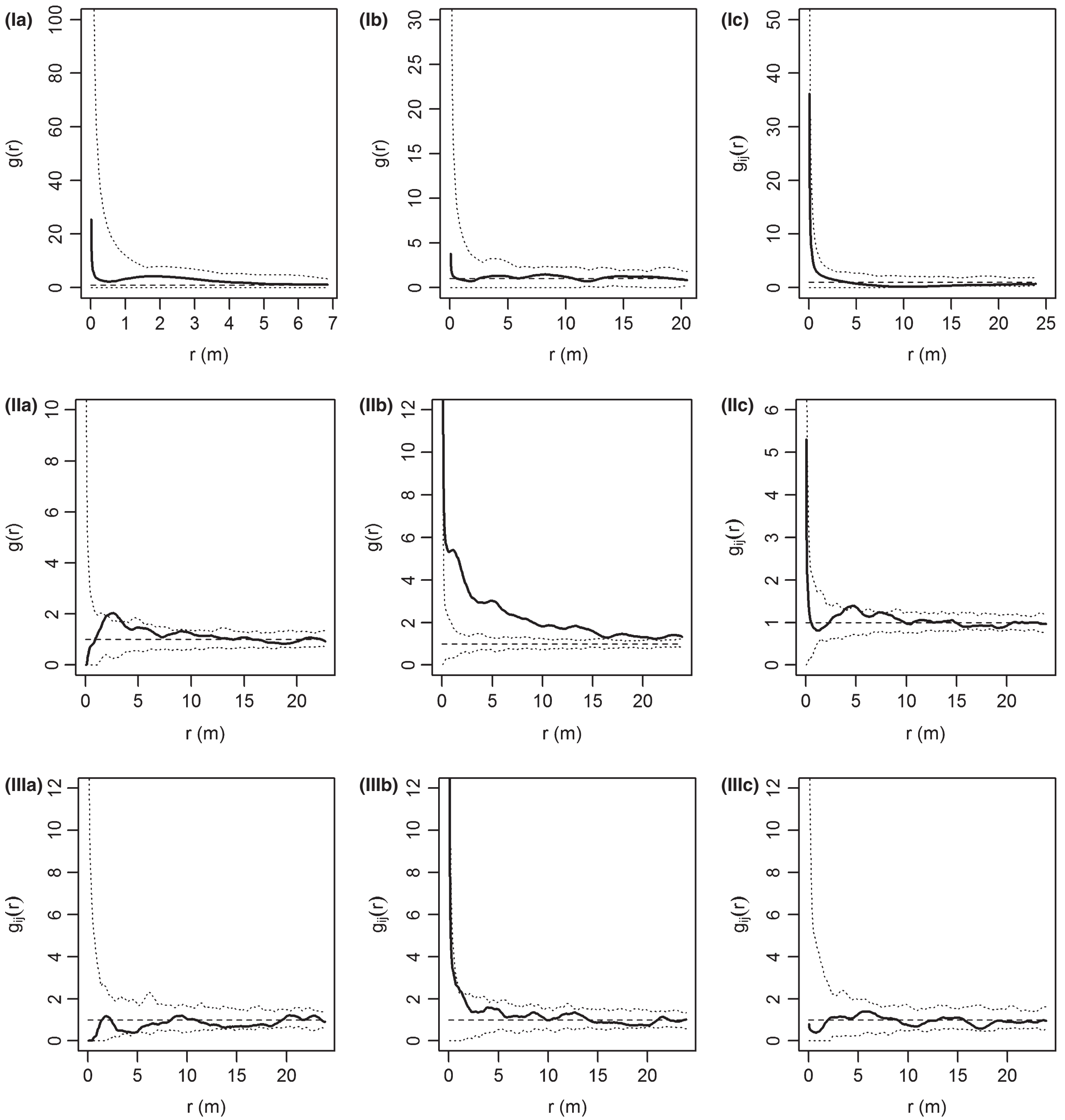

Fig 2 Graphs of the pair-correlation function for undamaged individuals [Saplings ungrazed (Ia), Females (Ib), and Females × Saplings ungrazed (Ic)]; damaged individuals [Adults-uprooted (IIa), Saplings grazed (IIb) and Adults-uprooted × Saplings grazed (IIc)] and cross-type pair-correlation function for undamaged and damaged individuals [Male × Saplings grazed (IIIa), Female × Saplings grazed (IIIb) and Female × Adults-uprooted (IIIc) in Konkombri stand (taken as example). Full bold lines show the statistic calculated from data. The horizontal dashed line shows the pair-correlation function expected from a Poisson process. Dotted lines are approximate 95% confidence envelopes for the null hypothesis (random/independent spatial pattern), obtained from the 500 independent simulations

Table 3 Effect of elephant pressure and stands on spacing (distance to nearest neighbour) of damaged and undamaged individuals of *B. aethiopum*: results of the nested ANOVA

	Distance to nearest neighbour (d_{ii}/d_{ij} in m)					
	Elephant pressure			Stands (Elephant pressure)		
Items, life stages and damages	df	*F*	*P*-value	df	*F*	*P*-value
Undamaged - Univariate analyses						
Adults (Males + Females)	1	15.89	0.000	3	2.10	0.132
Males	1	17.30	0.000	3	0.95	0.563
Females	1	19.20	0.000	3	0.99	0.387
Saplings ungrazed	NA	NA	NA	NA	NA	NA
Damaged - Univariate analyses						
Adults-uprooted (burned + not burned)	1	14.91	0.000	3	1.98	0.124
All adults (uprooted + live)	1	3.72	0.054	3	2.14	0.106
Saplings grazed	1	308.96	0.000	3	2.41	0.082
All saplings (grazed + ungrazed)	1	311.03	0.000	3	0.98	0.407
(Saplings + Juveniles) dead	NA	NA	NA	NA	NA	NA
Undamaged ($i \times j$) - Bivariate analyses						
Females × Males	1	25.18	0.000	3	0.07	0.976
Males × Ungrazed saplings	1	41.48	0.000	3	0.99	0.388
Females × Ungrazed saplings	1	8.97	0.003	3	1.79	0.162
Adults × Ungrazed saplings	1	45.55	0.000	3	1.04	0.335
Damaged (i×j) - Bivariate analyses						
Adults-uprooted × Grazed saplings	1	2.44	0.019	3	2.05	0.139
Adults-uprooted × (Sapl + Juvl) dead	1	100.24	0.000	3	6.14	0.000
Undamaged – Damaged ($i \times j$) - Bivariate analyses						
Males × Adults-uprooted	1	0.37	0.545	3	3.20	0.025
Males × Grazed saplings	1	8.90	0.003	3	2.10	0.132
Males × (Saplings + Juveniles) dead	1	20.66	0.000	3	1.95	0.151
Females × Adults-uprooted	1	2.35	0.127	3	1.24	0.298
Females × Grazed saplings	1	1.91	0.169	3	1.56	0.234
Females × (Saplings + Juveniles) dead	1	27.54	0.000	3	4.91	0.003
Adults × Adults-uprooted	1	0.40	0.526	3	2.86	0.090
Adults × Grazed saplings	1	8.52	0.004	3	0.93	0.415
Adults × (Saplings + Juveniles) dead	1	48.76	0.000	3	1.67	0.201
Ungrazed saplings × Adults-uprooted	1	1.47	0.237	3	0.80	0.507
Ungrazed saplings × Grazed saplings	1	0.01	0.934	3	0.53	0.666
Ungrazed saplings × (Sapl + Juvl) dead	1	6.46	0.018	3	1.24	0.298

df, Degree of freedom; *F*, Fisher statistics; *P*-value, probability value; Sapl, Saplings; Juvl, Juveniles; NA, not applicable.

However, grazed saplings and uprooted adults appeared to be closer than ungrazed saplings and live adults were 7.88 ± 0.41 m versus 61.53 ± 1.78 m for low EP and 10.60 ± 0.73 m versus 36.03 ± 2.16 m for high EP, respectively (Table 2).

Undamaged individuals versus damaged individuals. Irrespective of the EP and the stands, none of the damaged individuals (uprooted adults, grazed saplings, and dead saplings and juveniles) were spatially associated with neither live adults, adult males, adult females nor ungrazed saplings (Fig. 2-IIIa–c, Table 2). However, grazed saplings were always found to be significantly distant (*P*-value < 0.05, Table 3), about two times far from live adults in stands of high EP (14.56 ± 1.70 m) than they were in stands of low EP (8.27 ± 0.43 m; Table 2); suggesting that grazing extended to far from live adults in stands of high EP. Grazed saplings were closer to live adults (8.27 ± 0.43 m versus 14.56 ± 1.70 m) than they were to ungrazed saplings (13.17 ± 2.05 m versus

17.04 ± 2.81 m) and particularly closer to adult females (7.81 ± 0.60 m versus 12.48 ± 2.18 m) than to adult males (8.64 ± 0.60 m versus 16.76 ± 2.60 m) in stands of low and high EP, respectively (Table 2). In contrast, distance of uprooted adults to their nearest live adults did not vary with EP (*P*-value = 0.526, Table 3), in average 6.54 ± 0.25 m versus 6.67 ± 0.40 m in stands of low and high EP, respectively (Table 2). Dead saplings and juveniles were significantly closer (*P*-value = 0.000, Table 3) to undamaged individuals (adults, adult males, adult females and ungrazed juveniles) in stands of high EP (18.19 ± 2.23 m to 28.66 ± 2.46 m) than they were in stands of low EP (41.15 ± 1.44 m to 43.20 ± 1.82 m; Table 2).

Overall, grazed saplings were closer to live adults (9.92 ± 0.56 m) than ungrazed saplings were (54.81 ± 1.54 m; *t*-value = −27.30, df = 750, *P*-value = 0.000).

Discussion

Elephants make top-down foraging decisions (landscapes, habitats, species; Shrader *et al.*, 2012) and SP of treefall by elephants is clustered at landscape scale (Levick & Asner, 2013). This study provides insights into how EP might affect SP and tree-to-tree distance of individuals of a dioecious tree species at stand scale.

For living individuals, our results support previous findings that saplings of *B. aethiopum* are naturally aggregated and that whatever the sex, adults have a random pattern or are more loosely aggregated, and spatial distribution of males is independent from females (Barot, Gignoux & Menaut, 1999). The study also supports the overall trend towards a less aggregated pattern along plant life cycle (Liu, Li & Jin, 2014). These patterns did not change with EP, contrasting with our first hypothesis that high EP would affect SP of *B. aethiopum* individuals. Such findings thus suggest that EP did not affect the overall SP (random/independency, regular/repulsion or aggregated/attraction) of living individuals at stand scale.

Grazed saplings were always aggregated; congruently with the point that elephants often forage in groups (Calenge *et al.*, 2002). The findings that uprooted adults were aggregated in stands of low EP but randomly distributed in stands of high EP likely confirm the hypothesis of group foraging. Indeed, in stands of low EP, adults uprooting might be concentrated at some patchy points leading to aggregated patterns of uprooted adults. Conversely, in stands of high EP (assumed to be regularly visited by large elephant herds), the previous patchiness might be broken by the regular visits such that the prior aggregated pattern turns into a random pattern. Irrespective of the level of EP, Levick & Asner (2013) found an aggregated SP of treefall at landscape scale in the Kruger National Park suggesting a scale-dependent SP of treefall.

Our field data showed that both in stands of low and high EP, tree-to-tree distance between adult individuals has increased (1.5-fold and twofold increase, respectively). Thus, adult uprooting by elephants, whatever its intensity, results in relatively more distant living adult individuals. The study also showed that distance among adult females on one hand and among adult males on another hand has 1.5-fold increase in stands of high EP compared to stands of low EP. As for the distance of adult males to the nearest adult females, it has twofold increase in stands of high EP compared to stands of low EP. All these findings converge in that increasing EP induces spatial isolation in adult individuals as we predicted. As, the honeybee, *Apis mellifera* has been identified as the major pollinator of *B. aethiopum* (Thione, 2000) and reported to be a short distance pollinator (Diallo, 2001), increasing adult uprooting may increase pollination/reproduction failure (Berry, 2006), inducing lesser seed production and thus low seedlings input.

Ungrazed saplings were found far away from live adults, while grazed saplings were near live adults, especially adult females, as predicted by the Janzen–Connell escape hypothesis (Connell, 1971; Janzen, 1971, 1975).

From a genetic perspective, the increasing distance between individuals added to the lack of sufficient recruitment might also alter the spatial genetic structure within the species (Lowe, Harris & Ashton, 2004). Assessing how EP affects spatial genetic structure of its food-provider tree species will provide additional insights into elephant–plants interactions in savannahs ecosystems and effectively inform conservationists.

Overall, adult tree uprooting and increasing tree-to-tree distance by elephants coupled with the absence of juveniles in palm stands (Azihou, 2013) suggest a risk of local decline of *B. aethiopum* from the PNP. Because the PNP is not fenced and belongs to a regional network of protected areas (Arly in Burkina-Faso, trans-boundary Biosphere Reserve W in Benin, Burkina-Faso and Niger), elephants migrate freely across countries borders within the network of parks, and as such, a regional management plan of elephant populations will be the most effective way of addressing elephant–plant diversity relationships (O'Connor, Goodman & Clegg, 2007). Determining a threshold population of elephants beyond which this population poses severe threats to plant diversity regionally will be a key advance. A continued monitoring of elephant population at regional scale will then inform on when the threshold is reached and guide adequate decisions such as, for example, culling option. At the PNP scale, management actions should enhance the recruitment of saplings into juvenile palms, for example by the use of barbed wire to protect several patches of saplings from EP.

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References

Azihou, A.F. (2013) *Ecology of isolated trees in tropical savannas: modelling of plant species distribution and colonization of new habitats through long-distance dispersal and facilitation*. PhD Thesis, University of Abomey-Calavi. 162 p.

Azihou, A.F., Glele Kakaï, R., Bellefontaine, R. & Sinsin, B. (2013) Distribution of tree species along a gallery forest–savanna gradient: patterns, overlaps and ecological thresholds. *J. Trop. Ecol.* **29**, 25–37.

Baddeley, A. & Turner, R. (2005) spatstat: an R package for analyzing spatial point patterns. *J. Statist. Soft.* **12**, 1–42.

Barot, S., Gignoux, J. & Menaut, J.-C. (1999) Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. *Ecology* **80**, 1987–2005.

Barot, S., Gignoux, J., Vuattoux, R. & Legendre, S. (2000) Demography of a savanna palm tree in Ivory Coast (Lamto): population persistence and life-history. *J. Trop. Ecol.* **16**, 637–655.

Benot, M.L., Bittebiere, A.K., Ernoult, A., Clément, B. & Mony, C. (2013) Fine-scale spatial patterns in grassland communities depend on species clonal dispersal ability and interactions with neighbours. *J. Ecol.* **101**, 626–636.

Berry, E.J. (2006) *Population ecology of the harvested understory palm* Chamaedorea radicalis*: pollination biology, female fecundity, and source-sink population dynamics*. PhD dissertation. Miami University, 149 p.

Blake, S., Deem, S.L., Mossimbo, E., Maisels, F. & Walsh, P. (2009) Forest elephants: tree planters of the Congo. *Biotropica* **41**, 459–468.

Bouche, P., Lungren, C., Hien, B. & Omondi, P. (2004) Recensement aérien total de l'Ecosystème "W"-Arly-Pendjari-Oti-Mandouri-Kéran (WAPOK), 115 p.

Bouché, P., Douglas-Hamilton, I., Wittemyer, G., Nianogo, A.J., Doucet, J.-L., Lejeune, P. & Vermeulen, C. (2011) Will elephants soon disappear from West African Savannahs? *PLoS ONE* **6**, e20619.

Calenge, C., Maillard, D., Gaillard, J.-M., Merlot, L. & Peltier, R. (2002) Elephant damage to trees of wooded savanna in Zakouma National Park. *Chad. J. Trop. Ecol.* **18**, 599–614.

Campos-Arceiz, A. & Blake, S. (2011) Megagardeners of the forest: the role of elephants in seed dispersal. *Acta Oecol.* **37**, 542–553.

Chu, G., Wang, M. & Zhang, S. (2014) Spatial patterns and associations of dominant woody species in desert–oasis ecotone of South Junggar Basin, NW China. *J. Plant Interact.* **9**, 738–744.

Connell, J.H. (1971) On the role of Natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of Populations* (Eds P.D. Dem Boer and G.R. Grandwell). PUDOC, Wageningen.

Diallo, B.O. (2001) *Biologie de la reproduction et évaluation de la diversité génétique chez une légumineuse:* Tamarindus indica *L. (Caesalpinioideae)*. Thèse Université Montpellier II. Science et Technique du Languedoc, 119 p.

Diggle, P.J. (2003) *Statistical Analysis of Spatial Point Patterns*, 2nd edn. Academic Press, New York.

Giffard, P.L. (1967) Le palmier Ronier *Borassus aethiopum* Mart. *Bois For. Trop.* **116**, 3–14.

Gouwakinnou, G.N., Lykke, A.M., Djossa, B.A. & Sinsin, B. (2011) Folk perception of sexual dimorphism, sex ratio, and spatial repartition: implications for population dynamics of *Sclerocarya birrea* [(A. Rich) Hochst] populations in Benin, West Africa. *Agroforest. Syst.* **82**, 25–35.

Holdo, R.M. (2003) Woody plant damage by African elephant in relation to leaf nutrients in Western Zimbabwe. *J. Trop. Ecol.* **19**, 189–196.

Janzen, D.H. (1971) Escape of juvenile *Dioclea megacarpa* (leguminous) vines from predators in space and time in a deciduous tropical forest. *Am. Nat.* **105**, 97–112.

Janzen, D.H. (1975) Interactions of seeds and their insect predators/parasitoids in a tropical decidious forest. *Evolutionary Strategies of Parasitic Insects and Mites* (Ed Price, P. W.). Plenum Press, New York.

Kassa, B.D., Fandohan, B., Azihou, A.F., Assogbadjo, A.E., Oduor, A.M.O., Kidjo, F.C., Babatoundé, S., Liu, J. & Glèlè Kakaï, R. (2014) Survey of *Loxodonta africana* (Elephantidae)-caused bark injury on *Adansonia digitata* (Malvaceae) within Pendjari Biosphere Reserve, Benin. *Afr. J. Ecol.* **52**, 385–394.

Law, R., Illian, J., Burslem, D., Gratzer, G., Gunatilleke, C.V.S. & Gunatilleke, I. (2009) Ecological information from spatial patterns of plants: insights from point process theory. *J. Ecol.* **97**, 616–628.

Lejeune, P. (2001) Arpent 2.0, logiciel de saisie de données d'arpentage – Guide d'utilisation, FUSAGx. *Note Tech. For.* **5**, 1–12.

Levick, S.R. & Asner, G.P. (2013) The rate and spatial pattern of treefall in a savanna landscape. *Biol. Conserv.* **157**, 121–127.

Li, Y., Hui, G., Zhao, Z., Hu, Y. & Ye, S. (2014) Spatial structural characteristics of three hardwood species in Korean pine broad-leaved forest – validating the bivariate distribution of structural parameters from the point of tree population. *For. Ecol. Manage.* **314**, 17–25.

Liu, Y., Li, F. & Jin, G. (2014) Spatial patterns and associations of four species in an old-growth temperate forest. *J. Plant Interact.*, **9**, 745–753.

Loarie, S.R., Aarde, R.J.V. & Pimm, S.L. (2009a) Fences and artificial water affect African savannah elephant movement patterns. *Biol. Conserv.* **142**, 3086–3098.

Loarie, S.R., Aarde, R.J.V. & Pimm, S.L. (2009b) Elephant seasonal vegetation preferences across dry and wet savannas. *Biol. Conserv.* **142**, 3099–3107.

Lowe, A., Harris, S. & Ashton, P. (2004) *Ecological Genetics: Design, Analysis, and Application*. Blackwell, Oxford, UK, 326p.

Martínez, I., Taboada, F.G., Wiegand, T. & Obeso, J.R. (2013) Spatial patterns of seedling-adult associations in a temperate forest community. *For. Ecol. Manage.* **296**, 74–80.

O'Connor, T.G., Goodman, P.S. & Clegg, B. (2007) A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biol. Conserv.* **136**, 329–345.

P.A.P.E. (Programme d'Appui aux Parcs de l'Entente) (2013) Rapport de dénombrement pédestre de la faune dans les réserves de biosphère de la Pendjari et du W.

R Core Team. (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Riginos, C., Karande, M.A., Rubenstein, D.I. & Palmer, T.M. (2015) Disruption of a protective ant-plant mutualism by an invasive ant increases elephant damage to savanna trees. *Ecology* **96**, 654–661.

Ripley, B.D. (1981) *Spatial statistics*. Wiley, New York, NY, USA.

Schmidt, I.B., Mandle, L., Ticktin, T. & Gaoué, O.G. (2011) What do matrix population models reveal about the sustainability of non-timber forest product harvest? *J. Appl. Ecol.* **48**, 815–826.

Shrader, A.M., Bell, C., Bertolli, L. & Ward, D. (2012) Forest or the trees: at what scale do elephants make foraging decisions? *Acta Oecol.* **42**, 3–10.

Sokpon, N., Affoukou, M., Amahowe, I., Gandji, L., Gnonlonfin, L. & Sossou, B. (2008) Dynamique spatio – Temporelle des Formations végétales du Complexe Parc National de la Pendjari, Zones Cynégétiques de la Pendjari et de l'Atacora. CENAGREF, Benin.

Somanathan, H. & Borges, R.M. (2000) Influence of exploitation on population structure, spatial distribution and reproductive success of dioecious species in a fragmented cloud forest in india. *Biol. Conserv.* **94**, 243–256.

Stoyan, D. & Stoyan, H. (1994) *Fractals, Random Shapes and Point Fields*. Wiley, New York, 389 p.

Tehou, C.A. (2002) Les éléphants *Loxodonta africana* dans la Réserve de Biosphère de la Pendjari, nord-est République du Bénin: abondance, densité et répartition spatiale. *Pachyderm* **33**, 64–68.

Tehou, C.A., Kossou, E., Mensah, G.A., Houinato, M. & Sinsin, B. (2012) Indentification et caractérisation des formations végétales exploitées par l'éléphant *Loxodonta africana* dans la Réserve de Biosphère de la Pendjari au Nord-Ouest de la République du Bénin. *Pachyderm* **52**, 36–48.

Thione, L.A. (2000) *Biologie de la reproduction et étude de l'impact de l'exploitation des feuilles et des fruits sur la productivité des rôniers*. PhD dissertation, Université Cheikh Anta Diop.

Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D. & Duncan, P. (2011) Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biol. Conserv.* **144**, 902–912.

Wahungu, G.M., Mureu, L.K., Wato, Y.A., Mureithi, S.N. & Karanja, G.G. (2009) Seedling survival in *Manilkara butugi* Chiov. along a dispersal gradient in Kakamega forest, Kenya. *Afr. J. Ecol.* **48**, 783–790.

Yessoufou, K., Davies, J.T., Maurin, O., Kuzmina, M., Schaefer, H., Van der Bank, M. & Savolainen, V. (2013) Large herbivores favour species diversity but have mixed impacts on phylogenetic community structure in an African savanna ecosystem. *J. Ecol.* **101**, 614–625.

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