

Chimpanzees, dung beetles and seed dispersal: implications for habitat conservation of the West African chimpanzee *Pan troglodytes verus* in Taï National Park, Côte d'Ivoire

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Abstract

Seed dispersal is a key stage in the life cycle of plants, thus in forest regeneration, especially in the tropics. Chimpanzees are known as important seed dispersers and dung beetles play critical roles in secondary dispersal thus increasing the chance for seed post-dispersal success. Hence, understanding secondary seed dispersal by dung beetles is critical to our understanding of forest dynamics. The aim of this study was to evaluate the effects of successive dispersal by chimpanzees and by dung beetles on the surface dispersal and burial of the seeds of four plant species: (*Dacryodes klaineana* (Pierre) H.J. Lam, *Diospyros mannii* Hiern, *Pycnanthus angolensis* (Welw.) Warb. and *Uapaca guineensis* Muell) at three nesting site in the Taï National Park. To investigate this, 28 seeds i.e. seven seeds per plant species ($N = 75$, average $\pm$ SD: 28.24 ± 3.06 seeds) were introduced into 85 g of chimpanzee faecal matter. This set was exposed on the forest floor for 48h following an average faecal radius of 5 cm ($N = 40$, average $\pm$ SD: 5 ± 1.06 cm). From the observations made, it emerges an essentially surface dispersion, ie 45.6% of the seeds dispersed against 6.3% of seeds buried. The highest rate of vertically dispersed seeds, ie 10.31%, and average depth of burial, ie 7.45 cm, were quantified in the southern nesting sites. This distribution of seeds would not only be linked to the time of deposition of the faecal matter, but also and above all to the size of the secondary disperser.

Introduction

Tropical forests are characterized by high levels of biological diversity (Mayaux et al. 2013). Many hypotheses have been proposed to explain plant species richness and diversity in tropical forests including the biological interaction hypothesis between plants and their dispersers (Petre et al. 2015; deCastro-Arrazola et al. 2020; Pedersen and Blüthgen 2021). Indeed, more than 70% of fruiting plant species depend on animals for seed dispersal (Muller-Landau 2007; Beaune et al. 2012). At the local scale, the Janzen-Connell hypothesis states that the plant diversity observed in tropical forests is linked to a spatial variation in the probability of seedling recruitment (Janzen 1970; Connell 1971), this recruitment being higher away from mother plants where the density of conspecific species tends to be lower. Forests present a wide range of mammal-propagule relationships allowing seeds to escape competition (Janzen-Connell hypothesis or escape hypothesis), to escape predation, to colonize new sites, and to establish themselves in favorable microsites (targeted dispersal hypothesis).

Considered as a success story in rainforest conservation, the Taï National Park in south-western Côte d'Ivoire, protects more than 5000 km² of Guinean rainforest in a single block. The park represents a hotspot of biodiversity that boasts about 150 endemic plant species and is declared one of two protected areas in West Africa with high irreplaceability for biodiversity and endangered species (Le Saout et al. 2013) such as the chimpanzee *Pan troglodytes verus*, reclassified as « Critically Endangered » (Humle et al. 2016; Kühl et al. 2017) and known to be an excellent seed disperser. As in most frugivorous vertebrates, the choice of food is directly influenced by the availability in the environment of different species of plants that have a seasonal phenology (Ban et al. 2016), which implies movements in search of the food resource. In Taï, three chimpanzee communities are fully habituated to human presence and

regularly monitored: The Northern community, the Southern community, and the Eastern community. The size of the home range of the Northern community varies between 19-30 km², that of the Southern communities varies between 38-49 km², and that of the Eastern community varies between 32-43 km² (Samuni et al. 2021). With such large home ranges, chimpanzees can thus disperse seeds relatively far from the parent plants, which is an advantage for the survival of the seedling according to the Janzen-Connell hypothesis.

This endozoochoric transport of seeds by chimpanzees must not damage their germinative capacities to ensure the maintenance of forest dynamics. According to Lazure and Almeida-Cortez (2008) three mechanisms determine how frugivores affect seed germination: (i) by mechanical or chemical modification of the pericarp; (ii) by seed separation and pulp; and (iii) by a fertilizing effect of the faeces surrounding the seeds. In addition, Willson (1992) makes three assumptions about dispersal: (i) avoiding predators that often feed in response to seed density or proximity to the mother plant; (ii) avoid intra-specific competition; (iii) finding a suitable location (micro-habitat) for establishment. The final fate of dispersed seeds depends on several factors including the distance between the seed and the mother tree, the degree of seed agglomeration, the treatment received from dispersing agents, and the characteristics of the microsite in which the seeds are deposited (Karubian and Durães, 2009).

Once in the environment, animal droppings are highly sought-after by dung beetles as they represent an essential food resource (Halffter and Edmonds 1982). In tropical rainforests, adult dung beetles and their larvae preferentially feed on the faecal matter of large herbivorous mammals (Hanski and Cambefort 1991). By burying faecal matter, dung beetles perform essential ecological functions such as nutrient recycling, soil fertilization and aeration, and regulation of parasites (Nichols et al. 2008). More recently, their contribution to seed dispersal has been observed (Janzen 1982; Vulinec 2000; Andresen and Levey 2004; Andresen 2005; Culot et al. 2011; Petre et al. 2015; deCastro-Arrazola et al. 2020; Pedersen and Blüthgen 2021). The burying behaviour of dung beetles may attenuate the phenomenon of mortality-density dependence (Andresen and Feer 2005, Urrea-Galeano et al. 2019). Indeed, burial protects the seeds from predation by animals such as rodents (Midgley et al. 2015), particularly of smaller sized seeds (Andresen 2002a). Alternatively, burial at increased depth reduces the probability of seedling establishment (Vulinec et al. 2006). The burial depth of dung containing seeds is in turn influenced by dung beetle species specific traits and behaviour, and edaphic factors such as soil composition, soil compaction, and bedrock type (Halffter and Edmonds 1982).

Understanding the mechanisms of secondary seed dispersal by dung beetles is critical to our understanding of forest dynamics and seedling establishment (Urrea-Galeano *et al.* 2019).

This study aims to assess the role of dung beetles on secondary dispersal of seeds contained within the faecal matter of the Western chimpanzee *Pan troglodytes verus* within the nesting sites of three communities in the Taï National Park. Our research hypotheses are as follows: (H1) nesting behavior and size of the dung beetle influence the depth of seed burial; (H2) physical parameters such as soil

compaction and leaf litter influence the probability of seed burial; (H3) seed dispersal categories and distances are closely related to the size and nesting behavior of secondary dispersers i.e. dung beetles.

Methods

Study area and site selection

The Taï National Park covers an area of about 508,186 hectares, in south-western Côte d'Ivoire and extends between 5°08'192" and 6°23'790" N, and between 6°46'579" and 7°26'006" W (Fig. 1).

It is located on the borders of the departments of Guiglo, Taï, Tabou, San-Pedro, Méagui, Soubré and Buyo (Décret n° 2018-496 du 23 mai 2018). It represents the last and largest intact block of primary rainforest in West Africa and represents more than half of the total area of West African forest under high protection status. It is characterized by a subequatorial climate; hot and humid with four seasons: two rainy seasons, a long one from March to June and a short one from September to November, that are alternated by a long dry season from December to February and a short dry season from July to August (Chatelain et al. 2001). Rainfall varies from 1700 mm in the north-east to 2200 mm in the south-west of the park. The annual variation in temperature is around 4°C, between 24 to 28°C. Relative humidity is always very high and varies from 70 to 90% (Chatelain et al. 2001). During the 2019 study year, the average rainfall and temperature were 1877 mm and 25.2°C, respectively. The soil of the Taï National Park is of two types: highly desaturated and fragile ferralitic soils and more fertile hydromorphic gley and pseudogley soils drained by numerous permanent water streams which are shared between two large catchment areas and two basins of small coastal rivers (Perraud 1971). About 1,300 species of vascular plants have been recorded in the TNP, 12% of which are endemic (Adou et al. 2005). Vegetation is homogenous overall with two large plant formations, namely the hyper humid forest with "*Diospyros* spp. and *Mapania* spp. or pelohygrophilous forest, and the evergreen forest with "*Eremospatha macrocarpa* and *Diospyros mannii*" (Adou et al. 2005).

A floristic and structural survey of chimpanzee community habitats in northwestern TNP by Goné bi et al. (2016) identified 264 plant species belonging to 52 botanical families dominated by *Diospyros mannii* (Ebenaceae), *Calpocalyx brevibracteatus* (Fabaceae) and *Coula edulis* (Olacaceae).

These chimpanzees territories have high densities and land areas comparable to most tropical forests, in general, and forests that support chimpanzee communities, in particular (Goné bi et al. 2016). We collected data in the research area of the Taï Chimpanzee Project, where the chimpanzees of four neighbouring communities are followed and observed every day from sun rise to sun set (Wittig and Boesch 2019). We determined the Study plots by identifying the chimpanzee nesting sites of the last two months prior to the start of the study.

Experimental design

We established seven plots of 40 x 40 m in each of the chimpanzee nesting sites (North, South and East), thus resulting in a total of 21 plots. The main "pitfall trap" device for harvesting dung beetles was set up in center of each plot. To imitate the spatial pattern of aggregated defecation of chimpanzees in the nesting sites, we installed five devices horizontally on either side of the main device following the orientation 290° West - 70° East (Fig. 2).

Plant species studied

The seeds of four plant species, namely *Uapaca guineensis* Muell. Arg. (Phyllantaceae), *Diospyros mannii* Hiern (Ebenaceae), *Dacryodes klaineana* (Pierre) H.J. Lam (Burseraceae) and *Pycnanthus angolensis* (Welw.) Warb. (Myristicaceae) were selected for the study of dispersal by dung beetles. These seeds are regularly consumed by chimpanzees during the November-February period (Kasperek 2000). Further exploration of the droppings during the study period showed that 66% of the total seeds found in the droppings belonged to the four plant species chosen above. The average seed is compiled in the table 1.

Table 1

Seed dimensions (in cm) of the plant species studied (average $\pm$ SD, N = 75)

	Plant species			
	<i>Dacryodes klaineana</i>	<i>Diospyros mannii</i>	<i>Pycnanthus angolensis</i>	<i>Uapaca guineensis</i>
Length	1.65 $\pm$ 0.18	3.07 $\pm$ 0.21	1.66 $\pm$ 0.15	2.59 $\pm$ 0.1
Width	1.13 $\pm$ 0.13	1.49 $\pm$ 0.12	1.02 $\pm$ 0.07	1.27 $\pm$ 0.1
Thickness	0.82 $\pm$ 0.08	0.9 $\pm$ 0.1	1.07 $\pm$ 0.09	0.92 $\pm$ 0.05

Dacryodes klaineana (Pierre) H.J. Lam (Burseraceae): A medium sized, dioecious, evergreen, hypogeous germinating tree reaching 25-30 m high often branched a few meters above the ground. The shaft is branchless over 10 m, up to 60-120 cm in diameter. The leaves are composed of imperipinnate, opposite leaflets with inflorescent flowers in a raceme fascicle in the axils of the terminal leaves. The fruits are ovoid edible drupes of about 2 cm x 1 cm with a lemony taste (Kasperek 2000).

Diospyros mannii Hiern (Ebenaceae): A small tree with simple, alternate leaves. The flowers are unisexual, fasciculate and axillary. The calyx is hairy brown. The fruits are curious berries completely covered with brown hairs. The genus *Diospyros* has a wide range of distribution from Côte d'Ivoire to Gabon. There are six species within the study area: *Diospyros chevalieri* De Wild, *Diospyros heudelotii*, *Diospyros mannii*, *Diospyros sanza-minika* A. Chev, *Diospyros soubreana* F. White and *Diospyros vignei* F. White (Kasperek 2000).

Pycnanthus angolensis (Welw.) Warb. (Myristicaceae): An evergreen tree, monoecious or dioecious, medium to large in size and up to 25 – 35 (-40) m high. The straight, cylindrical shaft is branchless up to 15 (-25) m, reaching 120 (-150) cm in diameter. This species usually bears buttresses. The outer bark is greyish-brown with orange-brown exudate. The cyme is small, the alternate leaves are disticticulate, simple and whole, without stipules. The fruit is an ellipsoid to oblong or globular, yellowish-orange drupe with a fairly hard and solid wall. The seeds are ellipsoid, aromatic, dark brown with pink to red arils, lacinated almost to the base (Kasperek 2000).

Uapaca guineensis Muell. Arg. (Euphorbiaceae): This genus has a distribution that extends from Sierra Leone to Congo. It grows along rivers and wet, swampy ground. It has large, arched aerial roots (the stilt-roots) which support the tree. The leaves are large in terminal rosettes of simple leaves with small white to fairly large yellow flowers, dioecious tree. The fruit is a drupe of different sizes, ovoid. The genus *Uapaca* is particularly well represented within the Taï National Park, the species *Uapaca esculenta* A. Chev. Ex Aubrév. & Leandri, *Uapaca guineensis* Muell. Arg. and *Uapaca paludosa* Aubrév. & Leandri (Kasperek 2000).

Secondary seed dispersal

Determination of faecal material to be exposed

For better reproduction of a chimpanzee faecal sample, we evaluated the average mass of chimpanzee faecal matter (N = 200, average $\pm$ SD: 114.33 $\pm$ 49.46 g), the average diameter (N = 40, average $\pm$ SD: 10 $\pm$ 2.12 cm) and the average number of seeds by faecal sample (N = 75, average $\pm$ SD: 28.24 $\pm$ 3.06 seeds). We exposed 28 seeds, i.e seven seeds per plant species contained in 85g of faecal matters in the forest for the study, taking into account the average diameter measured. The average mass of the 28 seeds was estimated (N = 75, average $\pm$ SD: 29.47 $\pm$ 3.64 g). The whole faecal matter and seeds weighed 115 g.

Methodology for the study of seed dispersal

For each of North, South and East territories, we exposed 70 chimpanzee faeces inside which were inserted 28 seeds each, i.e ten faeces per nesting site. In total, we exposed 210 dropping over the whole of this study.

We directly deposited the faecal samples on the forest floor early in the morning for a 48-hour exposure. We indelibly marked each seed in order to avoid confusing them with seeds possibly present at the site of the devices or which would have been forgotten inside the faecal matter before the introduction of the marked seeds. A plastic sheet placed at 30 cm over each device prevented the seeds from being displaced by the rainwater. We estimated the proportion of faecal matter remaining on the surface after 48 h and counted the number of seeds on the surface. When it was lower than the number of seeds exposed initially, the soil was excavated following the orientation of the pedotrophic nests or over a maximum depth of approximately 50 cm and within a maximum radius of 1 m around a flag initially

placed in the center faecal matter. Seeds are indeed rarely moved over a horizontal distance exceeding 15 cm (Andresen 2001). Since the average radius of a faecal sample is 5 cm (N = 40, average $\pm$ SD: 5 ± 1.06 cm), we reduced the horizontal distances to be measured in the field by 5 cm in order to obtain an estimate of the actual value of horizontal distances. Seeds remaining on the surface after 48 h and located within 5 cm of the center are considered not to have been dispersed (Petre et al. 2015). Those buried were systematically considered dispersed.

The competitiveness of the species of dung beetles harvested in the different habitats is given in table 2.

Table 2

Abundance of individuals (percentage in brackets) belonging to the three competitiveness categories and result of the statistical test

	Habitats			Kruskal test		
	North	South	East	χ^2	df	p
Rollers	633 (21,41)	740 (35,34)	991 (36,41)			
Fast burying tunnelers	209 (7,07)	276 (13,18)	243 (8,93)			
Total category 1	842 (28,48)	1016 (48,52)	1234 (45,33)			
Slow burrowing tunnelers	0 (0)	0 (0)	0 (0)	6,543	2	0,038*
Small tunnelers	2105 (71,21)	1056 (50,43)	1466 (53,86)			
Total category 2	2105 (71,21)	1056 (50,43)	1466 (53,86)			
Dwellers (category 3)	9 (0,3)	22 (1,05)	22 (0,8)			

Individuals were prioritized into three categories, from most competitive to least competitive. The first category includes telecoprids ("Rollers"; genera *Sisyphus*, *Neosisyphus* and *Garetta*) as well as large nocturnal paracoprids burying faeces rapidly ("Fast burying tunnelers"; genera *Catharsius*, *Heliocopris* and *Diastellopalpus*). The second category includes small paracoprids (Tribe Onthophagini). The last category is constituted by the endocoprids (*Liatongus sjoestedti* (Felsche, 1904) and *Oniticellus pseudoplanatus* Balthasar, 1964).

Overall, the proportion of individuals belonging to the most competitive category is greater in the eastern nesting sites, but "fast burying tunnelers" of the genus *Heliocopris*, *Catharsius* and *Diastellopalpus* are more abundant in the southern nesting sites. Conversely, "rollers" are predominant in those of the East.

We observe a significant dependence of the distribution of individuals in the three habitat competitiveness categories.

Soil compaction

The rate of faecal matter burial can be greatly influenced by soil structure and compaction. For this, we evaluated the dry bulk density of the surface horizons, as an index of soil compaction, using the so-called “cylinder method”, described below.

We took three soil samples exactly 30 cm from the center point of each device that allowed secondary seed quantification. Here, we used a cylinder 10 cm high and 3 cm in diameter. It was driven into the ground with a hammer. We carefully cleaned the resulting soil sample of tiny roots and its contents poured into numbered and sealed plastic bags (Petre et al. 2015). We heated this content in an oven at 105°C. We weighed the soil sample subjected to heating every hour until the mass stabilized perfectly, meaning that the soil sample was dry. The evaluation of soil compaction was calculated using the following formula:

$$\text{Bulk dry density (g / cm}^3\text{)} = \frac{\text{Mass of dry soil}}{\text{Volume of soil}}$$

Litter quantification

We sample the litter an area of 1m² around each device that allowed the quantification of the seeds. We sieved using a 1 × 1 cm mesh and the resulting particles, namely the sieve and the large particles were weighed (Petre et al. 2015).

2.5- Data analysis

All statistical analyses were performed with the statistical software R version 4.1.0, at the 5% significance level.

The software allowed the verification of the normality and variances homogeneity of the insect abundances classified by nesting behavior and of the number of dispersed seeds on the one hand, but also of the litter data and of the soil compaction on the other hand. The Kruskal-wallis test (non-parametric test) and ANOVA (parametric test) were used for the comparison of means. The Kruskal-wallis post-hoc test was used to establish significant differences between the dispersion parameters.

Pearson correlation matrices tests were used to test correlations between the different parameters quantifying seed dispersal and dung beetle community parameters. When a significant correlation

between two parameters was observed, simple linear regression was used to determine a statistical model linking the two variables in question.

Results

General fate of seeds within the faecal material.

The handling of the faecal matter showed a greater use of it at the northern nesting sites (Kruskal test, $\chi^2 = 14.5$, $df = 2$, $p < 0.001$). Surface faecal matter estimates were 5.71 ± 9.72 for northern nest sites vs 13.8 ± 17.72 and 12.07 ± 19.27 for southern and eastern sites, respectively. Overall, a faecal exploitation rate of more than 85% was found. In the northern nesting sites, between 60 and 100% of the exposed faecal material was buried by dung beetles. This rate ranged from 30-100% for the southern nesting sites and varied from 0-100% for the eastern sites.

Similarly, seed fates were observed at the different nesting sites. Several seeds were "not found" in all habitats. The number of seeds not found was not significantly different by habitat (Kruskal test, $\chi^2 = 1.7$, $df = 2$, $p = 0.42$). Also, we counted a significant proportion of "non-dispersed" seeds. On average, 12.13 ± 4.67 seeds were not dispersed after 48 h in the northern habitat, 15.34 ± 6.55 in the southern habitat and 12.69 ± 5.22 in the eastern habitat. The mean number of non-dispersed seeds was greater in the Southern nesting site (Kruskal test, $\chi^2 = 6.49$, $df = 2$, $p = 0.04$) than in the North and East at the 5% threshold. Finally, the largest share of seeds was dispersed with an overall rate of 52.2% of dispersed seeds. There were significant differences between habitats for each parameter considered (Table 3).

Table 3 Average, number of measures, minima (Min) and maxima (Max) of seed dispersal distances at different nesting sites

Dispersal distances	Habitats	Number of measures	Min	Max	Average $\pm$ SD (cm)	Kruskal test		
						χ^2	df	p
Horizontal distance (surface)	North	1011	0,3	20,7	3,39 $\pm$ 2,89	35,8	2	< 0,001
	South	679	0,5	32,5	4,62 $\pm$ 4,97			
	East	992	0,2	30,5	3,03 $\pm$ 2,49			
Horizontal distance (Below surface)	North	72	0,5	10	3,01 $\pm$ 2,46	61,8	2	< 0,001
	South	163	0,5	22	8,31 $\pm$ 6,36			
	East	45	0,5	8	2,9 $\pm$ 1,97			
Overall horizontal distance	North	1083	0,3	20,7	3,37 $\pm$ 2,86	90,6	2	< 0,001
	South	842	0,5	32,5	5,34 $\pm$ 5,46			
	East	1037	0,2	30,5	3,03 $\pm$ 2,47			
Vertical distance	North	98	0,5	18	4,15 $\pm$ 5,6	115,03	2	< 0,001
	South	202	0,5	19	7,45 $\pm$ 5,06			
	East	75	0,5	3,5	0,99 $\pm$ 0,69			

The Kruskal-wallis post-hoc test performed for any type of dispersal revealed on average a higher number of dispersed seeds in the nesting sites of the southern habitat.

Surface dispersion

The percentage of surface dispersed seeds varied among nesting sites. It ranged from 10.71 to 78.57% for northern habitat nest sites, 0 to 96.43% for southern habitat nest sites, and finally 0 to 82.14% for eastern habitat nest sites. The distribution of seeds by surface distance category was significantly different by habitat (ANOVA, $F = 11.23$, $p < 0.001$). Two trends are observed across habitats. Overall, the number of seeds dispersed on the surface increased as the distance increased within the first three centimeters. Beyond three centimeters, the number of seeds moved is lower as distance increases. The highest rates were observed in the first five classes of intervals, from]0;1[to]5;10[.

Overall, the proportion of seeds dispersed 10 cm away or more from the center point of the fecal material remains low by habitat and plant species. This observation concerns 10.46% of the seeds of the nesting sites of the South habitat against respectively 3.45 and 2.03% for those of the North and the East. Most of the surface dispersal is measured within 10 cm of the center point of the exposed faecal material.

Vertical or depth dispersion

Vertical dispersal showed different uses of seeds in the different nesting sites. The number of vertically dispersed seeds ranged from 0 to 57.14% for the northern nesting sites, from 0 to 75% for the southern ones and finally from 0 to 17.86% for the eastern nesting sites. Only 375 (6.38 %) of 5880 seeds were buried. Seed distribution by vertical distance category was not significantly different by habitat (ANOVA, $F = 0.38$, $p = 0.9$). Overall, most seeds were dispersed below 3 cm in the northern and eastern habitat nest sites while the most seeds were observed above 3 cm depth in the southern ones (Fig. 2).

Concerning the larger *Diospyros mannii* seeds, 46 seeds were buried. Almost all of these, 43 seeds or 93.48%, were buried in the nesting sites of the southern habitat. More than 30% of these seeds were found at more than 10 cm of depth against 41.86% of the seeds buried in the interval [3;10[. In contrast, seeds buried at the North and East nesting sites were measured at less than 3 cm depth. Overall, seeds of all physical characteristics were buried more in the southern habitat than in the northern and eastern habitats. More seeds were buried at greater depths at southern nest sites.

Dispersal by seed species and nest sites

The dispersal measured in all the nesting sites of the three groups of chimpanzees differs according to the seed species. Concerning surface dispersion, it is more beneficial to *Diospyros mannii* and *Uapaca guineensis* seeds, which are larger (Kruskal test, $\chi^2 = 10.119$, $df = 3$, $p = 0.01758$). Conversely, the number of buried seeds (vertical dispersion) is greater in the seeds of *Dacryodes klaineana* and *Pycnanthus angolensis*, which are smaller (Kruskal test, $\chi^2 = 35.211$, $df = 3$, $p < 0.001$).

Regarding the surface dispersion of each nesting site, that measured in the southern (Kruskal test, $\chi^2 = 0.24756$, $df = 3$, $p = 0.9696$) and eastern (Kruskal test, $\chi^2 = 3.7441$, $df = 3$, $p = 0.2905$) is not influenced by seed size. Conversely, a greater number of seeds of *Uapaca guineensis* was dispersed in the northern nesting sites (Kruskal test, $\chi^2 = 16.53$, $df = 3$, $p < 0.001$).

As for depth dispersal, similar observations were observed in the North and East nesting sites. The seeds buried primarily are essentially small, namely *Dacryodes klaineana* and *Pycnanthus angolensis* both in the northern nesting sites (Kruskal test, $\chi^2 = 23.068$, $df = 3$, $p < 0.001$) and in those of the East (Kruskal test, $\chi^2 = 25.78$, $df = 3$, $p < 0.001$). Conversely, no significant variation was observed in vertical seed dispersal at southern nesting sites (Kruskal test, $\chi^2 = 2.106$, $df = 3$, $p = 0.5507$).

Quantification of litter and soil compaction at nesting sites

In general, the lowest litter weights were measured at the eastern nesting sites. From the data collected (Table 4), it appears that the amount of litter differs significantly between habitats for both coarse particles (Kruskal test, $\chi^2 = 41.8$, $df = 2$, $p < 0.001$) and sieve (Kruskal test, $\chi^2 = 20.7$, $df = 2$, $p < 0.001$).

Table 4

Average litterfall and soil compaction of different habitats

		Litter		Soil compaction		
		Large particle	Tamisat	Mass	Volume	Density
	North	1000,58±375,48 a	448,8±267,88 b	446,06±113,62	70,69	6,31±1,61 c
Habitats	South	816,65±3014,19 b	532,48±381,9 a	509,71±69,6	70,69	7,21±0,98 b
	East	620,39±256,18 c	301,74±252,98 c	543,52±62,11	70,69	7,69±0,88 a

Average $\pm$ SD values with different letters are significantly different at the 5 % level. Volume of cylinder (cm³) = $\pi r^2 h$ (d = 3 equals r = 1.5 cm, h = 10 cm, π = 3.1415926536)

Coarse particles were more abundant in the northern nesting sites in contrast to the more abundant sieve in the southern ones.

Concerning soil compaction, it was quantified that there was more compaction in the eastern nesting sites compared to the southern and northern ones (Kruskal test, $\chi^2 = 25.4$, df = 2, p < 0.001).

Regression analysis

Due to the multiplicity of correlation tests performed, only the regressions of significant correlations of the different habitats are presented here.

The relationship between dung beetles and seed dispersal at northern nest sites yielded 31 significant correlation relationships, 17 of which were negative. Simple linear regressions were run for each of the significant correlations (Table 5). The regression coefficient is relatively high for seven of them (r-Sq > 50%).

Table 5

Regression equations and coefficient of determination (R-Sq) for significant correlations at Northern nesting sites

Variable to explain (y)	Explanatory variable (x)	Regression equation	R-Sq (%)
Average horizontal distance	Number of endocoprids	$y = 4,47 x - 12,49$	38,36
	Number of kleptoparasites	$y = 3,66 x - 10,02$	25,75
Average vertical distance	Number of species	$y = - 3,96 x + 25,25$	39,34
Number of seeds scattered on the surface	Number of paracoprids	$y = - 0,3 x + 347,83$	0,93
	Number of endocoprids	$y = 0,06 x - 7,16$	53,14
	Number of kleptoparasites	$y = 0,04 x - 5,02$	29,26
	Number of species	$y = - 0,09 x + 37,12$	64,99
Number of seeds dispersed	Number of paracoprids	$y = - 0,03 x + 299,59$	9e-03
	Number of endocoprids	$y = 0,06 x - 7,76$	48,87
	Number of kleptoparasites	$y = 0,04 x - 5,80$	29,75
	Number of species	$y = - 0,09 x + 37,62$	55,69
Number of horizontally dispersed seeds	Number of paracoprids	$y = - 0,32 x + 353,91$	1,24
	Number of endocoprids	$y = 0,05 x - 7,36$	57,59
	Number of kleptoparasites	$y = 0,04 x - 5,82$	38,61
	Number of species	$y = - 0,08 x + 36,30$	59,25
Number of seeds dispersed only vertically	Number of paracoprids	$y = 13,14 x + 255,47$	51,24
	Number of telecoprids	$y = - 3,65 x + 90,97$	26,32
	Number of endocoprids	$y = - 0,17 x + 1,78$	13,75

	Number of kleptoparasites	$y = -0,17 x + 1,78$	13,75
	Number of individuals	$y = 9,26 x + 349,05$	23,03
	Number of species	$y = 0,32 x + 22,08$	21,57
Number of seeds dispersed horizontally and vertically	Number of telecoprids	$y = -7,27 x + 152,17$	31,6
	Number of individuals	$y = -11,04 x + 496,97$	9,89
Number of seeds buried	Number of paracoprids	$y = 8,1831x + 189,72$	28,95
	Number of telecoprids	$y = -4,01 x + 133,53$	46,36
	Number of endocoprides	$y = -0,09 x + 2,42$	5,71
	Number of kleptoparasites	$y = -0,02 x + 1,44$	0,3
	Number of species	$y = 0,22 x + 20,23$	14,27
Number of seeds not found	Number of telecoprids	$y = -0,83 x + 90,01$	29,48
	Number of endocoprides	$y = -0,03 x + 1,57$	7,99
	Number of species	$y = 0,12 x + 21,41$	68,28

Next, the relationship between dung beetles and seed dispersal in the southern habitat nesting sites yielded 35 significant correlation relationships, 14 of which were negative. The simple linear regressions run for each of the significant correlations are compiled in Table 6. The regression coefficient is relatively high for ten of them ($r\text{-Sq} > 50\%$).

Table 6

Regression equations and coefficient of determination ($R\text{-Sq}$) for significant correlations at Southern nesting sites

Variable to explain (y)	Explanatory variable (x)	Regression equation	R-Sq (%)
Average horizontal distance	Number of paracoprids	y = 32,81 x + 26,31	59,28
	Number of telecoprids	y = - 7,96 x + 125,91	6,26
	Number of kleptoparasites	y = 2,56 x - 3,61	17,58
	Number of species	y = 1,77 x + 13,94	55,41
Average vertical distance	Number of telecoprids	y = 23,65 x + 50,86	66,88
	Number of endocoprides	y = - 0,35 x + 3,23	6,14
	Number of kleptoparasites	y = - 0,90 x + 8,11	2,65
	Number of species	y = - 0,31 x + 21,43	2,05
Number of seeds scattered on the surface	Number of paracoprids	y = 0,88 x + 69,14	54,77
	Number of telecoprids	y = - 0,04 x + 98,22	0,16
	Number of endocoprides	y = 0,02 x + 0,68	19,62
	Number of kleptoparasites	y = 0,10 x - 3,75	37,53
	Number of species	y = 0,06 x + 15,16	78,08
Number of seeds dispersed	Number of paracoprids	y = 1,16 x + 8,98	71,14
	Number of telecoprids	y = - 0,23 x + 65,24	5,21
	Number of kleptoparasites	y = 0,12 x - 8,98	38,56
	Number of individuals	y = 1,28 x + 105,45	44,24
	Number of species	y = 0,06 x + 13,34	60,95

Number of horizontally dispersed seeds	Number of paracoprids	$y = 1,12 x + 20,1$	73,71
	Number of telecoprids	$y = - 0,17 x + 74,29$	3,04
	Number of kleptoparasites	$y = 0,12 x - 7,93$	40,68
	Number of individuals	$y = 1,15 x + 128,15$	39,68
	Number of species	$y = 0,05 x + 14,42$	54,29
Number of seeds dispersed only vertically	Number of paracoprids	$y = - 7,21 x + 198,14$	30,21
	Number of telecoprids	$y = 4,38 x + 68,43$	19,97
	Number of kleptoparasites	$y = - 0,71 x + 10,71$	14,4
Number of seeds dispersed horizontally and vertically	Number of telecoprids	$y = 1,24 x + 65,83$	27,85
	Number of endocoprides	$y = - 0,08 x + 4,39$	45,22
	Number of species	$y = - 0,10 x + 23,12$	30,64
Number of seeds buried	Number of telecoprids	$y = 1,56 x + 49,08$	42,1
	Number of endocoprides	$y = - 0,07 x + 4,54$	32,12
	Number of kleptoparasites	$y = - 0,08 x + 8,75$	2,95
	Number of species	$y = - 0,10 x + 23,68$	28,91
Number of seeds not found	Number of paracoprids	$y = 2,77 x + 111,05$	64,81
	Number of individuals	$y = 2,52 x + 227,13$	27,37

Finally, the one established between dung beetles and seeds dispersed in the eastern nesting sites yielded 24 significant correlation relationships, 12 of which were negative. The simple linear regression lines for each of the significant correlations is given in Table 7. The regression coefficient is relatively high for six of them ($r\text{-Sq} > 50\%$).

Table 7

Regression equations and coefficient of determination (R-Sq) for significant correlations at Eastern nesting sites

Variable to explain (y)	Explanatory variable (x)	Regression equation	R-Sq (%)
Average horizontal distance	Number of endocoprides	$y = -1,06 x + 3,49$	28,02
Average vertical distance	Number of paracoprids	$y = 247 x + 152,14$	37,75
	Number of telecoprids	$y = 534,72 x + 30,51$	61,04
	Number of kleptoparasites	$y = -27,78 x + 15,20$	8,9
	Number of individuals	$y = 753,18 x + 198,43$	82,16
Number of seeds scattered on the surface	Number of telecoprids	$y = -1,33 x + 301,13$	68,43
	Number of individuals	$y = -1,43 x + 522,76$	53,65
Number of seeds dispersed	Number of telecoprids	$y = -1,48 x + 357,78$	15,83
	Number of individuals	$y = -1,23 x + 528,04$	7,4
	Number of species	$y = 0,08 x + 8,45$	38,18
Number of horizontally dispersed seeds	Number of telecoprids	$y = -1,73 x + 388,8$	18,29
	Number of individuals	$y = -1,58 x + 575,02$	10,33
	Number of species	$y = 0,09 x + 8,25$	35,21
Number of seeds dispersed only vertically	Number of species	$y = 0,72 x + 17,957$	36,15
Number of seeds dispersed horizontally and vertically	Number of paracoprids	$y = 13,04 x + 114,61$	71,55
	Number of kleptoparasites	$y = -0,80 x + 15,15$	5,03
	Number of individuals	$y = 17,35 x + 228,05$	29,65
	Number of species	$y = 0,53 x + 17,76$	31,11

Number of seeds buried	Number of telecoprids	$y = - 5,66 x + 163,05$	11,78
	Number of kleptoparasites	$y = 1,59 x + 0,90$	50,39
	Number of individuals	$y = - 4,82 x + 367,11$	5,8
Number of seeds not found	Number of telecoprids	$y = 4,31 x + 96,26$	13,78
	Number of endocoprines	$y = - 0,06 x + 0,87$	26,76
	Number of individuals	$y = 5,58 x + 294,91$	15,71

Discussion

General fate of seeds in chimpanzee faeces at nesting sites

Animal droppings are a highly sought-after food-source for dung beetles and there is strong intra- and inter-species competition for dung in a given area (Hanski and Camberfort 1991). On average, more than 85% of the faecal matter placed in the various habitats was displaced after only 48 hours. Dung removal by dung beetles in the first few hours or even minutes is commonplace (Andresen 1999). The detection of faecal matter by dung beetles depends in part on the structure of the surrounding vegetation. This would influence the dispersion and diffusion of odors by circulating air currents or influence the drying of the faecal matter. However, the most important factor for the attractiveness of the faecal matter remains the diet of the dung producer. In general, the dung of omnivorous is more attractive as compared to that of herbivores, with carnivores being the least attractive (Hanski and Camberfort 1991; Whipple and Hoback 2012). Faecal material rich in nitrogen, such as that of humans and chimpanzees (Whipple and Hoback 2012) is more attractive to dung beetles, resulting in a greater abundance of individuals, which in turn would lead to greater competition and faster dung removal rates.

We observed low rates of seed burial at the various nesting sites. This was surprising considering that the dung beetle communities were strongly represented by paracoprids (dig galleries under the faecal matter) and thus, we would have expected a high proportion of seed burial. This low burial rate could be related to the level of competition between species as well as their abundance. Although the communities are largely represented by paracoprids, we found a low abundance of fast burying tunnelers in the different habitats. These are 8.97% of fast burying tunnelers for the eastern nesting sites against 7.07% for those in the North. Conversely, these represented 13.18% of the species collected in the southern nesting sites. Also, more than half or 59.9% of the species of the genus *Heliocopris* were collected in the southern nesting sites (Table 2). These dung beetles belong to the "fast burying tunnelers" and are known to bury faecal matter at great depths (Halffter and Edmonds 1982). The different burial rates obtained in the three habitats would be consistent with the different proportions of fast burying tunnelers collected. Most

of the seeds buried were by *Heliocopris diana*e Hope, 1842. Overall, only 3.83 and 5% of seeds were buried in the eastern and northern nesting sites, respectively, compared to 10.31% in the southern sites. These observations justify the competitive hierarchy established by Hanski and Cambefort (1991) which stipulates that the most competitive would be the "fast burying tunnelers", i.e. the large nocturnal paracoprids which bury faecal matter rapidly and in greater quantity. Similarly, measured mean vertical distances would be influenced by competition for space and resource. According to Andresen (2002b), when competition for space is intense, dung beetles tend to bury seeds more deeply.

Most of the seed dispersal was above ground, i.e. horizontally. Overall, more than 45% of the seeds were dispersed this way. These rates are very variable from one habitat to another. Thus, this dispersion concerned 34.64% of the seeds of the sites of southern nesting against 50.61% in those of the East. A greater proportion, 51.58%, was counted in the northern nesting sites. According to Andresen (2002b), small horizontal dispersal distances may be sufficient to significantly reduce competition between seedlings. The high horizontal dispersion rates would be related to the time of deposition. Indeed, diurnal telecoprid rollers such as *Gareta*, *Sisyphus* and *Neosisyphus* would be the first to exploit chimpanzee droppings favoring greater horizontal displacement. As a result, large nocturnal paracoprids (*Heliocopris*, *Catharsius* and *Diastellopalpus*) will have remains to exploit in the evening.

The average and maximum depths (Table 3) measured in our experiments are greater than those measured by Culot et al. (2009), Culot et al. (2011) and Santo-Heredia et al. (2010). Conversely, deeper measurements have been reported by Andresen and Levey (2004) and Petre et al. (2015). However, some authors such as Shepherd and Chapman (1998), Andresen (1999), Feer (1999) and Andresen and Levey (2004) have demonstrated a negative relationship between seed size and burial depth. In the present study, the results showed a positive relationship between seed size and average burial depth. A possible explanation could be related to the secondary disperser. Small seeds can be buried by any type of disperser. Conversely, large seeds would be buried primarily by the larger bodied and more competitive nocturnal "fast burying tunnelers" that quickly bury faecal material deeper, especially species of the genus *Heliocopris* as found in this study. This allows large seeds to be buried at great depths.

Our results indicate a low rate of seed burial in areas occupied by all three chimpanzee groups, indicating a low abundance of fast burying tunnelers in the dung beetle communities, especially species of the genera *Heliocopris*, *Diastellopalpus*, and *Catharsius*. Except for *Diastellopalpus noctis* (Thomson, 1858), which can utilize different types of dung, these species are generally associated with the faeces of large mammals such as elephants, humans, great apes and buffaloes (Moretto 2010). Nevertheless, more than 50% of the seeds were dispersed overall, probably reducing the density-dependent mortality phenomenon. Indeed, undispersed seeds, and subsequently the resulting seedlings, would be subject to density-dependent selection pressure related to two factors: (1) intra-specific competition for space and resources among seedlings, and (2) specific pathogens, predators, and herbivores (Janzen 1970; Connell 1971).

Unrecovered seeds

The loss of seeds would be linked to biotic factors. Hypotheses can be made. It is possible that the horizontal movement of seeds extends beyond the survey area. A study by Andresen (1999) showed telecoprids horizontal displacements of up to 118 ± 57 cm (mean $\pm$ SD). Also, Andresen (2002a) and Santos-Heredia et al. (2010) also measured a maximum horizontal seed dispersal distance of 49 and 60 cm, respectively, greater than that measured in this study (32.5 cm). It is important to remember that medium and large telecoprids (10 to 25 mm) are more specifically diversified and more numerous in Central and South American forests than in African forests, which probably explain the much greater distances measured in these studies. *Garetta diffinis* (14-19 mm), abundantly represented within the North and South nesting sites is the single large telecoprid of the studied area. It is very likely that the unrecovered seeds are the work of this species of telecoprid. A second hypothesis regarding these seeds would be related to depth dispersal. The maximum depth recorded in this experiment was 19 cm compared to 26.5 cm found by Petre et al. (2015) and 27 cm for Shepherd and Chapman (1998). It is highly likely that seeds are buried deeper, beyond our survey area. Finally, a last hypothesis would be related to the consumption of "unrecovered" seeds by granivores. Indeed, significant granivore activity was observed on about ten of our devices. In the experiments conducted by Shepherd and Chapman (1998), some seeds could not be found, and according to them, probably because of seed predation.

Effect of soil parameters on seed dispersal

The observed dispersal would not be solely dependent on seed size and secondary disperser size. The immediate environment of the faecal material at the scale of the device remains obviously an undeniable factor influencing the burial capacity of dung beetles. Thus, soil compaction and litter on the soil surface could be either an advantage or an obstacle to the seed dispersal process. The high density of the sieve forming a clumpy layer on the soil surface in the southern habitat and the high compaction in the eastern habitat suggest more constraints for the dung beetle communities living on these environments in the process of burying the faecal material. According to Fincher (1973), the level of compaction as well as litter would affect the burrowing behavior of dung beetles.

Conservation implications

Threats to the study site. Illegal gold mining in Taï National Park can greatly contribute to chimpanzee habitat destruction. Hunting is a significant factor that could greatly affect the numbers of primary dispersers (Nasi et al. 2011, Effiom et al. 2013) such as chimpanzees whose droppings are an undeniable source of food for coprophagous Scarabaeidae. The risk of infectious disease is a major concern. In 1994, chimpanzees at Taï National Park suffered an infection with a subtype of the Ebola virus that decimated 25% of the study community (Formenty et al. 1999).

Consequences. The consequences would be palpable and would result in reduced seed dispersal distance, agglomeration of seeds near the mother plant, leading to greater competition between seedlings (Muller-Landau 2007), a reduced recruitment rate (Beaune 2015) and consequently less regeneration of the plant species concerned (Wright et al. 2007). Homogenization of the plant community and a decrease in its diversity is expected in the long term (Terborgh et al. 2008; Beaune et al. 2012).

Recommendations. It would be beneficial to increase monitoring for poaching in and around Taï National Park as the only alternative to restoring large mammal communities. The goal is to maintain the Janzen-Connell model, promote secondary seed dispersal by dung beetles, and maintain forest dynamics, thus conserving plant species diversity and chimpanzee habitats.

Conclusion

Despite the dominance of paracoprids in dung beetle communities, our experiments showed low rates of seed burial in the different nesting sites. Nevertheless, a positive relationship between seed size and burial depth was observed, with larger seeds being buried at greater depths. Overall, the observed dispersal was essentially along the surface, i.e. horizontally, thus significantly decreasing the competition between the seedlings that would result from these seeds.

Declarations

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Author contributions K.K.S.K., K.D., PM and M.A. conceptualized the study; K.K.S.K., K.D., PM and M.A. designed the study; K.K.S.K. managed data collection; K.K.S.K. collected data in the field; R.M.W. provided infrastructure and logistical support for data collection; K.K.S.K. analysed the data; the manuscript was written by KSK and all authors commented on previous versions of the manuscript, read and approved the final manuscript.

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Data availability The datasets analyzed during the study will be available from the corresponding author on reasonable request.

Code Availability R code available from corresponding author.

Conflicts of interest/Competing interests We declare no conflict of interests.

Additional declarations for articles in life science journals that report the results of studies involving humans and/or animals Not applicable.

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Figures

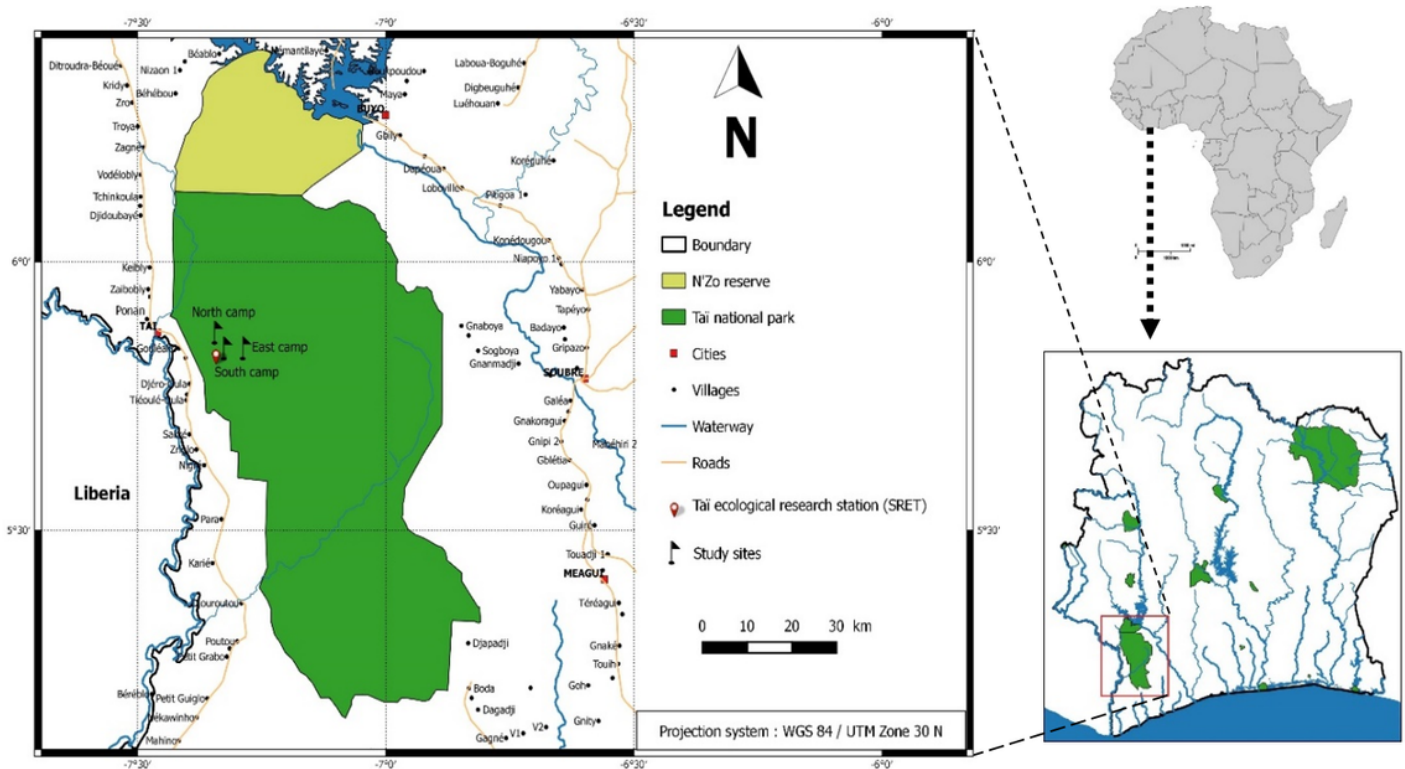
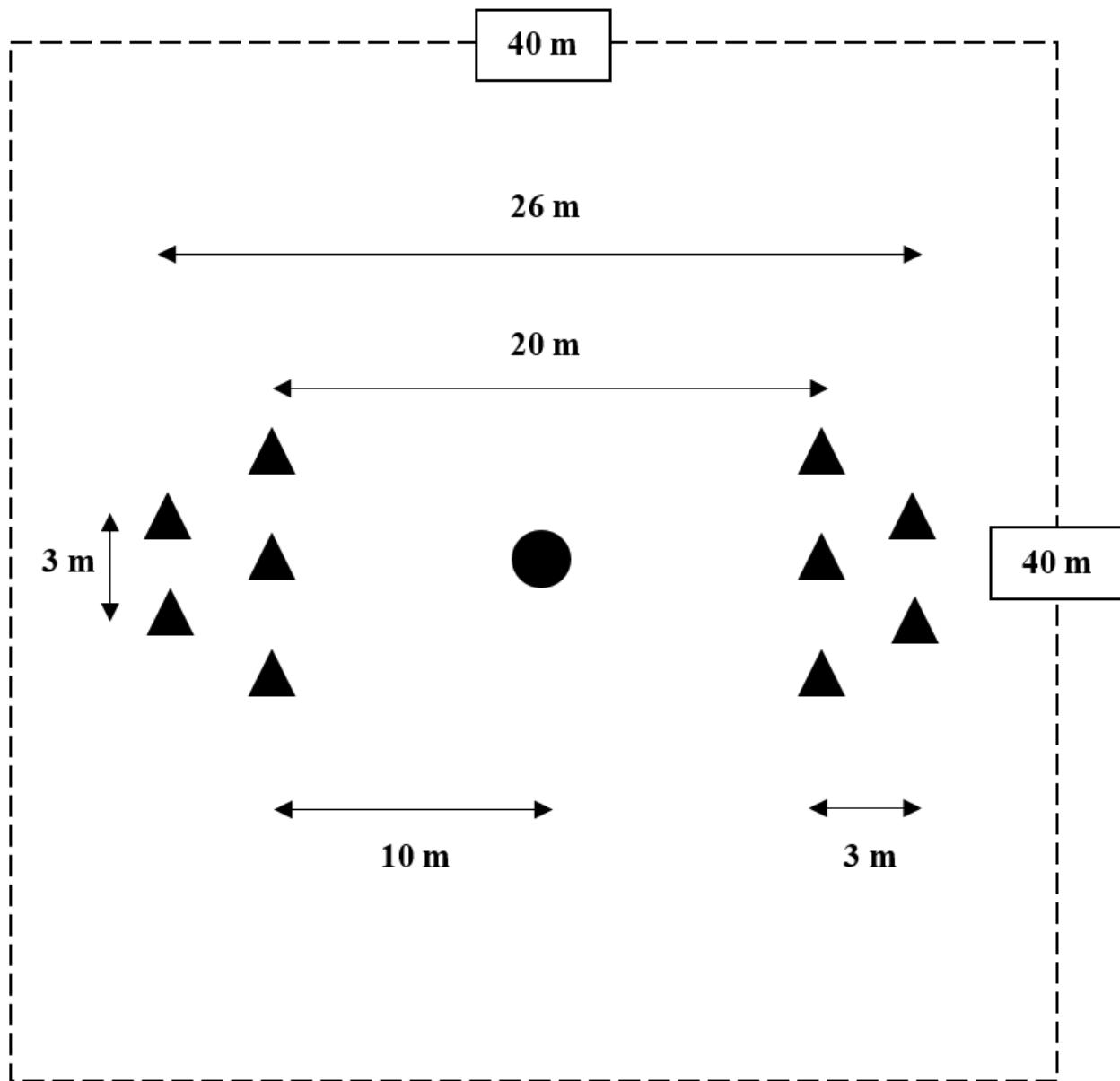


Figure 1

Location of the study area in the Tai National Park



Pitfall trap device for harvesting dung beetles
Device for studying seed dispersal

Figure 2

Experimental device of the study

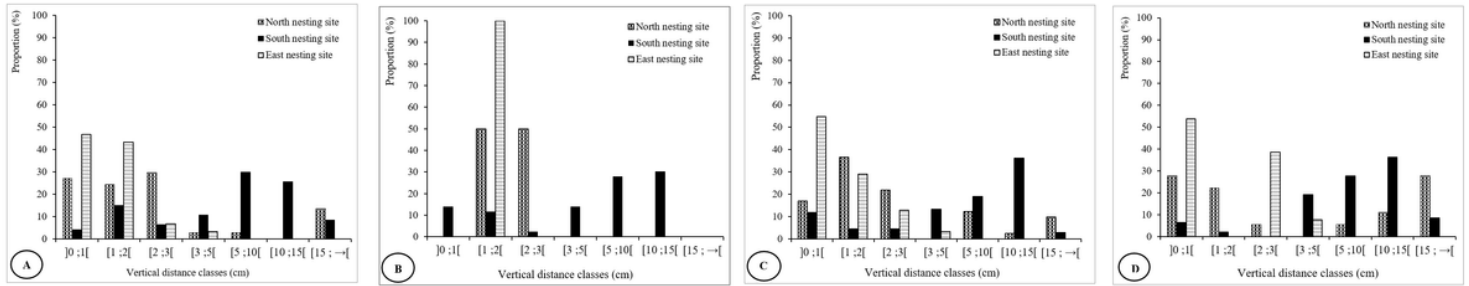


Figure 3

Percentage of seeds of different plant species buried vertically at different depths in the three habitats (A: *Dacryodes klaineana*, B: *Diospyros mannii*, C: *Pycnanthus angolensis*, D: *Uapaca guineensis*)