

BAYESIAN UPDATING OF THE FRUITING BIOLOGY OF *DIOSPYROS MESPILIFORMIS* HOCHST. EX A. DC IN REPUBLIC OF BENIN

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ABSTRACT

Fruiting and recruitment of trees are respectively dysregulating and declining throughout Afrotropical forests. The main objective of this research was to accurately estimate with robust methods of statistics inference the fruiting potential and spatial pattern of recruitment of the populations of the neglected wild edible fruit trees. The specific objectives were to (i) assess in the Bayesian framework the fruiting biology of *D. mespiliformis* Hochst. Ex A. DC following latitudinal gradient in republic of Benin and (ii) analyze the spatial pattern of the recruitment of *D. mespiliformis* surrounding the mother trees. Thirty and fifty-eight fruiting mother trees of *D. mespiliformis* were randomly selected respectively at the lowest and the highest latitudes. Number of fruits per tree, diameter at the breast height, height and crown areas were collected. Total number

of the individuals of recruitments of *D. mespiliformis* were recorded in the successive 5 m radius annulus surrounding mother trees. Overall, *D. mespiliformis* fruiting was higher at the highest latitudes (2708 fruits / tree) than at the lowest latitudes' vegetation ecosystems (247 fruits / tree). Markov Chain Monte Carlo resampling revealed contradictory trend. The main biotic driver for the highest fruits production is the height of *D. mespiliformis* at the highest latitudes while width crown area increases fruiting at the lowest latitudes. The populations of *D. mespiliformis* at the lowest latitudes produced the fleshiest endocarp fruits with the largest seeds at the opposite to the highest latitudes' populations that produced the longest and largest fruits. The spatial pattern of the recruitment was clumped in the radius of 5 m surrounding the mother trees ($D_x > 1 \text{ stem} / \text{m}^2$). Future researches have to address nutritional and breeding values of *D. mespiliformis*.

Keywords: tree reproductive biology, wild edible fruit trees, fruiting, Bayesian estimation, *Diopyros mespiliformis* Hochst. Ex A. DC.

1. INTRODUCTION

Fruiting and fruition are important demographic steps allowing to tree species to reproduce, disperse and to survive in their natural habitats (1, 2, 3, 4). To model the pattern, power of the tree species fruiting and dispersal dynamic throughout vegetations or habitats are the most important challenges in the analysis of demographic dynamics of the populations of tree species (5, 6, 4, 7). Fruits production favors not only tree species to survive from generations to generations but provides also foods to human (8), bird and animal species (9, 10). Wild edible fruits are the main foods and local economic resources for many endogenous people around the world (11, 12). Global domestic product of the nations with various and diverse wild edible fruit trees depends in large part on direct fruits trading and or fruits processing to various drinks and foods (13). Analysis of fruits production potential and nutritional values of the fruits of the wild fruit tree species are keys steps for a better value chain assessment of the wild edible fruits and subsequent national and regional policies setting for an increase of wild edible fruits production, an efficient commercialization and processing of fruits at industrial scale (14). The first desires of the consumers of fruits are the best physico-chemical characteristics of the fruits (15,16). Higher size and weight of the wild fruits and fleshy characteristic of the pulp and endocarp are the first physical characteristics that direct intense fruits harvesting and consumption by both humans and frugivorous animals (17). Both quantitative and qualitative production of fruits may be negatively impacted by several environmental and anthropogenic factors such as the ways and the intensity of barks and branches harvesting by humans (18, 19) (Growth differentiation hypothesis (20)) following the latitudinal gradient. Spatiotemporal variation of abiotic factors such as rainfall and temperature affects significantly fruiting and fruition of trees and are the main factors of the pattern of tree species fruition and dynamic (21, 22, 23) (resources availability hypothesis (24)). Biotic factors such as dendrometric parameters of the tree species play an important role in the fruiting

biology of tree species (25). Thus, the size of crown area, the height and the basal area could affect the quality and the quantity of fruits produced by a given tree species throughout its natural range size ecosystems (1, 2, 25). Diversity of natural ecosystems or habitats affect the reproductive biology and fruiting of trees and therefore drives demographic dynamic of the populations of the tree species (5).

Important ecological processes underlying tree species demography and survival are tree species fruitions and fruits dispersal capacity by mother trees (7). Furthermore, tree species demography and survival depend mainly on the regeneration ability of the mother trees and the growth potential of seedlings throughout the natural stands (26, 27, 28). Regeneration and recruitment are two ecological processes which allow seeds to germinate and to grow from seedlings via juveniles, sapling stages to recruit stage in the absence of natural predation (29) such as repeated intense herbivory (30).

Erosion of tree species genetic diversity and subsequent tree species extinction are mainly caused by lack or decrease of offsprings due to innate reproductive inability or intense seeds predation (1) or seedlings mortality in forest communities. The ways the individuals of the recruitments of tree species are spatially distributed are important ecological components in community ecology (31, 32, 33, 34). Density and diversity of tree species determine their spatial pattern across vegetation types (35). The spatial pattern of tree species is an indicator of abiotic and biotic factors importance or intensity and spatial variability throughout forests ecosystems (35, 36) and requires daily assessments for different generations of the individuals of tree species.

Targeted wild edible fruit tree of this study is *D. mespiliformis* Hochst. Ex A. DC, an evergreen tree species with large spatial repartition in Africa (37). *D. mespiliformis* rainfall requirement varies between 300-2000 mm and grows on the well-drained soils. *D. mespiliformis* is common to savannas and woodlands (38). Specific researches on the spatial pattern of its fruiting and recruitment remain less addressed in the western Afrotropical countries. Recent research in the northern part of republic of Benin assessed the morphotypes of *D. mespiliformis* with non-exhaustive number of morphological traits and with non-smart methods of statistics inference analysis background (39).

Some methods of data analysis or data science can fail to estimate or to predict accurately the true state or intrinsic characteristics of some biological and socio-ecological systems or processes (40, 41). Dealing with the most robust methods of data science in biological and socio-economic phenomena analyses become compulsory for biases reduction in decisions setting. Bayesian statistics inference (Bayes, 1770s) background (algorithmic calculus, resampling of main datasets, etc.) overcomes statistical analyses biases throughout any kind of database.

The main objective of this research was to accurately estimate with robust methods of statistics inference the fruiting potential and spatial pattern of recruitment of the populations of the neglected wild edible fruit trees. The specific objectives were to (i) assess in the Bayesian framework the fruiting biology of *D. mespiliformis* Hochst. Ex A. DC following latitudinal gradient in Benin and (ii) analyze the spatial pattern of the recruitment of *D. mespiliformis* surrounding the mother trees.

Based on the assumption of the effect of latitudinal gradient (42, 43) and resources availability (24) hypotheses on species diversity and biology, the main specific research hypotheses addressed are: (i) latitudinal gradient drives negatively *D. mespiliformis* fruiting with limited fruiting capacity at the highest latitudes (ii) vegetation types affect the fruiting capacity of *D. mespiliformis* with gallery forests and wetlands, the most important fruiting habitats (iii) dendrometric characteristics of *D. mespiliformis* affect its fruiting capacity differently following latitudinal gradient (iv) latitudinal gradient drives negatively physical traits variation of the fruits of *D. mespiliformis* with limited attractiveness consumption choice traits at the highest latitudes forest ecosystems and (v) mother trees of *D. mespiliformis* develop a repulsive behavior toward their offsprings.

2. MATERIAL AND METHODS

2.1 Study area

This study was carried out from the lowest latitudes to the highest ones of Benin republic in west Africa (Figure 1). Benin republic is located between 6°10' and 12°25' latitudes north and 0°15' and 3°55' longitudes east. The country is characterized by tropical climate with two rainy seasons in the southern and in the central part close to the southern part of the country and one rainy season in the northern part and the central part close to the northern part of the country and covers three chorological endemism centers (44, 45). The southern part of Benin covers the Guineo-Congolian endemism center with an average annual rainfall of 1200 mm and a range of temperature of 26°C and 35°C. The second endemism center is Guineo-Congolian-Sudanian transition endemism center that covers the central part of the country with an average annual rainfall ranging between 1050 mm and a temperature varying between 26 and 35°C. The highest latitudes' parts of the country correspond to the Sudanian endemism center with an average annual rainfall varying between 900 and 1100 mm and a temperature varying between 26-40°C (45). The main vegetations are dense semi-deciduous forests, savannah ecosystems, dry forests, gallery forests, riparian forests, wetlands, farmlands and fallows.

In Benin republic, over the last decades, 10741458 inhabitants were recorded (46) with diverse socio-economic activities. Agriculture is the first economic activity (47), followed by the stock farming and breeding, trade, fishery and craft industries. Non-timber forest products processing to foods and drinks is still at an embryonic stage and should be rethought for a better industrialization of the country.

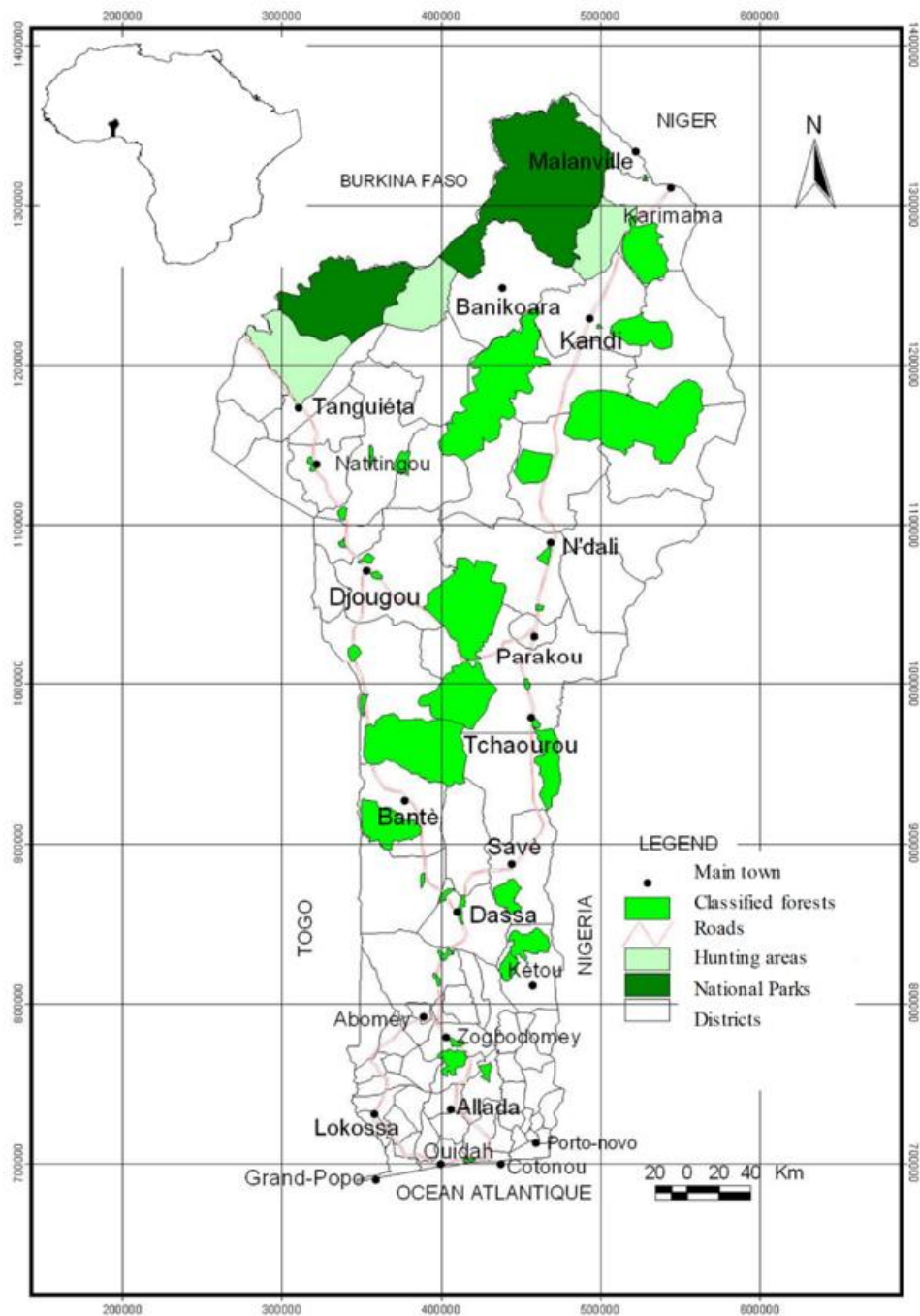


Fig. 1: Map of the study area showing the location of republic of Benin in Africa.

Figure 1 shows the main districts of republic of Benin and the forests and National Parks where the forest inventories were carried out.

2.2 Sampling design and data collection

2.2.1 Quantification of fruits production potential and physical traits of fruits of *D. mespiliformis* throughout vegetation types and latitudinal gradient in Benin

The fruiting biology data were collected at two very contrasted latitudinal gradient environments (the lowest versus the highest latitudes) of the country. Target populations of *D. mespiliformis* of the lowest latitudes were inventoried in the Guineo-Congolian endemism center while the populations of the highest latitudes were assessed in the Sudanian endemism center in order to address expected effect of very contrasted latitudinal gradient of abiotic and biotic factors on *D. mespiliformis* Hochst. Ex A. DC fruiting biology. Indeed, very isolated latitudinal gradient populations of the tree species are supposed to grow, reproduce differently with divergent functional traits diversity (42,43). Thirty and fifty-eight fruiting mother trees of *D. mespiliformis* were randomly chosen throughout vegetation types during fruiting period in the Guineo-Congolian endemism and Sudanian endemism centers respectively. The height of each target mother tree of *D. mespiliformis* was determined basing on the sight metrics of height measured from the highest and lowest sight of the tree at a suitable distance allowing to view the true summit of each target mother tree with clinometer sunto without sight biases. Diameters of crown area and the diameter at the breast height were measured with the tape pi. Total number of fruits per two important branches were also randomly collected. Variables samples of fruits were collected per each target individual of *D. mespiliformis* and diameter, size and endocarp size of each fruit, size and diameter of each seed were measured with ruler caliper (Figure 2). Clinometer sunto, tape pi and ruler caliper are the most accurate instruments in forest inventory science.



Fig. 2: Measurement of physical traits of fruits of *D. mespiliformis* throughout forest ecosystems.

The figure 2 is an example of measurement of physical trait of the fruits of *D. mespiliformis* during forest inventories. The ruler caliper was used to measure physical traits of fruits of *D. mespiliformis*.

2.2.2 Collection of spatial pattern data of the recruitments of *D. mespiliformis*

The spatial pattern of the recruitments of *D. mespiliformis* were assessed per vegetation type in the two target contrasted endemism centers. Several successive circular plots of 5 m radius were established surrounding each target mother individual of *D. mespiliformis* (adapted from 34). Inside each annulus or circular plot, total number of the individuals of recruitments of *D. mespiliformis* were recorded. Diameter at the breast height and total height of each targeted mother tree were measured.

2.3 Data analysis

2.3.1 Assessment of latitudinal gradient pattern effect of environmental factors on production potential and physical traits variation of fruits of *D. mespiliformis* in Benin

A quick view of the tree species survival likelihood assessment throughout the natural stands is most of time approached by measuring the capacity of the tree species to produce fruits and propagules in nature (48). The quantity of fruits produced by a given mother tree of *D. mespiliformis* is computed by multiplying the average number of fruits per branch by the overall branches of each tree.

Basal area (G) (Eq.1), height (Eq.2) and crown area (Eq.3) were computed for each individual of *D. mespiliformis*.

$$G = \frac{\pi}{4} d_i^2 \tag{Eq.1}$$

$$\text{Height} = \frac{(V_h - V_b) \times \text{distance}}{100} \tag{Eq.2}$$

$$\text{crown area} = \frac{\sum_{i=1}^n \pi \times D_i^2}{4n} \tag{Eq.3}$$

where d_i corresponds to diameter of a given fruiting tree i , V_h and V_b are respectively up and down sighted values measured with clinometer sunto from an unbiased distance of accurate height of tree measurement. D_i corresponds to a given diameter i of the crown for the same tree and n is the total number of diameters measured for the crown. Bayes Factor metric (bf) (Eq.4) is computed per fruit production driving factors and per their additive common and interactive effects to determine the main drivers of the capacity of fruits production of *D. mespiliformis* throughout vegetation types at national scale in Benin.

$$bf = \text{generalTestBF}(\text{Total_fruit} \sim \text{Endemism} \times \text{Habibat}, \text{data} = \text{DiospFruiting}) \text{ (Eq. 4)}$$

A further analysis based on Bayesian generalized linear mixed effect model of Poisson family was performed by simulating initial dataset via Markov Chain Monte Carlo with 3000 iterations. In order to select the most important populations of *D. mespiliformis* that can produce attractive fruits for dietary, the average values of size and diameter of the fruits, size and diameter of the seeds and size of endocarp of the fruits were computed per individual of *D. mespiliformis* tree species and submitted to combined clustering and principal component analyses.

To implement the statistical analyses, the packages brms (49)), BayesTools (50) and BayesFactor (51) of the R statistic software were used to define specific macro languages compulsory for the statistical analyses implementation.

2.3.2 Analysis of the spatial pattern of the recruitments of *D. mespiliformis* surrounding the mother trees throughout vegetation types in contrasting chorological endemism centers in Benin

The way the individuals of tree species are dispersed in a given vegetation directs often management plans of trees throughout natural forests. The individuals of the tree species can disperse by living often together (clumped spatial pattern), randomly or regularly throughout their natural ecosystems (32, 33). There are several ways to analyze the spatial pattern of tree species. Two methods, distance to the nearest neighborhood individuals (32, 33) and density of individuals per vegetation survey unity index (Green index (31)) are often used to analyze the spatial pattern of tree species. However, to assess local dispersal ability of tree species, analysis of the spatial pattern of the individuals of the recruitments surrounding the mother tree species (Eq. 5) is often the most appropriated method (34).

$$D_x = \frac{\sum N_x}{\sum A_x} \text{ (Eq.5)}$$

D_x is the neighborhood density, N_x is the number of individuals of the recruitments of *D. mespiliformis* in a given annulus surrounding target mother tree and A_x the area of the annulus. The advantage of the neighborhood density spatial pattern index is related to its ability to analyze the spatial pattern of the individuals of the recruitments at specific distances from the mother trees (34). This study used just the average density of recruitment of *D. mespiliformis* per annulus area. Inclusion of the heterospecific species leads to relative neighborhood density computation by including the overall density of tree species per annulus. $D_x = 1$ corresponds to random distribution while $D_x > 1$ corresponds to aggregative distribution and $D_x < 1$ indicates an hyperdispersion (34).

3. RESULTS

3.1 Latitudinal gradient pattern effect of environmental factors on production potential and physical traits variation of fruits of *D. mespiliformis* in Benin

3.1.1 *Diospyros mespiliformis* fructification throughout chorological endemism centers and habitats

Bayes Factor metric values obtained reveal that both endemism center and habitat types variation influence the fruits production capacity of the individuals of *D. mespiliformis* within its areas of occurrence throughout the country (Table 1). Habitat types represent the most important driver that influenced *D. mespiliformis* fructification. The lowest average quantity of fruits per tree was observed in the dense semi-deciduous forests (183) in the Guineo-Congolian endemism center (Table 2). The most important average quantity of fruits per tree was observed on tertiary individuals of *D. mespiliformis* (3933) and on Savannas-fallow-farmlands (3459) in the Sudanian endemism center. The populations of *D. mespiliformis* of gallery forests and wetlands showed similar fruits production capacity (1752 and 1689 respectively). The results of Bayesian generalized linear mixed effect model of Poisson family omitting the effects of the habitats types after 3000 datasets resampling via Markov Monte Carlo chains reveal an evidence of higher fruits production capacity of the individuals of *D. mespiliformis* located in Guineo-Congolian endemism center than those in the Sudanian endemism center (Table 3). Most of the Markov Monte Carlo chains did not converge (Figure 3).

Table 1: Bayes Factor results on the driving factors of the number of fruits per individual of *Diospyros mespiliformis*

Driving Factors	Bayers Factor
Endemism	$1.047565 \times 10^{141} \pm 0\%$
Habitats	$5.488746 \times 10^{226} \pm 0\%$
Endemism + Habitats	$1.642302 \times 10^{227} \pm 1.61\%$
Endemism + Habitats+ Endemism×Habitats	$1.458442 \times 10^{227} \pm 1.16\%$

Table 2: Average number of fruits per individual tree of *Diospyros mespiliformis* per habitat

Endemism	Habitats	mean	cv (%)
Sudanian	Gallery Forest	1752	61.9335
	SFF	3459	96.8498
	Termitary	3933	75.0914
	Wetland	1689	59.2599
Guineo-Congolian	DSF	183	23.172
	TDSF	312	28.8507

SFF: Savanna-Fallow-Farm ecosystems, DSF: Dense Semi-deciduous Forest, TDSF: Typical Dense Semi-Deciduous-Forest, CV: coefficient of variation.

Table 3: Bayesian Generalized linear mixed effect model of Poisson family on the number of fruits of *Diospyros mespiliformis*

Group-Level Effects							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Habitats							
sd(Intercept)	0.92	0.98	0.03	3.15	1.99	4	17
Habitats:Plots							
sd(Intercept)	0.64	0.21	0.34	0.89	1.75	5	30
Population-Level							
Intercept	3.62	0.81	2.03	5.26	1.00	2089	2222
Intercept	4.74	1.16	1.84	5.88	1.83	4	23
Sudanian	1.54	0.62	0.63	2.78	2.00	4	14

Sd : standard deviation, Est.Error : estimated error, CI : credibility interval, Rhat : potential scale reduction statistic, also known as the Gelman-Rubin statistic, Bulk_ESS : Effective sample size for rank normalized values using split chains, Tail_ESS : Tail effective sample size.

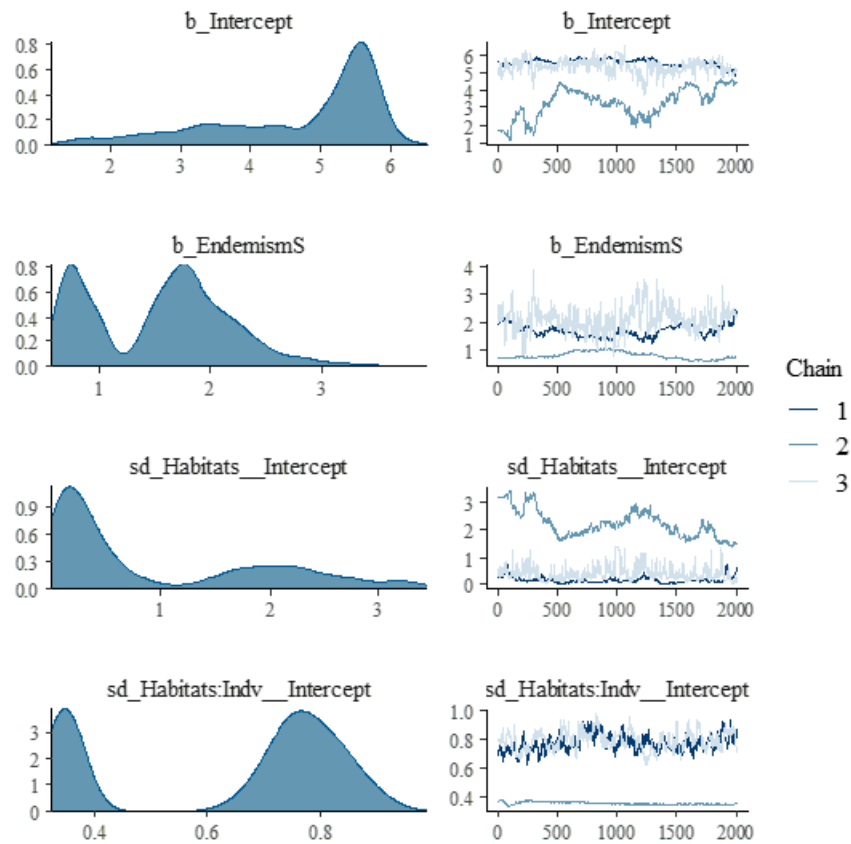


Fig. 3: Map of convergence pattern of Markov Monte Carlo chains.

Figure 3 shows convergence pattern of Markov Chains Monte Carlo resampling of initial fruit production data of *D. mespiliformis*.

3.1.2 Biotic drivers of *Diospyros mespiliformis* fructification

Diospyros mespiliformis fructification was affected differently by dendrometric parameters of the individuals of *D. mespiliformis* throughout the chorological endemism centers (Table 4). Among three dendrometric parameters assessed, crown diameter was the functional traits that showed an evident effect on the fruits production quantity of *D. mespiliformis* in the Guineo-Congolian endemism center. Large crown diameter individuals are supposed to produce more fruits than the small crown diameter trees. In the Sudanian endemism center, only the height of the individuals of *D. mespiliformis* influenced significantly their ability of fruit production. The tallest individuals produced more fruits than the shortest ones.

Table 4: Bayesian Generalized linear mixed effect models of Poisson family on *Diospyros mespiliformis* fructification

Endemism	Group-Level Effects							
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	
GC	Habitats							
	sd(Intercept)	0.72	0.58	0.04	1.46	3.2	3	11
	Habitats:Plots							
	sd(Intercept)	1.68	1.66	0.4	4.03	2.95	4	11
	Population-Level							
	Intercept	38.35	86.14	-42.78	159.25	3.83	3	11
	Height	0.11	0.46	-0.33	0.73	3.6	3	11
	Basal area	-0.05	0.06	-0.13	0	3.74	3	11
	Crown area	0.47	0.31	0.08	0.88	3.74	3	11
	S	Habitats						
sd(Intercept)		2.33	3.08	0	6.68	4.21	3	NA
Habitats:Plots								
sd(Intercept)		0.3	0.12	0.12	0.43	2.97	3	NA
Population-Level								
Intercept		38.06	50.88	-8.8	111.69	3.66	3	11
Height		0.58	0.6	0.08	1.43	3.07	3	NA
Basal area		-0.02	0.03	-0.08	0	3.54	3	11
Crown area		-0.19	0.32	-0.64	0.1	3.41	3	11

GC : Guineo-Congolian endemism center, S : Sudanian endemism center, sd : standar deviation, Est.Error : Estimated Error, CI : credibility interval, Rhat : potential scale reduction statistic, also known as the Gelman-Rubin statistic, Bulk_ESS : Effective sample size for rank normalized values using split chains, Tail_ESS : Tail effective sample size, NA ! Not Available.

3.1.3 Pattern of physical traits of fruits of *Diospyros mespiliformis* throughout the chorological endemism centers following the latitudinal gradient in Benin

Combined clustering and principal component analyses on the physical traits' values of the fruits of individuals of *D. mespiliformis* following latitudinal gradient from south to north revealed three clusters or morphotypes of the populations of *D. mespiliformis* at national scale in Benin (Figure 4). Distinctively, the southern populations, the individuals of the lowest latitudinal gradient located in the Guineo-Congolian Endemism center (Cluster 2) were characterized mainly by the deepest endocarp thickness with some individuals with the widest diameter of seed. The populations of *D. mespiliformis* of the highest latitudinal gradient were separated into two morphotypes. The first morphotypes (cluster 1) is characterized by the individuals with the longest fruits and widest seeds at the opposite to the second morphotypes (cluster3) dominated mainly by the individuals with the largest diameter of fruits and the longest fruits and seeds.

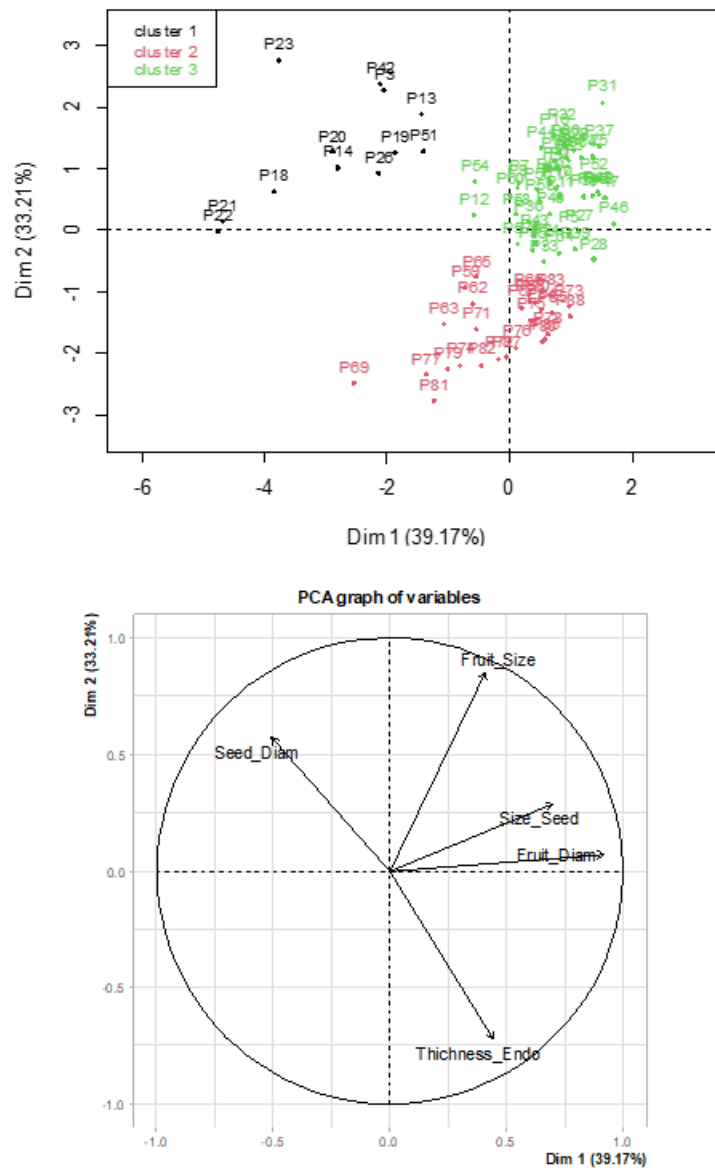


Fig. 4: Map of morphotypes populations of *Diospyros mespiliformis* in relation to the physical traits of their fruits throughout chorological endemism centers following latitudinal gradient.

P=Plant, Thickness_Endo= Thickness of Endocarp, Fruit-Diam = Fruit Diameter, Size_Seed= Size of seed, Seed_Diam = Seed diameter, Fruit_Size = Fruit Size.

Figure 4 is the map of the principal component analysis on physical traits of the fruits of the individuals of *D. mespiliformis* measured from the populations at the lowest latitudes (Guineo-Congolian endemism center) versus the populations at the highest latitudes (Sudanian endemism

center) across the country. Very closest individuals are clumped with the same color and represent one morphotype of the species.

3.2 Spatial pattern of the recruitments of *D. mespiliformis* surrounding the mother trees throughout vegetation types in contrasting chorological endemism centers in Benin

Neighborhood density results reveal a clumped distribution pattern ($D_x > 1 \text{ stem/ m}^2$) of the individuals of the recruitments in the radius of 5 m surrounding *D. mespiliformis* mother trees (Table 5). Both aggregative and hyperdispersion patterns were observed between 5 m and 10 m radius. Overall, very few individuals were observed beyond 10 m radius surrounding the mother trees.

Table 5: Average neighborhood density of the recruitments of *D. mespiliformis* surrounding the mother trees in two contrasting chorological endemism centers in Benin

	Habitats	0-5m	5-10m	10-15m	15-20m	20-25m	25-30m	30-35m	35-40m
SGC	Farmlands	4.73	0.33	0.00	0.03	0.00	0.09	0.03	0.00
	Gallery Forest	4.27	1.09	0.00	0.00	0.00	0.00	0.00	0.00
	Fallow	3.12	0.36	0.00	0.00	0.00	0.00	0.00	0.00
	Savanna	1.66	0.61	0.48	0.00	0.00	0.00	0.00	0.00
Global		3.45	0.60	0.12	0.01	0.00	0.02	0.01	0.00
S	Farmland	1.50	0.75	0.50	0.00	0.00	0.00	0.00	0.00
	Gallery Forest	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Fallow	1.14	1.00	0.29	0.00	0.00	0.00	0.00	0.00
	Savanna	2.38	0.57	0.08	0.00	0.00	0.00	0.00	0.00
Global		1.34	0.58	0.22	0.00	0.00	0.00	0.00	0.00

SGC = Sudano-Guineo-Congolian transition endemism center, S= Sudanian endemism center.

4. DISCUSSION

4.1 Fruits production potential and physical traits of the fruits of *D. mespiliformis* throughout vegetation types and latitudinal gradient in Benin

The main findings of this study highlight contrasting effect of latitudinal gradient (42, 43), chorological endemism centers and vegetation types (44) on the quantity of fruits produced by target mother trees of *D. mespiliformis* in republic of Benin. The quantity of fruits recorded during forest inventories throughout the populations of *D. mespiliformis* encountered in Guineo-Congolian endemism center (the lowest latitudes’ populations of the species) is lower than the one of fruits recorded per individual of *D. mespiliformis* in the Sudanian endemism center (the highest latitudes’ populations of the species). Thus, the research hypothesis according to which the lowest latitudes’ populations of *D. mespiliformis* produce higher quantity of fruits than the highest latitudes’ populations is not verified for the sampling effort involved in the forest inventories of this research. This opposite pattern of fruits production by the populations of *D. mespiliformis* throughout the two contrasted ecological regions is linked to the presence of important and various

monkey species in the Guineo-Congolian endemism center and especially in the strictly protected dense semi-deciduous Lama reserve forest. Despite the fact that Lama reserve forest has the most important populations of *D. mespiliformis*, the fruiting trees were regularly visited by various monkey species with stronger fruits predation diet behavior as stated by previous researches in the natural forest ecosystems (1, 9). However, this weak fruit availability penalization due to natural fruits predators in Guineo-Congolian endemism center is corrected by robust Bayesian generalized linear mixed model of Poisson family estimates obtained after 3000 iterations resampling scheme from Markov Monte Carlo simulations. Indeed, Markov Monte Carlo simulations take into account penalized and incertitude situations related to the shape of the survey designs and spatial and temporal variation effect of the characteristics of the fruits during different times of forest inventory. This pattern of estimated fruits production obtained from established statistical models is extremely true given that very wide crown area and higher size trees of *D. mespiliformis* were encountered in the Lama reserve forest. Indeed, the size and the crown area of tree species are often positively correlated with higher fruits production by tree species (52, 53). Thus, estimative and predictive framework from Bayesian generalized linear mixed effect model of Poisson family on these biotic drivers of the fruiting capacity of the individuals of *D. mespiliformis* indicates that higher fruits production capacity of *D. mespiliformis* is positively linked to the crown area size of the individuals of *D. mespiliformis* located in the Guineo-Congolian endemism center when fruits eaters or predators are absent. At the opposite, it is the height of the individuals of *D. mespiliformis* that favors higher quantity of fruits production at the highest latitudes' populations in the Sudanian endemism center. Basal area variation did not induce an evidence of fruiting capacity variation of *D. mespiliformis* as already found out by Venter and Witkowski (53) for the main basal area calculation component such as the diameter for the *Adansonia digitata* trees in another tree fruiting biology study. These findings confirm the opposite or neutral effect of some of the functional traits of *D. mespiliformis* on its fruiting biology hypothesis. Personal observations during the forest inventories confirm this trend where the smallest and shortest trees produced higher quantity of fruits as well as the largest trees.

By focusing on the physical traits alone of the fruits of the individuals of *D. mespiliformis*, the main findings reveal three morphotypes populations of *D. mespiliformis* from the lowest latitudes to the highest latitudes of the country. The populations of *D. mespiliformis* in Guineo-Congolian endemism center produced especially fruits with deeper endocarp and wider diameter of seeds at the opposite to the populations of *D. mespiliformis* in the Sudanian endemism center. Indeed, water availability plays often an important role in the fruiting processes and mainly in the quality of the fruits produced by tree species (24, 22, 54). The populations of the wild fruit trees at the highest rainfall regions or ecosystems and seasons produce often fleshier fruits than the fruits of their conspecific trees in the driest environments (54). Thus, afforestation and reforestation programs have to target the fruits from these populations for breeding trials to provide the highest value

fruiting trees and fruits for regional and local trade of the fruits. The main findings contradict recent findings from two other endemism centers (Sudanian and Sudano-Guineo-Congolian) respectively in the northern and central part of the country where four morphotypes of *D. mespiliformis* were inventoried (39). This discrepancy of the pattern of both scientific findings on the morphotypes of *D. mespiliformis* throughout the country is linked to difference in the morphological traits used in the previous research with regard to the ones of this research. Three of the morphological or physical traits (endocarp thickness of the fruits, the length and diameter of the seeds) used in this study were not taking into account by Gnonlonfin *et al.* (39) who focused on the length and width of the leaves, the length and diameter of the fruits and the number of seeds per fruit to determine the main morphotypes of *D. mespiliformis*. Furthermore, spatial variation of ecological conditions of the populations of *D. mespiliformis* sampled between the Sudanian and the Guineo-Congolian-Sudanian endemism centers created also important variation in this difference. Indeed, both endemism centers are widely differentiated by latitudinal gradient and rainfall pattern, vegetation types, soils types and temperature pattern (resources availability hypothesis (24)) which are also important sources of variation of fruits quantity production pattern throughout natural stands. Thus, the research hypothesis according to which vegetation types that harbor the individuals of *D. mespiliformis* drive its fruiting biology is confirmed. Molecular characterization of the populations of the species is required to bring out true morphotypes of *D. mespiliformis*. To collect the organs of *D. mespiliformis* for molecular analysis, geographic coordinates of each tree species and related samples of soils must be collected for analysis of the effects of climatic and soils' conditions variability on the genetic morphotypes of *D. mespiliformis*.

4.2 Spatial pattern of the recruitments of *D. mespiliformis* surrounding the mother trees throughout vegetation types in contrasting chorological endemism centers in Benin

Overall, spatial pattern analysis of the recruitments of the populations of *D. mespiliformis* revealed a lower fruits dispersal ability of the individuals of *D. mespiliformis*. Indeed, most of the individuals of the recruitments of *D. mespiliformis* were located between 0 and 10 m radius surrounding their mother trees with clumped distribution between 0 and 5 m radius surrounding the mother trees. Thus, the hypothesis of repulsive behavior of the mother trees toward their offsprings is rejected. Indeed, the weight of the seeds and the height of the mother trees play important roles in the spatial distribution of the individuals of their recruitment (55). Heavy seeds are less so far dispersed from the mother trees in the absence of dispersers agents such as mega-frugivorous (1, 7). Higher dispersal ability allows often to the fruits and seeds to disperse so far from mother trees and to germinate and to grow from seedlings to young trees. So far from the mother trees, the individuals of recruitment escape from expected allelopathy behavior of some mother trees and also from the negative conspecific trees interaction behaviors for nutrients over the growth periods (2, 55).

Habitat types and endemism centers affected the intensity of the clumped spatial pattern of the recruitments of *D. mespiliformis* surrounding the mother trees with more clumped spatial patterns in the farmlands, gallery forests, fallows and especially in the Guineo-Congolian endemism center at the opposite to the recruitments of the populations of *D. mespiliformis* encountered in the sub-humid areas in the Sudanian endemism center. Indeed, most of the seedlings of some tree species die during dry seasons in the Sudanian endemism center. Most of the mother trees assessed were also encountered in the national parks, where their seedlings and juveniles are often browsed by mammalian herbivores which reduce or limit the growth of important individuals of their recruitments (Growth differentiation hypothesis (20)) as already indicated by other researches (56, 30).

5. CONCLUSION

Wild edible fruit trees feed both human and fauna and contribute to important part of global domestic production of some nations. *D. mespiliformis* is one of these dietary tree species largely distributed from the lowest latitudes to the highest ones in Benin republic. *D. mespiliformis* fruiting was lower at the highest latitudes and varied differently across vegetation types. Any increase of the height and the crown diameter of the individuals of *D. mespiliformis* induces significant increasing fruiting capacity of the individuals of *D. mespiliformis* and the effect was specific to chorological endemism centers. *D. mespiliformis* has lower dispersal capacity with clumped individuals of recruitment surrounding the mother trees in the radius of 5 m. The populations of *D. mespiliformis* are subdivided in three morphotypes with the populations of the fleshiest fruits and widest seeds located in the Guineo-Congolian endemism center. Future researches have to address nutritional and pharmacological properties of the fruits and other organs of *D. mespiliformis*. Breeding researches are also required.

AUTHOR CONTRIBUTIONS

Isidore Gnonlonfoun was the main designer of the research. He led all of the statistical analyses, reviewed and edited the manuscript. Yacoubou Orou Se Guene led data collection with the paraecologists under direction of the forester Elie Zinsou during vegetation surveys, did data curation and drafted the manuscript. Murielle Farrelle Eurydice Soglo, Vignon Descroix Alain Gnonlonfoun measured the characteristics of the fruits and established database. Joel Oscar Houessou, Essolliouwèm Peguedou contributed to statistical analyses. Oré Adédiran Goudégnon and Morel Tiomon contributed to manuscript revision. Marcos Aboubacar and Madjidou Oumorou supervised the research.

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CONFLICT OF INTEREST STATEMENT

Authors of this research did not receive any financial or logistic supports from any funder or supporter that can lead to the conflict of interest.

DATA AVAILABILITY STATEMENT

All of the database used to write this manuscript are available upon request.

REFERENCES

- [1]. Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104, 501–528.
- [2]. 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 Boer, P. J. D. & Gradwell, G.). Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, pp. 298-312.
- [3]. Tesfaye, G., Teketay, D., Fetene, M., & Beck., E. (2010). Regeneration of seven indigenous tree species in a dry Afromontane forest, southern Ethiopia. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 205 (2), 135-143. <https://doi.org/10.1016/j.flora.2008.12.00>.
- [4]. Swamy, V., Terborgh, J., Dexter, K. G., Best, B. D., Alvarez, P., & Cornejo, F. (2011). Are all seeds equal? Spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest. *Ecology Letters*, 14, 195-201. <https://doi.org/10.1111/j.1461-0248.2010.01571.x>.
- [5]. Gaoue, O. G., & Ticktin, T. (2008). Impacts of bark and foliage harvest on *Khaya senegalensis* (Meliaceae) reproductive performance in Benin. *Journal of Applied Ecology*, 45 (1), 34–40. <https://doi.org/10.1111/j.1365-2664.2007.01381.x>.
- [6]. Gaoue, O. G., & Ticktin, T. (2010). Effects of harvest of non-timber forest products and ecological differences between sites on the demography of African mahogany. *Conservation Biology*, 24, 605–614. <https://doi.org/10.1111/j.1523-1739.2009.01345.x>.
- [7]. Koike, S., Tochigi, K., & Yamazaki, K. (2023). Are seeds of trees with higher fruit production dispersed farther by frugivorous mammals? *Journal of Forest Research*, 28(1), 64-72. <https://doi.org/10.1080/13416979.2022.2120073>.
- [8]. Omotayo, A. O., & Aremu, A. O. (2020). Underutilized African indigenous fruit trees and

- food–nutrition security: Opportunities, challenges, and prospects. *Food and Energy Security*, 9 (3), e220. <https://doi.org/10.1002/fes3.220>.
- [9]. Nombimè, G., & Sinsin, B. (2003). Les stratégies de survie du singe à ventre rouge (*Cercopithecus erythrogaster erythrogaster*) dans la Forêt Classée de la Lama. *Biogeographica*, 79(4), 153-166.
- [10]. Sinasson, S. G. K., Shackleton, C. M., & Sinsin, B. (2021). Nationwide Assessment of Population Structure, Stability and Plant Morphology of Two *Mimusops* Species along a Social-Ecological Gradient in Benin, West Africa. *Forests*, 12 (11), 1575. <https://doi.org/10.3390/f12111575>.
- [11]. Angelsen, A., Jagger, P., Babigumira, R., Belcher B., Hogarth, N. J., Bauch, S., & Wunder, S. (2014). Environmental income and rural livelihoods: A global-comparative analysis. *World Development*, 64 (1), S12-S28. <https://doi.org/10.1016/j.worlddev.2014.03.006>.
- [12]. Sardeshpande, M., & Shackleton, C. (2019). Wild edible fruits: A systematic review of an under-researched multifunctional NTFP (non-timber forest product). *Forests*, 10(6), 467. <https://doi.org/10.3390/f10060467>.
- [13]. Huang, H., Zhu, Y., Fu, X., Zou, Y., Li, Q., & Luo, Z. (2022). Integrated natural deep eutectic solvent and pulse-ultrasonication for efficient extraction of crocins from gardenia fruits (*Gardenia jasminoides* Ellis) and its bioactivities. *Food Chemistry*, 380, 132216. <https://doi.org/10.1016/j.foodchem.2022.132216>.
- [14]. Avocèvou-Ayisso, C., Sinsin, B., Adégbidi, A., Dossou, G., & Van Damme, P. (2009). Sustainable use of non-timber forest products: Impact of fruit harvesting on *Pentadesma butyracea* regeneration and financial analysis of its products trade in Benin. *Forest Ecology and Management*, 257, 1930-1938. <https://doi.org/10.1016/j.foreco.2009.01.043>.
- [15]. Nyambe, M. M., Hakwenye, H., & Benyamen, M. S. (2019). Nutritional and anti-nutritional composition of *Diospyros mespiliformis* and *Hyphaene petersiana* fruits from Namibia. *International Science and Technology Journal of Namibia*, 13, 2-11. <https://istjn.unam.na/index.php/istjn>.
- [16]. Safari, F., Hasanpour, H., & Alijanpour, A. (2022). 'Investigation of fruit, seed, and leaf characteristics of some hackberry (*Celtis australis* L.) genotypes in East Azerbaijan Province'. *Forest Research and Development*, 8(4), 389-402. <https://doi.org/10.30466/jfrd.2022.54179.1604>.
- [17]. Zarafshar, M., Akbarinia, M., Sattarian, A., & Hosseini, S.M. (2009). Endocarp diversity of *Celtis australis* L. with Iran and Northern Africa ecotypes. *Journal of Wood and Forest Science and Technology*, 16 (4), 109-114.
- [18]. Haarmeyer, D. H., Schumann, K., Bernhardt-Römermann, M., Wittig, R., Thiombiano, A., & Hahn, K. (2013). Human impact on population structure and fruit production of the socio-economically important tree *Lannea microcarpa* in Burkina Faso. *Agroforestry*

- Systems*, 87, 1363-1375. <https://doi.org/10.1007/s10457-013-9644-7>.
- [19]. Gaoue, O. G., Jiang, J., Ding, W., Agosto, F. B., & Lenhart, S. (2016). Optimal harvesting strategies for timber and non-timber forest products in tropical ecosystems. *Theoretical Ecology*, 9, 287-297. <https://doi.org/10.1007/s12080-015-0286-4>.
- [20]. Herms, D., & Mattson, W. (1992). The dilemma of plants: to grow or defend. *Quarterly Review of Biology*, 67, 283-335. <https://doi.org/10.1086/417659>.
- [21]. Goldschmidt, E.E. (2013). The Evolution of Fruit Tree Productivity: A Review. *Economic Botany*, 67, 51-62. <https://doi.org/10.1007/s12231-012-9219-y>.
- [22]. Gnonlonfoun, I., Assogbadjo, A. E., Gnanglè, C. P., & Glèlè Kakaï, R. L. (2019). New indicators of vulnerability and resilience of agroforestry systems to climate change in West Africa. *Agronomy for Sustainable Development*, 39(2), 1-12. <https://doi.org/10.1007/s13593-019-0566-2>.
- [23]. McKeon, C. M., Kelly, R., Börger, L., De Palma, A., & Buckley, Y. M. (2023). Human land use is comparable to climate as a driver of global plant occurrence and abundance across life forms. *Global Ecology and Biogeography*, 32 (9), 1618-1631. <https://doi.org/10.1111/geb.13713>.
- [24]. Coley, P. D., Bryant, J. P., & Chapin, F. S. (1985). Resource availability and plant antiherbivore defense. *Science*, 230, 895-899. <https://doi.org/10.1126/science.230.4728.895>.
- [25]. Villacorta, C. D. A., Gomes, H. S. Z., Guedes, M. C., & de Toledo, J. J. (2023). Size and crown shape predict reproductive maturity of *Carapa guianensis* in upland and floodplain forests in the northeastern Amazon. *Biotropica*, 0, 1-2. <https://doi.org/10.1111/btp.13256>.
- [26]. Kaproth, M. A., & McGraw, J. B. (2008). Seed viability and dispersal of the wind-dispersed invasive *Ailanthus altissima* in aqueous environments. *Forest Science*, 54(5), 490-496. <https://doi.org/10.1093/forestscience/54.5.490>.
- [27]. Snell, R. S., Beckman, N. G., Fricke, E., Loiselle, B. A., Carvalho, C. S., Jones, L. R., Lichti, N. I., Lustenhouwer, N., Schreiber, S. J., Strickland, C., Sullivan, L. L., Cavazos, B. R., Giladi, I., Hastings, A., Holbrook, K. M., Jongejans, E., Kogan, O., Montañó-Centellas, F., Rudolph, J., ... & Schupp, E. W. (2019). Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB Plants*, 11, 1-19. <https://doi.org/10.1093/aobpl a/plz016>.
- [28]. Juncosa- Polzell, A. S., Tecco, P. A., & Vergara- Tabares, D. L. (2023). Seed dispersal of a fleshy- fruited invasive shrub is affected by changes in the frugivorous bird assemblage along an elevational gradient. *Austral Ecology*, 00, 1-18. <https://doi.org/10.1111/aec.13423>.
- [29]. Ribbens, E., Silander, J. A., & Pacala, S.W. (1994). Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, 75, 1794-1806.

- <https://doi.org/10.2307/1939638>.
- [30]. Morrison, T. A., Holdo, R. M., & Anderson, T.M. (2016). Elephant damage, not fire or rainfall, explains mortality of overstorey trees in Serengeti. *Journal of Ecology*, 104, 409-418. <https://doi.org/10.1111/1365-2745.12517>.
- [31]. Green, R. H. (1966). "Measurement of non-randomness in spatial distributions." *Researches on Population Ecology*, 8, 1-7.
- [32]. Ripley, B. D. (1977). Modelling spatial patterns. *Journal of the Royal Statistical Society Series B*, 39, 172-212.
- [33]. Ripley, B. D. (1981). Spatial statistics. J. Wiley, New York. NY.
- [34]. Condit, R., Ashton, P. S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S. P., Foster, R. B., Itoh, A., LaFrankie, J. V., Lee, H. S., Losos, E., Manokaran, N., Sukumar, R., & Yamakura, T. (2000). Spatial patterns in the distribution of tropical trees. *Science*, 288, 1414-1418. <https://doi.org/10.1126/science.288.5470.1414>.
- [35]. Wu, W., Yang, P., Tang, H., Zhou, Q., Chen, Z., & Shibasaki, R. (2010). Characterizing spatial patterns of phenology in cropland of China based on remotely sensed data. *Agricultural Sciences in China*, 9, 101-112. [https://doi.org/10.1016/S1671-2927\(09\)60073-0](https://doi.org/10.1016/S1671-2927(09)60073-0).
- [36]. Birch, J. D., & Lutz, J. A. (2023). Spatial patterns of seedlings dominated by proximity to deadwood and adult trees for *Pinus flexilis* and *Pinus longaeva*. *Forest Ecology and Management*, 121049. <https://doi.org/10.1016/j.foreco.2023.121049>.
- [37]. Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., & Simons, A. (2009). Agroforestry database: a tree reference and selection guide. Version 4.0. [Internet] World Agroforestry Centre (ICRAF), Nairobi, Kenya. <http://www.worldagroforestry.org/resources/databases/agroforestry>. Accessed May 2011. El-Kamali H.H. 2011. *Diospyros mespiliformis* Hochst. ex A. DC. [Internet] Record from PROTA4U. Lemmens, R.H.M.J., Louppe, D. & Oteng-Amoako, A.A. (Editors). PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, Netherlands. <http://www.prota4u.org/search.asp>. Accessed 1 February 2024.
- [38]. Arbonnier, M. (2002). Arbres et arbustes et lianes des zones sèches d'Afriques de l'ouest. CIRAD-MNHN, 573p.
- [39]. Gnonlonfin, L., Biaoun, H., & Ouinsavi, C. A. I. N. (2022). "Morphological variation in *Diospyros mespiliformis* (Ebenaceae) among different habitats in Benin, West Africa." *Journal of Ecology and The Natural Environment*, 14 (2), 44-55. <https://doi.org/10.5897/JENE2022.0925>.
- [40]. Hodges, C.B., Stone, B.M., Johnson, P.K., Carter III, J.H., Sawyers, C.K., Roby, P.R., & Lindsey, H.M. (2022). Researcher degrees of freedom in statistical software contribute to unreliable results: A comparison of nonparametric analyses conducted in SPSS, SAS,

- Stata, and R. *Behavioral Research*. <https://doi.org/10.3758/s13428-022-01932-2>.
- [41]. Kraemer, H.C. (2019). Is it time to ban the P value? *JAMA Psychiatry*, 76, 1219-1220.
- [42]. Fischer, A. G. (1960). Latitudinal variation in organic diversity. *Evolution*, 14, 64-81. <https://doi.org/10.2307/2405923>.
- [43]. Pianka, E.R. (1966). Latitudinal Gradients in Species Diversity: A Review of Concepts. *The American Naturalist*, 100 (910), 33-46. <https://doi.org/10.1086/282454>.
- [44]. White, F. (1983). The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO. UNESCO, Natural Resources Research, 20, 1-356.
- [45]. Adomou, A. C. (2005). Vegetation patterns and environmental gradients in Benin: implications for biogeography and conservation. PhD thesis Wageningen University, Wageningen ISBN 90-8504-308-5.
- [46]. INSAE (Institut National de la Statistique et de l'Analyse Economique), (2016). Effectifs de la population des villages et quartiers de villes du Bénin. Rapport final, RGPH-Recensement Général de la Population et l'Habitat 4e édition. Cotonou, Bénin, Institut national de la statistique et de l'analyse économique, 85 p.
- [47]. Boffa, J. M. (1999). Agroforestry parklands in sub-Saharan Africa. Food and Agriculture Organization, FAO Conservation Guide, Rome, Italy, p34.
- [48]. Visser, M. D., Jongejans, E., van Breugel, M., Zuidema, P. A., Chen Yu-Yun., Kassim, A. R., & de Kroom, H. (2011). Strict mast fruiting for a tropical dipterocarp tree: a demographic cost-benefit analysis of delayed reproduction and seed predation. *Journal of Ecology*, 99, 1033-1044. <https://doi.org/10.1111/j.1365-2745.2011.01825.x>.
- [49]. Bürkner, P. (2017). "brms: An R Package for Bayesian Multilevel Models Using Stan." *Journal of Statistical Software*, 80(1), 1-28. <https://doi:10.18637/jss.v080.i01>.
- [50]. Bartoš, F. (2021). BayesTools: Tools for Bayesian Analyses. R package version 0.2.17, <https://CRAN.R-project.org/package=BayesTools>.
- [51]. Morey, R. D., & Rouder, J. N. (2014). BayesFactor version 0.9.9: An R package for computing Bayes factor for a variety of psychological research designs. Software <http://bayesfactorpcl.r-forge.r-project.org/>.
- [52]. Lamien, N., Tigabu, M., Guinko, S., & Oden, P.C. (2007). Variations in dendrometry and fruiting characters of *Vitellaria paradoxa* populations and multivariate models for estimation of fruit yield. *Agroforestry Systems*, 69, 1-11. <https://doi.org/10.1007/s10457-006-9013-x>.
- [53]. Venter, S. M., & Witkowski, E. T. F. (2011). Baobab (*Adansonia digitata* L.) fruit production in communal and conservation land-use types in Southern Africa. *Forest Ecology Management*, 261, 630-639. <https://doi.org/10.1016/j.foreco.2010.11.017>.
- [54]. Dunham, A. E., Razafindratsima, O. H., Rakotonirina, P., & Wright, P. C. (2018). Fruiting phenology is linked to rainfall variability in a tropical rain forest. *Biotropica*, 50, 396-404.

- <https://doi.org/10.1111/btp.12564>.
- [55]. Okuda, T., Kachi, N., Yap, S. K., & Manokaran, N. (1997). Tree distribution pattern and fate of juveniles in a lowland tropical rain forest – implications for regeneration and maintenance of species diversity. *Plant Ecology*, 131, 155-171. <https://doi.org/10.1023/A:1009727109920>.
- [56]. Goheen, J. R., Palmer, T. M., Keesing, F., Riginos, C., & Young, T.P. (2010). Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *Journal of Animal Ecology*, 79, 372-382. <https://doi.org/10.1111/j.1365-2656.2009.01644.x>.