

Seed dispersal by duikers in selectively logged rainforests: Overlooked dispersal of an important animal community

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ABSTRACT

Seed dispersal by frugivores is a key process which is necessary for the regeneration of plant communities. The decrease in the abundance of fruit-eating mammals due to anthropogenic pressures impacts on the proper functioning of forest ecosystems.

In this study, for the first time we evaluate seed dispersal by duikers (Bovidae, frugivores and the most hunted animals of the rainforests of central Africa: Congo basin), using germination trials of seeds contained in their dung and rumen. The influence of selective timber harvesting on this dispersal was also examined by comparing duiker community occupancy between a logged and an unlogged site.

Our results revealed a community of four duiker species *Cephalophus silvicultor*, *Philantomba congica* and two species of 'red' duiker (*C. callipygus* and *C. castaneus*). A total of 79 plant species (5481 seedlings) were found in the dungs of all duikers and a total of 37 species (5225 seedlings) were observed in the rumens of red duikers and *P. congica*. *Phyllanthus* sp. and *Musanga cecropioides* were the dominant taxa in dung and rumen contents respectively. Taxa of high commercial value such as *Erythrophleum suaveolens*, *Milicia excelsa* and *Nauclea diderrichii* were also observed. The lack of a clear difference between the plant communities dispersed by the duiker species (assessed by β -diversity) showed that they play redundancy rather than complementary dispersal roles.

Duikers play an underestimated role in the restoration of environments disturbed by logging or shifting cultivation as most of the species observed are pioneer colonizing species. Furthermore duiker communities appear to be affected little by selective logging.

1. Introduction

Seed dispersal is an essential mechanism for forest regeneration. It allows the reduction of competition between seedlings; it contributes to the creation of new populations through the colonisation of new environments and it promotes genetic mixing through the exchange of individuals between populations (Lapenta and Procópio-de-Oliveira, 2008; Traveset et al., 2014; Delibes et al., 2019). Seed dispersal can be achieved by several vectors including water, wind, gravity or animals (Jordano et al., 2011). Through their combined action, these vectors

contribute to the long-term functioning of ecosystems and associated ecosystem services, including carbon sequestration, or the availability of wood and non-timber forest products (Forget et al., 2011).

The plant-animal mutualistic network is one of the most important complexes in terrestrial ecosystems. In tropical areas, up to 95 % of plant species depend on animals for their dispersal (Beaune et al., 2013). Plants provide frugivores with the food resources they need to survive, and in return, frugivores disperse seeds away from the parental environment (González-Varo, 2010; Jordano, 2013). The effectiveness of frugivores as seed dispersers depends on their ability to deliver viable

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seeds in environments suitable for germination (Garber, 1986; Reid, 1989) since it has been shown that some species that consume the fruits are more predators than seed dispersers (Tutin and Fernandez, 1993; Garber and Lambert, 1998). It is usually assessed by the quantity and quality of dispersed seeds (Schupp et al., 2010). The quantitative aspect corresponds to the temporal and spatial availability of fruits or seeds, while the qualitative component corresponds to the processing of the seeds by the animal (Lapenta and Procópio-de-Oliveira, 2008; Schupp et al., 2010; Schleuning et al., 2015). Three treatment mechanisms by frugivores can promote seed germination: (1) removal of the pulp reduces the presence of inhibitory chemicals; (2) mechanical scarification (chewing) and chemical scarification (passage through the digestive tract) favour the permeability of the seed to gases and water; and (3) ejection of the seed inside fertilising faecal material favours germination and growth (Schupp et al., 2010; Muñoz-Gallego et al., 2019). Many studies point to a positive effect of the intestinal tract on seed germination (e.g. Haurez, 2015 or Muñoz-Gallego et al., 2019). However the final fate of seeds depends not only on their condition after handling or passage through the intestinal tract but also on the locations of deposit (e.g. sites of less competition or less predation) (Jordano, 2000; Zwolak and Sih, 2020). Directed dispersal of seeds into habitats favorable to their germination (e.g. open habitats, sites of less crowding, etc.) is one of the most important services provided by frugivores (Zwolak and Sih, 2020).

Given their importance in forest regeneration and the sustainability of metapopulations, the decline of frugivores would lead to a change in the composition of forests and, in turn, the extinction of certain taxa (Bond, 1995; Beaune et al., 2013). Indeed, several authors (Wang et al., 2007; Vanthomme et al., 2010) have shown a positive correlation between the abundance of frugivorous mammals and the recruitment of plant species. The more an environment is devoid of fauna, the less efficient the seed dispersal network is. The modification of dispersal systems by the effect of hunting pressure actually leads to a clumping of seeds at the foot of trees, and consequently to an increased genetic differentiation between plant populations (Giombini et al., 2017). Hunting activities can be facilitated by logging activities. Timber exploitation occupies large areas, reaching 28 % of central Africa's rainforests (Congo basin) (FRMi, 2018). Although selective, it impacts animal communities by facilitating access to remote areas for hunters and poachers when the road network is not controlled (Robinson et al., 1999).

Furthermore, settlement of logging company employees in camps or villages near forests increases hunting activities and makes harvesting unsustainable (Bennett and Gumal, 2001).

In the face of human activities, research on plant-animal mutualistic relationships and on the resilience of animal communities (the main vectors of seed dispersal) is necessary to establish an adequate conservation strategy for forest ecosystems, particularly in tropical areas where biological diversity is high and anthropogenic pressures are increasing. In central Africa, which is one of the world's hotspots of biodiversity, most of the research on the plant-animal interaction network has focused on large mammals and/or those with a high protection status, such as elephants, gorillas and other primates (e.g. Maurois et al., 1997; Haurez, 2015). Very few studies have focused on ruminants (Hounbégnon et al., 2019).

Ruminants are often considered seed predators because of their powerful digestive system (fine chewing and efficient microbial digestion) (Bodmer, 1991). Nevertheless, Baltzinger et al. (2019) suggested the possibility of dispersal of small seeds via dung. Furthermore, their digestive system makes them vectors of a particular type of endozoochory called partial endozoochory or endozoochory spitting (Forget et al., 2007; Baltzinger et al., 2019). This is because intact or roughly crushed fruits and seeds are first stored in the rumen. After some time, the bolus is regurgitated for fine chewing of the elements (rumination) (Schwarm et al., 2008). During this process, the tough or large seeds are returned to the rumen for a second fermentation, or are spat out by the

animal. The seeds expelled in this way may be viable (Herrera, 2002; Forget et al., 2007). This partial endozoochory is rarely studied due to the difficulty of tracking ruminants in their natural environment (McConkey et al., 2018).

Although duikers account for a significant proportion of the mammalian biomass of African rainforests, their role in seed dispersal has been little studied (Morgan, 2007). Duikers (Cetartiodactyla, Bovidae) represent the main venison products in central Africa (Delvingt et al., 2001; Mockrin, 2009), and are therefore subject to high hunting pressure, which may be exacerbated by unsustainable logging activities. Poulsen et al. (2011) note that logged forests, even in the absence of hunting activities, would not maintain the same duiker densities as unlogged forests, although Clark et al. (2009) show that species respond differently. On the other hand, there would not be a direct effect of logging on the duiker community in both the short term (4 years) and long term (25 years) (White, 1992).

Fruit makes up to 90 % of the diet of these sympatric ruminants. The rest of their diet is supplemented by leaves, fungi and animal matter (Hounbégnon et al., 2019). The great variability of their size, from 5 kg to 80 kg (genera *Philantomba* and *Cephalophus*), could predispose them to the dissemination of a large diversity of seeds (Hounbégnon et al., 2019). However, the fineness of chewing and their digestion process presents a high destruction potential for swallowed seeds (Newing, 2001). Alexandre (1982), however, reported the presence of seeds of *Solanum verbascifolium* L. and *Musanga cecropioides* R.Br. ex Tedlie in the dung of *Cephalophus niger* Gray, 1846 in West Africa. Gautier-Hion et al. (1985) and Feer (1995) observed seed regurgitation during rumination by some captive duiker species (*Philantomba congica* Lönnberg, 1908; *C. callipygus* Peters, 1876; *C. castaneus* Thomas, 1892; *C. silvicultor* Afzelius, 1815).

The objective of this study is to assess the role of duikers in seed dispersal and to examine whether this role could be altered by selective timber harvesting. To do this, in a forestry concession in south-east Cameroon: (i) we characterised the duiker community living in forests with different logging histories, and (ii) we analysed the dung and rumen contents of this community.

2. Materials and methods

2.1. Study area

The research took place in the Forest Management Units (FMUs), between 3°01' N and 3°44' N; 13°20' E and 14°31' E granted to the Pallisco forestry company and its surroundings in South-eastern Cameroon (Fig. 1). The rainforest is a transition between the evergreen and semi-deciduous types (classified as *Celtis* forest by Fayolle et al., 2014). The climate is equatorial, with two rainy seasons (April-June and September-November). Annual precipitation is 1640 mm (Worldclim, 2015), and the average annual temperature is 23.1 °C (Hijmans et al., 2005). The geological substratum consists of volcanic intrusions and metamorphic rocks, and the soils are ferralsols (Jones et al., 2013).

Timber harvesting in these forests is selective, with an average of one to two trees felled per hectare every 30 years (Umunay et al., 2019). As part of the FSC (Forest Stewardship Council) certification, Pallisco has taken measures to combat poaching (guarded or blocked roads, surveillance patrols, raising awareness, etc.). In accordance with Cameroonian legislation, self-subsistence hunting of resident villages is allowed. The density of mammals is intermediate between that observed in the neighbouring protected area, the Dja Biosphere Reserve, and in the community forests managed by local populations (Lhoest et al., 2020). Mathot and Doucet (2006) and Lhoest et al. (2020) noted, through the use of indirect animal records (faeces and footprints) and camera traps respectively, the presence of the "red" duiker group (*Cephalophus* spp.), the blue duikers (*Philantomba congica*) and the yellow-backed duikers (*Cephalophus silvicultor*).

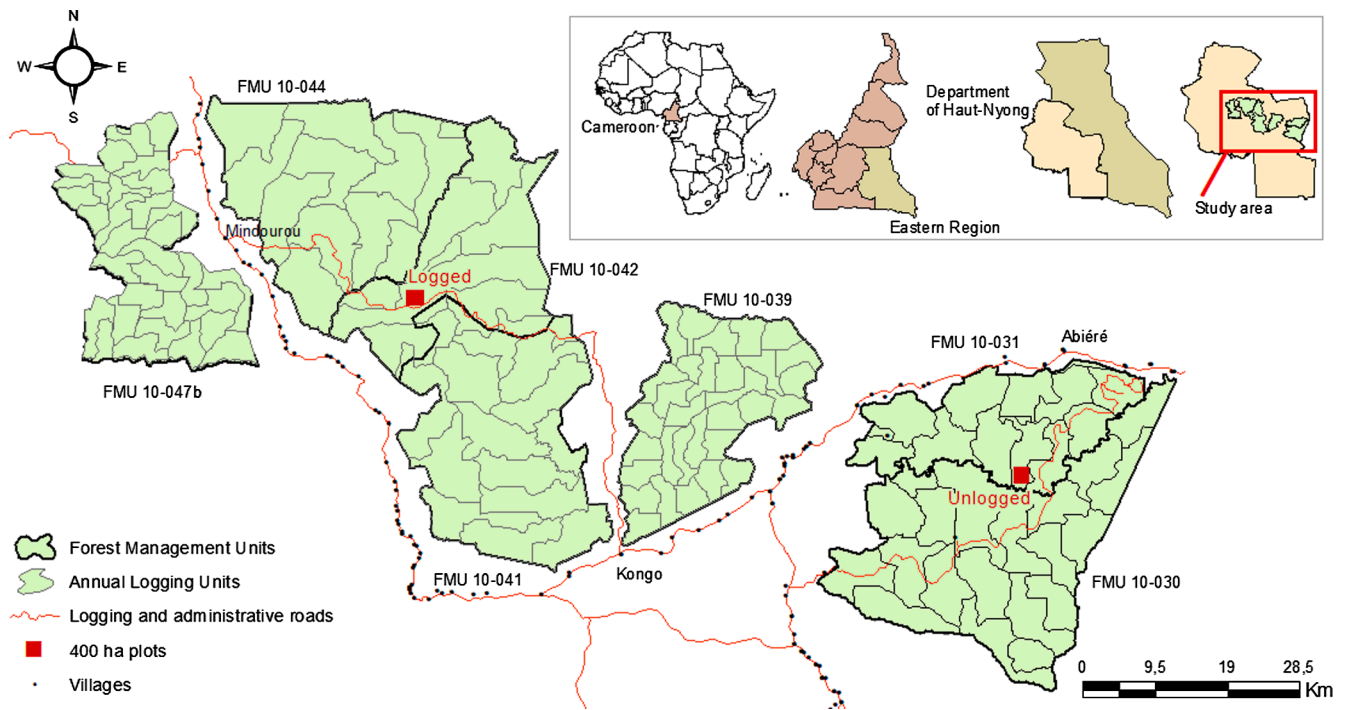


Fig. 1. Location of the study sites and sampling plots.

2.2. Data collection

2.2.1. Duiker inventory

The composition and dynamics of the duiker community was studied by camera trap surveys conducted from 2016 to 2019 in two 400 ha plots, 80 km apart: a forest logged in 2013 (FMU 10–042, Annual Logging Units 9), and an unlogged forest (FMU 10–031, Annual Logging Units 11) (Fig. 1). Thirty-two camera traps (Bushnell Trophy Cam HD Aggressor and Moultrie M–1100i) with passive infrared sensors were deployed, with 16 devices per plot. One camera was set up every 0.5 km as performed by Bowkett et al. (2008) for antelope surveys. The camera traps were set up at the same sampling points for each survey. They were tied to the base of trees and directed towards the animal tracks (Fonteyn et al., 2020). In order to allow good detection and identification of species, the cover of grasses and lianas was slightly reduced in the angle of view of the cameras within a range of 3 m (Houngbégnon et al., 2020). The cameras operated 24/7 for at least 63 days, resulting in a minimum of 1008 camera days (63 days × 16 cameras) per plot, as recommended by O'Brien et al. (2010).

2.2.2. Dung and rumen collection

Dung and rumen collections were made during several seasons in order to take into account phenological variability. The dungs were collected in each of the two plots (400 ha camera trap plots) by walking along 21 tracks, each 2 km long and 100 m apart. Collections were made in June 2016 (wet season), April to June 2017 (wet season), July 2017 (short dry season) and January to March 2018 (dry season). Due to the difficulty of associating dungs with different duiker species, three groups were distinguished according to the size of the dungs and by extension their dungs (Fimbel et al., 2000; van Vliet and Nasi, 2007). These were: (1) the blue duiker group (genus *Philantomba*, ~5kg), characterised by small dung pellets, (2) the red duiker group (genus *Cephalophus* except *C. silvicultor*, 18–27 kg) with medium-sized dung pellets, and (3) the yellow-backed duiker group (*C. silvicultor*, ~80 kg) with large dung pellets. According to the recommendations of Soto-Calderón et al. (2009), ten pellets of dung were preserved in silica gel for genetic analyses to associate the dung with different duiker species.

Rumen contents were obtained in outlying villages (the study was explained and villagers' consent was obtained) of the FMU from April to July 2017 and from January to March 2018 and finally during all seasons from April 2018 to June 2019. Duikers from subsistence hunting were first identified on the basis of physical traits described by Groves et al. (2011). They were then dissected and the rumen contents were collected. Some rums were brought in directly by hunters or households. In this case, the identification of duiker species was done by genetic analysis of CO1 (Cytochrome Oxidase 1) of previously collected tissue (ear or rumen portion) and preserved in 96 % ethanol (Soto-Calderón et al., 2009).

The genetic analyses in both cases were carried out by the Genetics and Conservation Laboratory (GeCoLAB) of the University of Liege.

2.2.3. Plant species identification

The dung samples collected were taken to a processing site (outside the forest) where they were gently washed and cleaned of debris. They were then placed on the surface of the jars filled with soil that had been steamed (90 °C for 90mn) to destroy the germinative power of any seeds it might contain (Zebaze et al., 2021). The rumen contents were washed and the seeds collected were placed in the pots treated in the same way as the dug pots.

All pots were protected from exogenous seed supply by a fine mesh screen (1x1mm) and regularly watered with running water. The identification of seedlings resulting from the germination of dung and rumen seeds was carried out by specialists of the Tropical Forestry Laboratory of the University of Liege - Gembloux Agro-Bio Tech when they had reached an appropriate stage of development, between six months and one year after potting. Species not directly identified were collected and placed in a herbarium for later identification. Pteridophytes were excluded from the analyses, as their spores, due to their tiny size, could not be stopped by the mesh of the net.

Once the plant species were identified, a set of traits was assigned to each species to examine whether duiker taxa disperse preferentially a type of species. The following traits were considered: plant life forms (grass, woody: trees and shrubs), and seed behaviour to dehydration (orthodox: seeds resilient to dehydration; recalcitrant: seeds less

resilient to dehydration). The seed weight of each species was also specified (the average seed weight of the genus was considered for the species for which information on seed weight was not available). Information on the traits and the seed weight was obtained from the website of the Royal Botanical Gardens of Kew (Kew Science), the website of the Conservatory and Botanical Garden of Geneva (CJB), and the website of the Global Biodiversity Information Facility (GBIF). The commercial value of dispersed species was also assessed based on its use as timber and considering timber production statistics (FRMi, 2018).

2.3. Data analysis

2.3.1. Camera trap data analysis

The photos taken by the camera traps were processed in *Camera Base* (Tobler, 2015). The different species were identified based on their physical traits (Groves et al., 2011). An interval of at least 10 min (between two photos) was considered to determine an independent detection event of the same species at the same camera trap location (Lhoest et al., 2020). The relative abundance index (RAI) of each species was estimated by calculating the average daily detection (Fonteyn et al., 2020). The population dynamics of duikers were assessed using the multiseason occupancy model (MacKenzie et al., 2006). For this purpose, we divided each annual inventory period (primary periods) into five sampling sections (secondary periods) of 14 days each. This allowed us to retain as much data as possible without having too many missing observations within a given sampling section (Tempel & Gutiérrez, 2013). If a camera captured at least one duiker during a sampling section, we assigned 1 to the detection history. We assigned 0 when no animals were captured. If a sample point was not recorded during a section (camera malfunction, or failure to deploy the camera at that point due to a logistical problem), we treated it as a missing observation, as suggested by MacKenzie et al. (2006) and Tempel & Gutiérrez (2013).

The multiseason occupancy model contains the following parameters (MacKenzie et al., 2006):

- The probability of occupancy (ψ), which corresponds to the fraction of landscape units where a species is present.
- The probability of detection (p), which is the probability that a species will be detected at an occupied site.
- The probability of colonisation (ψ_t), which is defined as the probability that a site unoccupied in year t is occupied by a species in year $t + 1$.
- The extinction probability (ϵ_t), which represents the probability that a site occupied by a species in year t is unoccupied in year $t + 1$.

In addition, in order to clarify the impact of plot type (logged, unlogged) on duiker occupancy, we added a “TypeForest” covariate (logged plot: 1; unlogged plot: 0). As the surveys were carried out in different seasons, we associated the time (year or season) of sampling (t) with the probability of detection. The parameters ψ and ϵ were kept constant (no covariate), as the variation of these parameters with sampling time and plot type was not the focus of this study. Four models were applied for each species detected. Specifically, the simplest model where all parameters are held constant $\psi(p)\psi(\epsilon)$, the model where the probability of occupancy is influenced by the plot type $\psi(\text{TypeForest})p(\epsilon)$, the model where the probability of detection varies with sampling time $\psi(p(t))\psi(\epsilon)$, and the more general model where occupancy and probability of detection are influenced by plot type and sampling time respectively $\psi(\text{TypeForest})p(t)\psi(\epsilon)$. The comparison of AICs (Akaike’s Information Criterion) allowed the selection of the best model (smallest AIC) (Burnham and Anderson, 2002). However, models with $\Delta\text{AIC} < 2$ (difference in AIC between models) were considered equivalent (Burnham and Anderson, 2002; Sadoti et al., 2013). The impact of plot types on the probability of occupancy was assessed by the size of the sum of the AIC weights of the models carrying the covariate “TypeForest”: $\sum \omega_{\text{AIC}}(\text{TypeForest})$, (Burnham & Anderson, 2004;

MacKenzie et al., 2006). Finally, the rate of change of occupancy (λ) between two inventory years was calculated ($\lambda_t = \psi_{t+1}/\psi_t$). If $\lambda_t > 1$, this implies an increase in occupancy between year t and year $t + 1$.

Since the study area is situated within a FSC-certified logging concession, involving the control of wildlife hunting and a limitation of logging impacts on wildlife (Lhoest et al., 2020), we do not expect a significant impact of selective logging on duiker occupancy.

2.3.2. Seed dispersal model

For each dung and rumen sample, the numbers of species and seedlings were calculated. Next, the numbers of dispersed species per duiker taxon were estimated with the Jackknife (Jack1) and Chao indices (Doh, 2019). Rarefaction curves were also made to assess the completeness of the sampling (Gotelli & Colwell, 2001).

The relative abundance RA (number of seedlings of a given species/total number of seedlings of all species) and the relative frequency RF (proportion of samples containing the given species) were determined. The importance value index (IVI = RA \times RF) was calculated to distinguish the dominant species (highest IVI) (Osipov, 2021). We then identified the characteristic species (indicator species) of each duiker group by calculating the indicator value index (*Indval*) (Dufrene and Legendre, 1997). The *Indval* equation is worded below (Dufrene and Legendre, 1997; Doh, 2019). Given that duikers are mostly frugivores, we expect the dominant and indicator species to be a woody (trees and shrubs).

$$\text{Indval} = (N_{\text{individuals}_{ij}} \times N_{\text{rd}_{ij}} / N_{\text{individuals}_i} \times N_{\text{rd}_j}) \times 100$$

With rd representing rumen or dung samples, *Indval* the Indicator value of species i in rd group j , $N_{\text{individuals}_{ij}}$ is the mean number of individuals of species i in the rd of group j , $N_{\text{individuals}_i}$ is the number of individuals of species i in all groups, $N_{\text{rd}_{ij}}$ is the number of rd in the group j where species i is present, N_{rd_j} is the total number of rd in that group. $N_{\text{individuals}_{ij}}/N_{\text{individuals}_i}$ is a measure of specificity (based on the abundance of species i), and $N_{\text{rd}_{ij}}/N_{\text{rd}_j}$ is a measure of fidelity (based on incidence of species i).

Differentiations between the plant communities of the three duiker groups were assessed by beta diversity (β -diversity) based on an occurrence matrix (presence: 1; absence: 0). Beta diversity was estimated by using Sørensen’s dissimilarity (β_{SOR}) (Baselga & Orme, 2012). The greater the beta diversity, the less similar the specific composition of communities (Marcon, 2015). Beta diversity was partitioned into two components in order to clarify differences between groups: (i) turnover (β_{SIM} , Simpson dissimilarity), which represents the difference in species composition caused by species replacement, (ii) and nestedness (β_{NES}), which indicates the nesting in species composition or the difference in species composition caused by species loss (Baselga, 2010). Beta diversity was estimated at two levels: (i) multiple-unit dissimilarities, which involves beta diversity of all rumens and all dungs without distinction of duiker groups (between N samples of all rumens and N samples of all dungs), beta diversity between all three duiker groups, and beta diversity between samples (rumens and dungs respectively) of each group; (ii) pairwise dissimilarities, which involves beta diversity between pairs of duiker groups. Since duikers consume (1) various fruits (Houngbégnon et al., 2019) and (2) vary greatly in body size, resulting in variable fruit size selection across species (Newing, 2001), we expect the dispersed plant community to be different within species samples (dungs and rumens) as between species with a comparable turnover.

Furthermore, differences in plant species composition between duiker groups were visualised by a Non-metric Multidimensional Scale (NMDS) based on occurrence matrix and Bray-Curtis distance (Oksanen et al., 2020). We plotted the pots as lozenges (with colors corresponding to duiker groups), and plants species as points, with size proportional to their seed weight (seed weight was log-transformed because of the wide spread in the data). Finally, differences in plant traits (grass, woody, orthodox, recalcitrant) between duiker groups were tested by Permutational Multivariate Analysis of Variance (PERMANOVA).

The statistical analyses were performed using R software (R Core Team, 2018). The packages *RPresence*, function *occMod* (type = “do.1”) (MacKenzie and Hines, 2018); *labdsv*, function *indval* (Dufrene and Legendre, 1997); *vegan*, function *adonis2* and *metaMDS* (Oksanen et al., 2020); *betapart*, *beta.multi* and *beta.pair* functions (Baselga and Orme, 2012) were used to determine: duiker occupancy dynamics, indicator species, plant trait differences, NMDS representation, and beta diversity (multiple-units and pairwise dissimilarities) respectively. The tests involving simulations were done on the basis of 1000 replications.

2.3.3. Genetic analysis

The genetic identification of duiker species was performed using the amplification of a small fragment of the mitochondrial Cytochrome Oxidase 1 (COI) gene as proposed in Gillet et al. (2015). The sequencing of the obtained PCR fragment was performed following Next Generation Sequencing technologies using an Illumina automatic sequencer (Next-seq model).

More precisely, the libraries were prepared following the two-steps PCR approach combined with Illumina’s dual indexing strategy: a 133 bp minibarcode was amplified using the primer couple developed by Gillet et al (2015). The PCR was carried out in 25 µl reaction volume using 5 µl of KAPA HiFi Fidelity buffer, 0.75 µl of dNTPs, 0.75 µl of each primer, 1 µl of KAPA HiFi DNA Polymerase, 13.25 µl of PCR-grade water and 3.5 µl of DNA extract. The PCR conditions consisted in an initial denaturation step at 95 °C for 5 min, followed by 38 cycles of denaturation at 95 °C for 30 s, annealing at 45 °C for 45 s, and extension at 72 °C for 30 s, followed by a final extension step at 72 °C for 10 min. The resulting PCR products were purified using 20 µl of Agencourt AMPure XP beads (Beckman and Coulter) in 25 µl of PCR product.

A second PCR was performed to add the dual indexes and the adaptor required by the Nextseq sequencer, following the protocol proposed by Illumina. A second purification was performed (using the same protocol than for the first purification) followed by a quantification of each resulting purified PCR product using a FISHER Quant-iT PicoGreen® dsDNA Assay Kit. All samples were then diluted to 5 ng/µl and pooled together. The pool was sent alongside with pools from other projects to the GIGA NGS platform from the University of Liege for sequencing on a Nextseq Illumina Sequencer.

The raw sequences were treated by using a modified version of the bio-informatical script used in André et al (2017), and consisting of a mix of FASTX Toolkit and USEARCH (Edgar, 2010) functions. The resulting sequences were compared with published sequences available in the BOLD database (Ratnasingham and Hebert, 2007).

3. Results

3.1. Duiker communities and impact of logging

A sampling effort of 6048 trap nights was carried out over the four years of the survey. Four species of duiker were detected: *C. castaneus* and *C. silvicultor* (0.3 event/day); *Cephalophus callipygus* (0.6 event/day); and *Philantomba congica* (1.4 event/day).

To assess the dynamics of occupancy, the model including the variation of the detection probability was selected for *C. castaneus* and *C. silvicultor*. The model without covariates (simple model) was the best for *P. congica* (Table 1). *Cephalophus callipygus* was excluded from the multiseason analysis due to insufficient data to assess occupancy within the first and second year of the survey.

The probability of occupancy of *C. castaneus* varied from year to year from 0.36 [SE 0.18] to 0.49 [SE 0.14], and for *C. silvicultor* it varied from 0.47 [SE 0.1] to 0.61 [SE 0.26]. *Philantomba congica* recorded the highest occupancy probabilities, fluctuating between 0.64 [SE 0.07] and 0.80 [SE 0.15] (Fig. 2). For each species, the sum of the AIC weights of the models including the covariate “TypeForest” is not greater than the weight of the rest of the models (*P. congica* $\sum \omega_{AIC}(\text{TypeForest}) = 0.28$; *C. castaneus* and *C. silvicultor* $\sum \omega_{AIC}(\text{TypeForest}) = 0.36$ respectively)

Table 1

Multi-season occupancy model likelihood selection based on AIC for three duiker species. Selected models are in bold. Bold values represent significantly different models ($\Delta AIC > 2$).

	Models	AIC	ΔAIC	ω_{AIC}
	Probability of detection influenced by the sampling time	233.81	0	0.41
<i>C. castaneus</i>	Simplest model (no covariates used)	235.06	1.25	0.22
	Occupancy influenced by the plot type	235.18	1.37	0.21
	Occupancy and probability of detection influenced by plot type and sampling time respectively	235.80	1.99	0.15
	Probability of detection influenced by the sampling time	291.25	0	0.48
<i>C. silvicultor</i>	Occupancy and probability of detection influenced by plot type and sampling time respectively	292.38	1.12	0.28
	Simplest model (no covariates used)	293.41	2.16	0.16
	Occupancy influenced by the plot type	294.95	3.70	0.08
<i>P. congica</i>	Simplest model (no covariates used)	469.16	0	0.44
	Probability of detection influenced by the sampling time	470.14	0.98	0.27
	Occupancy influenced by the plot type	470.90	1.74	0.18
	Occupancy and probability of detection influenced by plot type and sampling time respectively	472.08	2.92	0.10

ΔAIC : difference in Akaike’s Information Criterion (AIC) between models, ω_{AIC} : AIC weights.

(Table 1), implying that plot type (logged, unlogged) does not affect the probability of duiker occupancy. The statistics for the occupancy and detection probabilities of each species are given in the Appendix (Table A1).

The rate of change in occupancy was >1 for *C. castaneus* between the years 2016–2017 and 2018–2019, reflecting an increase in occupancy. For the other years, the rate of variation in occupancy fluctuated between 0.88 [SE 0.25] and 0.99 [SE 0.01], reflecting a slight decrease (~ 1) in occupancy for the species concerned (Table 2). Depending on the species, the probability of colonisation ranged from 0.32 [SE 0.27] to 0.67 [SE 0.21], and the probability of extinction from 0.29 [SE 0.08] to 0.83 [SE 0.14] (Table 2).

3.2. Richness of vegetal species in dungs and rumens

A total of 424 dung samples (1 sample = 251 ± 176 dung pellets) were collected, and 5481 seedlings obtained. They belonged to 79 plant species, representing 22 families. Red duiker dung had the highest number of species (3535 seedlings, 69 species, $n = 212$ samples) followed by *P. congica* (1163 seedlings, 49 species, $n = 183$ samples) and *C. silvicultor* (783 seedlings, 34 species, $n = 29$ samples) (Fig. 3A). The average number of seedlings and species by duiker group varied from 6.4 to 27.0 seedlings/dung, and from 1.7 to 2.6 species/dung, respectively (Appendix, Table A2). 41.8 % of the species obtained are woody. The most dominant species (highest Importance Value Index) in the dung is *Phyllanthus* sp., with an IVI of 15.7 %, 6.6 % and 9.6 % for *P. congica*, *C. silvicultor*, and red duikers respectively (Table 3). Two timber species were poorly represented (Low IVI). These are *Milicia excelsa* (*P. congica* IVI = 0.1 %, red duiker IVI = 0.01 %) and *Nauclea diderrichii* (red duiker IVI = 0.01 %) (Appendix, Table A3).

The rumens of two groups of duikers were collected: *P. congica* (2975 seedlings, 28 species, $n = 61$ rumens), and red duikers (2250 seedlings, 27 species, $n = 26$ rumens) (Fig. 3B). From the 87 rumens processed, 37 species belonging to 18 families were obtained. An average of 48.8 seedlings/rumen and 1.9 species/rumen were recorded for *P. congica*, and 86.5 seedlings/rumen and 2.8 species/rumen for red duikers (Appendix, Table A2). The species obtained from the rumens are mostly woody (trees and shrubs: 70.3 %). *Musanga cecropioides* is the most dominant taxon, with an IVI of 28.2 % for *P. congica* and 29.2 % for red

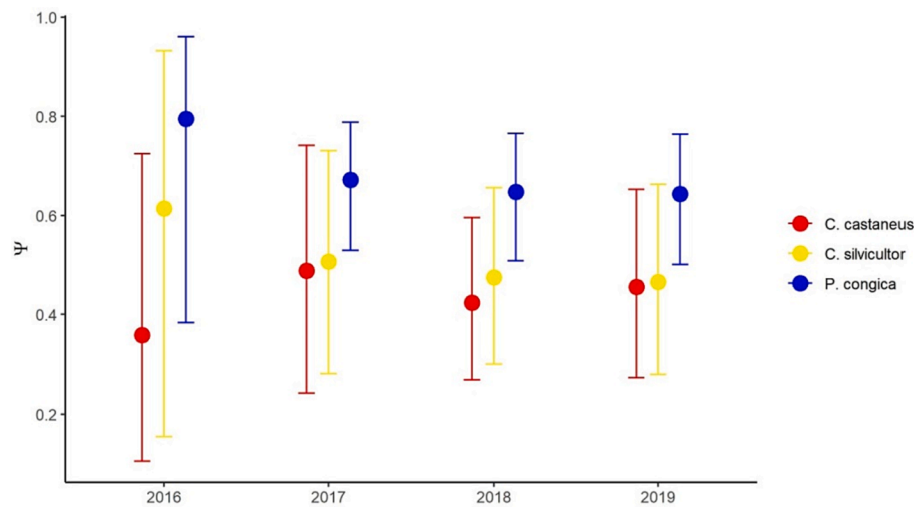


Fig. 2. Temporal trends in occupancy of three duiker species in the FMU (Logged and unlogged plots). Error bars denote 95 % confidence intervals (the length of the error bars for 2016 is related to more missing data compared to other years.) ψ : Occupancy probability. Estimates were obtained using 4 years' survey data and multiseason occupancy models.

Table 2
Occupancy dynamics of three duiker species through years. λ : occupancy change rate; γ : colonisation; ϵ : extinction; SE: Standard Error; CI: Confidence Intervals.

	Parameters	Values	SE	95 % CI
<i>C. castaneus</i>	$\lambda_{2016-2017}$	1.36	0.89	0.37–3.10
	$\lambda_{2017-2018}$	0.88	0.25	0.38–1.36
	$\lambda_{2018-2019}$	1.08	0.18	0.72–1.43
	γ	0.67	0.21	0.25–0.92
	ϵ	0.83	0.14	0.40–0.97
<i>C. silvicultor</i>	$\lambda_{2016-2017}$	0.83	0.25	0.34–1.31
	$\lambda_{2017-2018}$	0.94	0.17	0.61–1.26
	$\lambda_{2018-2019}$	0.98	0.08	0.81–1.15
	γ	0.32	0.27	0.04–0.85
	ϵ	0.38	0.25	0.07–0.83
<i>P. congica</i>	$\lambda_{2016-2017}$	0.84	0.15	0.56–1.13
	$\lambda_{2017-2018}$	0.96	0.05	0.87–1.06
	$\lambda_{2018-2019}$	0.99	0.01	0.97–1.02
	γ	0.52	0.12	0.29–0.73
	ϵ	0.29	0.08	0.16–0.46

duikers (Table 3). Two timber species were observed and poorly represented, namely *Erythrophleum suaveolens* (Red duikers IVI = 0.001 %, *P. congica* IVI < 0.001 %) and *Milicia excelsa* (*P. congica* IVI = 0.009 %) (Appendix, Table A4).

Analysis of indicator species indicated *Ficus wildemaniana* (Indval = 0.1, $P = 0.042$) and *Strophanthus gratus* (Indval = 0.1, $P = 0.041$) as indicator species for red duiker rumen contents (Table 3). In the dung of *C. silvicultor*, *Paspalum conjugatum* (Indval = 0.2, $P = 0.018$), *Kyllinga* sp. (Indval = 0.1, $P = 0.011$), *Oplismenus burmannii* (Indval = 0.1, $P = 0.005$), *Ficus barteri* (Indval = 0.03, $P = 0.044$), and *Ficus wildemaniana* (Indval = 0.1, $P = 0.004$) represented the indicator species, while *Ageratum conyzoides* (Indval = 0.1, $P = 0.029$) was the indicator species for red duiker dung. No indicator species were noted for *P. congica* in either dung or rumen.

3.3. Vegetal species diversity and traits in dungs and ruments

Beta diversity is dominated by the substitution of plant species for both the dung set (β -diversity = 0.99, Turnover = 0.99) and the rumen set (β -diversity = 0.98, Turnover = 0.95) without distinction of group (Appendix, Fig. A1). This trend was also observed in all duiker groups

separately, with turnover ranging from 0.85 (β -diversity = 0.93, Red duiker ruments) to 0.98 (β -diversity = 0.99, Red duiker dungs). This implies that the specific composition of plants communities is not similar within a group of duikers and for all groups considered together. This dissimilarity is explained by the replacement of some plant species by other from one sample (dung or rumen) to another.

The relatively low β -diversity (similar specific composition of plants community) between the dung of the different duiker groups (Appendix, Fig. A1) is linked to a nestedness of up to 71.4 % of the β -diversity (*C. silvicultor* and Red duikers: β -diversity = 0.42; *P. congica* and Red duikers: β -diversity = 0.27). This indicates that between these groups of duikers considered the biotas of dung samples with smaller numbers of species are subsets of the biotas at richer samples. In contrast, the low β -diversity between the ruments of *P. congica* and Red duikers is mainly explained by turnover (β -diversity = 0.34, Turnover = 0.33) (Appendix, Fig. A1). Overall, duikers have a comparable turnover between species as within species.

Plant life forms (grass, woody) of the species are not related to any duiker group (PERMANOVA, Dung: $F = 0.6, P = 0.6$; Rumen: $F = 0.9, P = 0.4$). This observation is identical for the seed behaviour to dehydration (orthodox, recalcitrant) of the plant community from rumen contents (PERMANOVA, $F = 2.4, P = 0.1$). Which involves that there is no particular selection in the life forms or behaviour (physiology) of the dispersed seeds. The species observed in the dung are mostly orthodox seeds (Appendix, Table A3).

The NMDS representation does not show clear segregation patterns in the composition of the dung and rumen plant communities (Fig. 4). However, heavy seeds are more present in the rumen than in the dung (Fig. 4, Appendix, Tables A3 and A4).

3.4. Duiker specific identification

A total of 51 dung samples were submitted for genetic identification. Three samples were associated with *C. silvicultor*, five with *C. callipygus*, nine with *P. congica*, and twelve with *C. castaneus*. Nineteen of the collected ruments were identified by CO1 genetic analysis and 54 ruments by direct observation of the species. All 73 ruments identified belong to *C. callipygus* ($n = 1$), *C. castaneus* ($n = 11$), or *P. congica* ($n = 61$).

Appendix Table A5 and Table A6 show the plant species observed in dung (genetic identification of duikers) and rumen (genetic and direct identification) samples respectively.

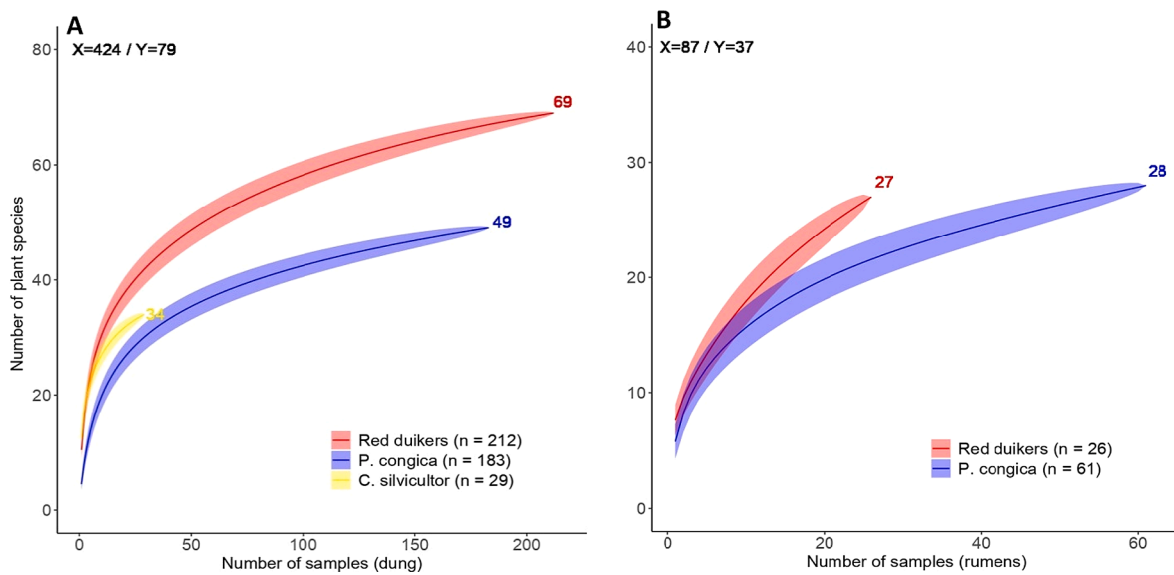


Fig. 3. Species rarefaction curves with increasing samples of dung (A) and rumen (B) showing average (lines) and standard deviation (shading) for diuker species. Numbers near the curves represent alpha diversity. X: total number of samples, Y: gamma diversity, n: number of samples for each diuker species.

4. Discussion

Although duikers are assumed to be seed dispersers due to their frugivorous diet (Beaune et al., 2013), or their ability to eject seeds during rumination (Feer, 1995), our study is the first to confirm this role based on rumen and dung seed germination trials.

4.1. Duiker community and impact of logging

The studied duiker community consisted of four species: *C. callipygus*, *C. castaneus*, *C. silvicultor*, and *P. congica*. Line transect and camera trap surveys performed in the same area by Mathot & Doucet (2006) and Lhoest et al. (2020) respectively confirm the presence of these same species.

Our analyses showed no significant difference in occupancy of duikers between the logged and unlogged plot, confirming our prediction. This indicates that the dispersal role of the duiker community would not be altered as a result of certified logging. Indeed, through its FSC certification, Pallisco is committed to sustainable management of the forest concession by ensuring, among other things, the ecological integrity of the forests through reduced impact logging (on average one to two trees per ha every 30 years), and the protection of wildlife (through surveillance patrols) (Lhoest et al., 2020). In Gabon, White (1992) also found no impact of logging on duiker populations in low intensity logging forests (non-certified), while in Northern Congo, Poulsen et al. (2011) noted that in the absence of hunting activities, *P. congica* was significantly more abundant in unlogged than in logged FSC forests. However, impact of logging on duikers population remain poorly documented.

4.2. Seed dispersal patterns

Germination trials revealed many fertile seeds (often very small) in duiker dungs and rumens. The average number of fertile seeds ranged from 6.4 to 27.0 per dung and from 48.8 to 86.5 per rumen. At the community level, 79 species were known to be dispersed by duikers (species observed in dung). Studies on ungulate communities show that they can disperse between 10 and 191 plant species by endozoochory (Baltzinger et al., 2019). Even though duikers are known to be mainly frugivorous, they disperse mainly herbaceous plants (58.2 %) through their dung. This result is supported by the research of Albert et al. (2015), who point out that the plants dispersed by ungulates are mainly

grasses typical of open habitats. Indeed, small herbaceous seeds can be inadvertently ingested by duikers when eating fruits or leaves (Janzen, 1984). Furthermore, the small size of the seeds of herbaceous plants explains why they are ingested in greater quantities than woody plants. As a result, some herbaceous species are the dominant and indicative of certain duiker groups, which is not consistent with our prediction.

According to Gautier-Hion et al. (1985) and Feer (1995) the release of seeds from rumens takes place in resting sites, usually far from seed sources. The regurgitated seeds are said to be tough, often large and proportional to the size of the ruminant. Thus, duikers could regurgitate seeds over a critical threshold of 2.2 cm, 2.8 cm, and 4.7 cm in diameter for *P. congica*, red duikers, and *C. silvicultor* respectively (Feer, 1995). However, small seeds can be dispersed both by conventional endozoochory (release of seeds through dung) and partial endozoochory (release of seeds during rumination) (Janzen, 1982; Castañeda et al., 2018). When the large seeds are rejected, some of the small seeds may remain attached to them and be expelled. When resting sites are reused, there could be a concentration of regurgitated seeds and thus increased seedling mortality as a result of competition (Delibes et al., 2019). *Cephalophus castaneus* and *P. congica* sometimes reuse resting sites (Castelló, 2016). However, they stir up the site with their hooves before each rest (Castelló, 2016), which could mitigate competition between seedlings.

Dissimilarity in dispersed taxa between duiker groups is as high as 42.0 %, probably related to the preferential habitats (mature forests, old secondary forests, gallery forests, etc.) of duikers. Unlike the other species, *P. congica* can thrive in a wide range of forests (Groves et al., 2011; Kingdon and Hoffmann, 2013). This would explain the lower dissimilarity between *P. congica* and all other duikers. However, duiker populations predominantly disperse the same species (relatively low β -diversity between groups). Contrary to our expectation, this finding shows that the studied frugivore species play overlapping rather than complementary dispersal roles. Baltzinger et al. (2019) demonstrated that sympatric ungulates can provide an overlapping seed dispersal service. Indeed, a fundamental property of mutualistic assemblages in ecosystems is high functional redundancy, favoured by the convergence of biological traits between the species that compose them (Bascompte and Jordano, 2013; Schleuning et al., 2015). Nevertheless, the role of species in dispersal is not technically redundant, as the combined functional action of all species is useful for maintaining ecosystems (Stringer et al., 2020).

Table 3

Ten most dominant species in dung (A) and rumen (B) according to the IVI. IVI: importance value index, RA: relative abundance, RF: relative frequency, Indval: indicator value index and its p-value (Pval). Ns: Not significant.

	IVI%	RA%	RF%	Indval%	Pval
(A) Dungs					
Species in <i>P. congica</i>					
<i>Phyllanthus</i> sp.	15.696	33.8	46.5	0.120	Ns
<i>Oxalis</i> sp.	0.627	5.0	12.6	0.052	Ns
<i>Cardamine</i> sp.	0.552	7.2	7.7	0.015	Ns
<i>Mitracarpus hirtus</i>	0.422	11.0	3.8	0.016	Ns
<i>Musanga cecropioides</i>	0.398	4.0	9.8	0.016	Ns
<i>Oxalis barrelieri</i>	0.207	2.9	7.1	0.030	Ns
<i>Panicum laxum</i>	0.199	4.0	4.9	0.008	Ns
<i>Axonopus compressus</i>	0.141	2.2	6.6	0.021	Ns
<i>Torenia thoursii</i>	0.141	4.3	3.3	0.004	Ns
<i>Ageratum conyzoides</i>	0.117	2.2	5.5	0.003	Ns
Species in <i>C. silvicultor</i>					
<i>Phyllanthus</i> sp.	6.605	12.8	51.7	0.214	Ns
<i>Paspalum conjugatum</i>	3.743	21.7	17.2	0.157	0.018
<i>Ficus wildemaniana</i>	1.069	10.3	10.3	0.102	0.004
<i>Kyllinga</i> sp.	0.881	5.1	17.2	0.124	0.011
<i>Cardamine</i> sp.	0.581	5.6	10.3	0.067	Ns
<i>Oplismenus burmannii</i>	0.546	4.0	13.8	0.115	0.005
<i>Panicum laxum</i>	0.507	2.9	17.2	0.081	Ns
<i>Laportea aestuans</i>	0.242	7.0	3.5	0.030	Ns
<i>Mitracarpus hirtus</i>	0.199	1.9	10.3	0.0320	Ns
<i>Fimbristylis</i> sp.	0.189	5.5	3.5	0.0320	Ns
Species in Red duikers					
<i>Phyllanthus</i> sp.	9.598	16.4	58.5	0.192	Ns
<i>Ageratum conyzoides</i>	2.148	15.7	13.7	0.125	0.029
<i>Musanga cecropioides</i>	1.211	7.1	17.0	0.13	Ns
<i>Torenia thoursii</i>	0.562	10.8	5.2	0.039	Ns
<i>Paspalum conjugatum</i>	0.467	3.0	15.6	0.012	Ns
<i>Panicum laxum</i>	0.393	3.8	10.4	0.039	Ns
<i>Kyllinga</i> sp.	0.273	2.6	10.4	0.024	Ns
<i>Oxalis barrelieri</i>	0.198	1.5	13.2	0.076	Ns
<i>Cyperus</i> sp.3	0.193	2.6	7.6	0.039	Ns
<i>Ficus</i> sp.1	0.181	5.5	3.3	0.022	Ns
(B) Rumens					
Species in <i>P. congica</i>					
<i>Musanga cecropioides</i>	28.240	82.0	34.4	0.152	Ns
<i>Phyllanthus</i> sp.	4.249	8.1	52.5	0.167	Ns
<i>Oxalis barrelieri</i>	0.242	1.3	18.0	0.17	Ns
<i>Landolphia</i> sp.	0.195	2.0	9.8	0.023	Ns
<i>Xylopia hypolampra</i>	0.095	1.5	6.6	0.062	Ns
<i>Oxalis</i> sp.	0.082	0.7	11.5	0.025	Ns
<i>Bridelia micrantha</i>	0.019	1.1	1.6	0.016	Ns
<i>Drymaria cordata</i>	0.018	1.1	1.6	0.016	Ns
<i>Kyllinga</i> sp.	0.016	0.2	8.2	0.009	Ns
<i>Paspalum conjugatum</i>	0.012	0.2	4.9	0.021	Ns
Species in Red duikers					
<i>Musanga cecropioides</i>	29.245	58.5	50.0	0.279	Ns
<i>Phyllanthus</i> sp.	6.394	9.8	65.4	0.446	Ns
<i>Ficus wildemaniana</i>	2.442	21.2	11.5	0.115	0.042
<i>Landolphia</i> sp.	0.852	3.7	23.1	0.177	Ns
<i>Oxalis</i> sp.	0.273	1.4	19.2	0.15	Ns
<i>Kyllinga</i> sp.	0.113	1.0	11.5	0.103	Ns
<i>Ficus</i> sp.	0.106	2.8	3.9	0.038	Ns
<i>Strophanthus gratus</i>	0.025	0.2	11.5	0.106	0.041
<i>Paspalum conjugatum</i>	0.021	0.2	11.5	0.066	Ns
<i>Melanthera</i> sp.	0.017	0.2	7.7	0.066	Ns

4.3. Role of duikers in the restoration and regeneration of logged forests

The home range of duikers can be up to 200 ha depending on the species (Feer, 1988), which could allow duikers to disperse seeds over long distances of about 2 km (diagonal of a 200 ha square) from the mother plant. Whether herbaceous or woody, most of the species found in dung and rumen are orthodox pioneer colonisers, which play a major role in the recovery of disturbed environments such as fallows. Most of these seeds, if not in favourable conditions for germination, especially in terms of light, remain dormant and become part of the soil seed bank. Studies in Cameroon (Dainou et al., 2011) and Congo (Douh, 2019) confirm the predominance of orthodox pioneer coloniser species in the

soil seed bank. These studies identified many species also observed in this study: *Ageratum conyzoides*, *Alstonia boonei*, *Celtis adolfi-frideric*, *Chromolaena odorata*, *Commelina diffusa*, *Eleusine indica*, *Erigeron* sp., *Erythrophleum suaveolens*, *Ficus calyprata*, *Ficus craterostoma*, *Ficus* sp., *Ficus wildemaniana*, *Mitracarpus hirtus*, *Musanga cecropioides*, *Nauclea diderrichii*, *Phyllanthus* sp., *Sabicea* sp., *Trema orientalis*, *Vismia* sp. Many of these species are known to be involved in the healing of areas disturbed by shifting cultivation.

In addition, the presence of fertile seeds in the dungs and rumens of some commercially valuable species such as *Milicia excelsa*, *Nauclea diderrichii* and *Erythrophleum suaveolens*, gives duikers added value for their conservation in timber forests. The duiker community completes the array of dispersers of these species whose regeneration is deficient in mature forest (Dainou et al., 2012; Duminil et al., 2016). The first two, with very small seeds, are found in the dung. The third can only be expelled by regurgitation.

4.4. Limitations of the study

Our work took place in a particular environment where the management of forest resources is controlled according to the FSC label. Therefore, the results should only be interpreted at the scale of our study area, as it is currently managed.

Our study did not consider vegetation types as well as seasonal variations in the two plots. This could influence our results on rate of change in occupancy of duikers.

The grouping of duiker populations into three groups according to faecal size is widely adopted in the literature. However, it may be subject to bias (van Vliet et al., 2007). For instance, the dungs of a young red duiker could be mistaken for those of an adult blue duiker. Generally, the dungs of the rare species *C. silvicultor* are identified in the field without error (due to their large size) (van Vliet et al., 2007). Our genetic analyses have provided more precision on the seeds dispersed by species. However, they could not cover all the samples collected due to the costs. Similarly, some of the analysed samples could not be identified due to the rapid degradation of DNA in tropical environments (Soto-Calderón et al., 2009).

Our research was carried out in a controlled environment, it therefore cannot identify with certainty which seeds are able to germinate and successfully establish themselves *in natura*. Moreover, our study specifically focused on species for which the seeds germinated. It therefore cannot make a statement about the diet of duikers. Furthermore, the plant species obtained were identified between six months and one year after potting, as is generally recommended (Baltzinger et al., 2019). However, studies have reported germination of some seeds between three and seven years after the start of the experiments (Young, 2012; Jaroszewicz et al., 2013). Furthermore, our study focused exclusively on partial and conventional endozoochory. Seeds that duikers could disperse by their fur and hoofs (fur-epizoochory and hoof-epizoochory) were not taken into account.

5. Conclusion

Our results demonstrated for the first time the presence of fertile seeds in the dungs and rumens of duikers from the rainforests of central Africa. Although duikers are known to be frugivorous, they can disperse both herbaceous and woody plants, which gives them an important ecological role in forest regeneration, particularly in the recovery of areas disturbed following logging or by shifting cultivation. By dispersing commercially valuable species, duikers also help to maintain timber production capacity in the long term. Controlling hunting pressure, as is done in forest concessions that are certified for sustainable management, seems essential to ensure the resilience of forest ecosystems.

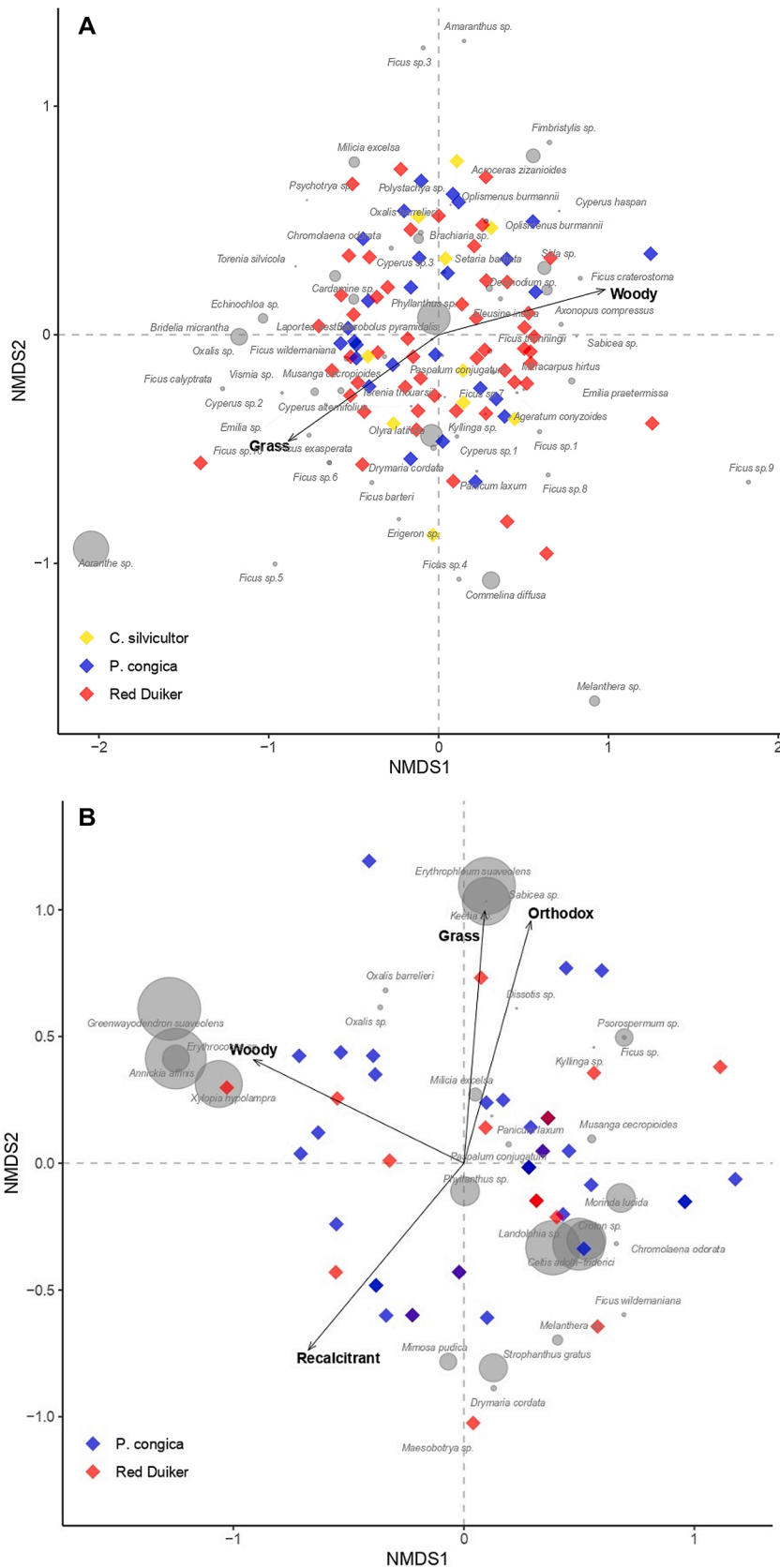


Fig. 4. Non-Metric Multidimensional Scaling (NMDS) ordination plot illustrating differences among plant species in duiker dung (A) and duiker rumen (B) in species space. Colours (blue, yellow, red) correspond to the different groups of duikers. Gray points correspond to plant species, with point size proportional to the weight of the plant seed. Arrows show the projection of supplementary variables. For better visualisation, seed weight has been log-transformed; dung and rumen samples < 4 and 2 plant species respectively have been removed. NMDS stress value was 0.25 for dung and 0.14 for rumen. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

CRedit authorship contribution statement

Fructueux G.A. Hounbégnon: Conceptualization, Formal analysis, Investigation, Funding acquisition, Validation, Visualization, Writing – original draft, Writing – review & editing. **Jean-François Gillet:** Resources, Validation, Visualization, Writing – review & editing. **Johan Michaux:** Conceptualization, Supervision, Visualization, Writing – review & editing. **Yves Brostaux:** Formal analysis, Validation, Visualization, Writing – review & editing. **Donatien Zébazé:** Formal analysis, Resources, Validation, Visualization, Writing – review & editing. **Simon Lhoest:** Formal analysis, Validation, Visualization, Writing – review & editing. **Cédric Vermeulen:** Conceptualization, Supervision, Visualization, Writing – review & editing. **Bonaventure Sonké:** Conceptualization, Supervision. **Jean-Louis Doucet:** Conceptualization, Formal analysis, Funding acquisition, Supervision, Validation, Visualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120650>.

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