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ORIGINAL PAPER

# Seed dispersal strategies and the threat of defaunation in a Congo forest

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**Abstract** Seed dispersal mode of plants and primary interactions with animals are studied in the evergreen Afrotropical forest of LuiKotale, at the south-western part of Salonga National Park (DR Congo). We first analysed seed dispersal strategies for (a) the plant species inventoried over a decade at the study site and (b) the tree community in 12 × 1 ha census plots. Our analyses of dispersal syndromes for 735 identified plant species show that 85 % produce fleshy fruits and rely on animals for primary seed dispersal. Trees depending on animals for primary dispersal dominate the tree community (95 %), while wind-dispersed and autochorous trees are rare in mixed tropical forests. A list of frugivorous vertebrate species of the ecosystem was established. Among the fruit-eating vertebrate species identified in the ecosystem, forest elephants and bonobos are threatened with extinction (IUCN, The IUCN red list of threatened species, 2012). Although most of the species listed previously are internationally and regionally protected, all the species we observed dispersing seeds are hunted, fished or trapped by humans in the area. With the exception of bush pigs, seed predators, mainly small-sized animals, are generally not targeted by hunters. As a consequence, we expect human pressure on key animal species to impact the plant community. We suggest defaunation to be considered as major conservation problem. Thus, not only for the sake of animal species but also for that of plant species conservation, anti-poaching measures should have priority in both "protected" and unprotected areas. Defaunation could bring a new impoverished era for plants in tropical forests.

**Résumé** Dans la forêt tropicale humide de LuiKotale, au sud-ouest du parc national de la Salonga (RD Congo), nous avons analysé (a) l'ensemble des stratégies de dispersion des plantes inventoriées dans le site d'étude depuis une décennie, puis (b) des plantes

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recensées dans l'inventaire de la communauté d'arbres sur 12 parcelles de 1 ha. D'après l'analyse des syndromes de dispersion de 735 espèces de plantes identifiées, 85 % produisent des fruits adaptés pour la consommation par des animaux qui dispersent leurs graines. Les arbres dont la dispersion primaire est zoochore dominent la communauté (95 %), alors que les arbres autochores et dispersés par le vent sont rare. Nous avons identifié les espèces de vertébrés frugivores de l'écosystème, parmi lesquelles les éléphants de forêts et les bonobos qui sont menacés d'extinction (IUCN 2012). Bien que protégés internationalement, tous ces animaux sont chassés, pêchés ou piégés. Les prédateurs de graines, principalement des petits animaux (rongeurs et oiseaux), ne sont pas des espèces cibles pour la chasse à l'exception des potamochères. La pression humaine devrait affecter la communauté végétale par l'élimination d'espèces clefs de l'écosystème. La défaunation risque d'être la cause d'une nouvelle ère d'appauvrissement spécifique des plantes de forêt tropicale. Cette défaunation doit être considérée comme un problème majeur de conservation. Les mesures anti-braconnage doivent être une priorité dans les zones protégées et « non protégés » et ceci non pas seulement pour la conservation des espèces animal mais aussi pour la conservation des espèces végétales.

**Keywords** Seed dispersal · Defaunation · Democratic Republic of the Congo · Forest ecology · Frugivores · Human pressure · Seed predators · Tropical rainforest · Zoochory

## Introduction

A critical problem in tropical forest conservation is hunting and poaching for the commercial bush meat trade, and this is particularly true in the Congo Basin (Bowen Jones and Pendry 1999; Wilkie and Carpenter 1999; Fa et al. 2002). The Congo Basin is of particular interest investigating the link between defaunation and forest conservation, as it is home to the second largest rainforest block in the world. Almost half of its forests (about 154 million ha) are located in the Democratic Republic of Congo (DRC) (FAO 2010). A total of 60 % of the DRC is covered by forest with high biodiversity, but these areas where defaunation is particularly severe are among the least studied in Africa (Bowen Jones and Pendry 1999; Hart et al. 2008). With a total extraction of 4.9 tons of wild mammal meat each year (vs. 0.15 in Neotropical forests (Fa et al. 2002), the rate of exploitation has been judged unsustainable for Afrotropical forests. Causes and consequences of the on-going "bush meat crisis" (Peres and Palacios 2007) are similar across Africa, and where still available, large and medium-sized animals are the most targeted species (Wright et al. 2007; Poulsen et al. 2009). This impact on animal species and populations has an impact on plants (Terborgh et al. 2008): Ecosystems are shaped by animal–plant interactions, and many plant species depend on animals for seed dispersal (Forget et al. 2006, 2011; Dennis 2007).

To evaluate the impact of hunting on plant species, we need to (1) estimate how many plant species are dependent on animals for seed dispersal; (2) census primary seed dispersers and seed predators; and (3) assess their relative hunting pressure.

(1) In tropical areas, zoochory is dominant and seems to outperform other dispersal modes such as barochory (by gravity), hydrochory (by water), anemochory (by wind) or autochory (by ballistic mechanisms) (Gautier-Hion et al. 1985; Willson 1993; Jordano 2000; Levey et al. 2002). However, community-scale assessments are rare in the Afrotropics. Studies must therefore assess the abundance and diversity of zoochorous plant species in the ecosystem.

Recent studies indicate that seed dispersal plays a prominent role in recruitment limitation, gene flow, metapopulation dynamics, colonisation potential and plant migration in response to past and future climate change, maintenance of biodiversity, and more (Schupp et al. 2010). As predicted by models (Muller-Landau 2007) and shown in field surveys (Forget and Jansen 2007; Stoner et al. 2007; Wright et al. 2007; Terborgh et al. 2008; Brodie et al. 2009; Vanthomme et al. 2010), defaunation leads to the empty forest syndrome (Redford 1992; Terborgh et al. 2008) with noticeable consequences for the structure and dynamics of the habitats concerned. Currently, three not mutually exclusive conclusions are possible concerning the impact of hunting for tropical forest plant communities: (1) Hunting reduces the amount and efficiency of seed dispersal for plant species whose seed dispersal agents include hunted animals (Beckman and Muller-Landau 2007; Wang et al. 2007); (2) hunting alters the species composition of the seedling and sapling layers (Stoner et al. 2007); (3) selective hunting (i.e. pressure on large/medium-sized instead of small animals) leads to differential predation on seeds, with more predation on small seeds (Mendoza and Dirzo 2007). As a consequence of hunting pressure, the tropical forest with plant species disseminated by animals might change with regard to biodiversity, species dominance, survival, demography, and spatial and genetic structure (Wright et al. 2007). Although studies have assessed diversity and abundance of plant species in central African ecosystems such as the Congo Basin (Howe and Smallwood 1982; Idani et al. 1994; Boubli et al. 2004), certain areas are underexplored and require urgent assessment due to the continuing rapid decline in biodiversity.

(2) Plants can interact with many different animals, such as seed predators and/or seed dispersers (Gautier-Hion et al. 1985; Jordano et al. 2003). Some of these animals are prey for hunters while others are not (or are caught opportunistically). Differential human pressure on fauna could affect plant reproductive parameters. Seed predators (e.g., small rodents) may be less affected by human predation than primary seed dispersers (such as primates, bats, and birds; Wilkie and Carpenter 1999). Therefore, a census of primary seed dispersers and seed predators is required.

Among the seed predator guild, some species are strictly seed predators (e.g., bush pigs: Beaune et al. 2012b) while others are also secondary dispersers (scatter hoarders, ruminants: Feer 1995; Vander Wall et al. 2005; Nyiramana et al. 2011; Beaune et al. 2012a).

(3) The relative hunting pressure on seed predators depends on a variety of factors such as a species' conspicuousness, its arboreality, or body mass. The latter i.e. shows a large variation not only between but also within species (with weights from <1 to >100 kg, e.g., bush pig). Within the seed predator community, the seed size panel predated is thought to be linked to seed predator size: the differential predation hypothesis (DPH). The removal of large/medium-sized seed predators such as bush pigs (one of the preferred prey of hunters; Wilkie and Carpenter 1999) could trigger differential predation on seed species; with large-seeded plants escaping predation with consequences on seed mortality and recruitment (Mendoza and Dirzo 2007).

Here we provide an assessment of seed dispersal strategies within a plant community in a Congo forest. In this study (1) we determine plant strategies and estimate the number of species within a tree community that are dependent on animals for seed dispersal and the relative importance of their abundance/dominance relative to other strategies; (2) we inventory the community of vertebrates interacting with seeds (primary seed dispersers and seed predators) and assess whether or not an animal is hunted by humans; (3) we present the first data on ichthyochory in Africa. Reports on fruit-eating fish are limited although fruits of some trees that inhabit riverine and seasonally inundated forests are already known to be eaten by fish (Hulot 1950; Horn et al. 2011).

## Methods

### Study site

The LuiKotale research site (LK) is located within the equatorial rainforest at 2°47′S–20°21′E, at the south-western fringe of the Salonga National Park (DRC), and in the same continuous forest block as that park Fig. 1. Classified as a world heritage site, Salonga National Park is the largest protected rain forest area in Africa and the second largest protected rainforest in the world (33.346 km$^2$, Grossmann et al. 2008). The study site is a primary evergreen tropical lowland rainforest ancestrally owned and used by Lompole village (17 km away). The site covers >60 km$^2$ with a network trail of 76 km. Since 2001, subsistence hunting and harvesting within the site has ceased for the sake of research (Hohmann and Fruth 2003). The climate is equatorial with abundant rainfall (>2,000 mm/year), a short dry season in February and a longer one between May and August. Mean temperature at LuiKotale ranges between 21 and 28 °C, with a minimum of 17 °C and a maximum of 38 °C (2007–2010). Five major vegetation types are distinguished in the site: (1) mixed tropical forest on *terra firme*, (2) monodominant forest dominated by *Monopetalanthus* sp. (3) monodominant primary forest dominated by *Gilbertiodendron dewevrei* (4) temporarily inundated mixed forest (5) permanently inundated mixed forest.

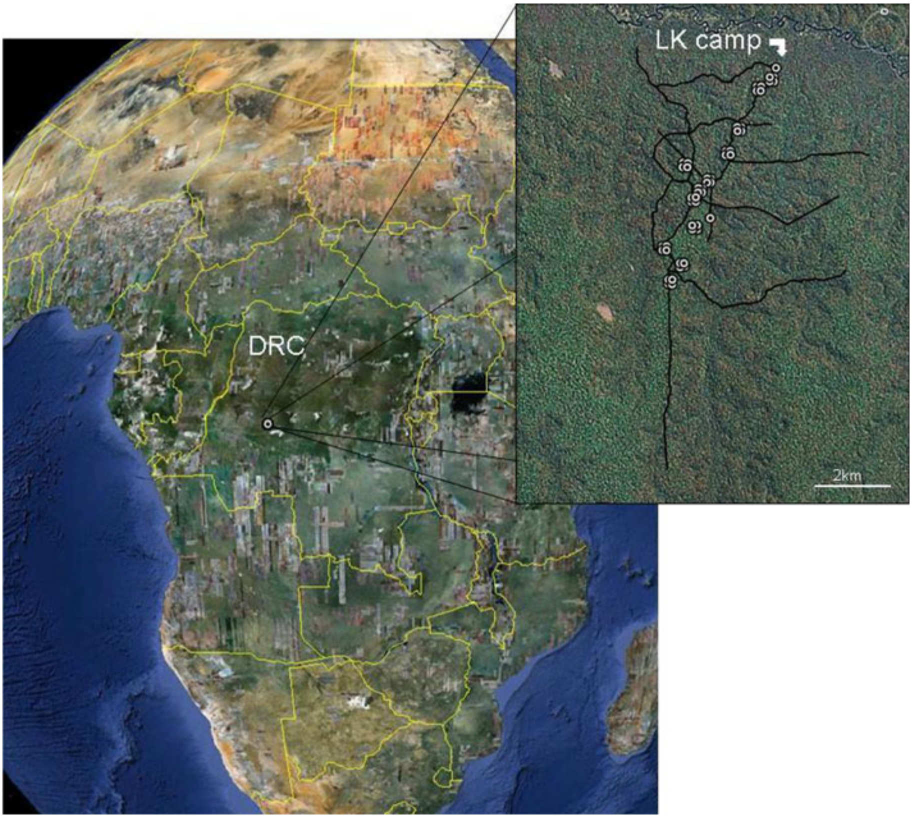


**Fig. 1** Map of the field site and location of plots (*white dots*), with main transects shown as *black lines*

Well-drained habitats (1–3) dominate site cover, with 73 % of heterogeneous forest composition and 6 % of homogeneous composition. Seasonally or permanently flooded habitats (4, 5) represent 17 and 4 % of the cover respectively (Mohneke and Fruth 2008).

## Plant species and dispersal mode

Between 2002 and 2010, botanical data collection took place as part of the long-term project-The *Cuvette Centrale* as a Reservoir of Medicinal Plants: Fertile plant material was collected at least in triplicate along natural trails (31 km), standardized transects (8 km), in plots, and opportunistically. Each plant was identified by vernacular name, described, tagged with a unique collection number, and herborised. The dried vouchers were shipped to Kinshasa, taxonomically determined and incorporated into the herbarium of the INERA at Kinshasa University (herbarium code: IUK). Copies of specimens were shipped to herbaria in Belgium (National Botanic Garden of Belgium: code BR, Meise) and Germany (Botanische Staatssammlung München: code M, Munich) for verification and identification by specialists.By May 2010, the herbarium consisted of 7,300 vouchers (Fruth 2011). For the purpose of our study, the dispersal strategies of each inventoried species from LK were categorized through diaspore anatomy and tissue analysis as (1) zoochore (fleshy fruit indicating zoochory by primary dispersers) (2) hydrochore (drift fruit) (3) anemochore (achene or samara) or (4) autochore. (dehiscent tissue). If fruit was unavailable, dispersal strategy was inferred from literature (Gautier-Hion et al. 1985; White and Abernethy 1997; Geerinck 2005).

## Abundance and diversity of animal-dispersed trees

From February to June 2011, 12 plots of 1 ha (100 $\times$ 100 m) were randomly positioned in mixed tropical forest. Within these plots, all trees $\geq$10 cm DBH (diameter at breast height) were measured and identified in order to assess the relative importance of zoochorous trees in the community. Plot difference was tested with a Shapiro–Wilk normality test and tree densities and average DBH were calculated by one-way analysis of variance (ANOVA) (Boubli et al. 2004).

The proportional abundance of zoochorous trees found in the plots was compared to the theoretical proportion according to the number of zoochorous species censused on the plots, using a Binomial test (with power analysis of the test specified if $H_0$ rejected). Analyses were performed using R 2.13 (R Development Core Team 2011).

## Vertebrate seed dispersers and predators

*Mammals*. From January 2010 to June 2011, a list of terrestrial frugivorous mammals was compiled from ad libitum direct visual observation and camera traps (Two Wildeview series3 & three Bushnell® Trophy Cam™: Video mode 60 s/1 s interval/normal sensitivity, were installed for 82 days and nights) at the LK site. The LK site was explored on and off the trail system (> 10 km/day) and species were recorded opportunistically. To identify seed predators, camera traps were randomly positioned throughout the forest and baited with different seeds (Beaune et al. 2012b).

*Birds*. Frugivorous birds were opportunistically observed from January 2010 to June 2011 and complemented with data from earlier studies conducted by Surbeck (Fruth and Hohmann 2005) and Cohen (BirdLife-International 2011).

*Fishes*. Fishes were captured by local fishermen in the Lokoro River and affluents for subsistence and commerce. Catches were brought to camp for census. Stomach contents were analysed from March to June 2011 in order to find seeds in the bolus.

All animal species were identified and their main interaction with seeds (1-primary seed disperser; 2-seed predator; 3-neutral) inferred from literature, video records and unpublished data observation from the field site (Gautier-Hion et al. 1985; Kingdon 1997; Bourson 2011; Beaune et al. 2012a, b). Observed frugivores were considered to be seed dispersal vectors when intact seeds were horizontally moved in space by endo- or ecto-zoochory. Seed predators were observed destroying seeds (Beaune et al. 2012b). Through lack of evidence of secondary dispersal, only primary dispersal was considered. Species status followed the IUCN red list of threatened species (IUCN 2012). The local threat was assigned for each species (poached, hunted or fished) by crosschecking questionnaires from experienced local hunters ($n = 28$), the literature (Wilkie and Carpenter 1999; Poulsen et al. 2009) and ad libitum observation of catches from January 2010 to June 2011.

## Results

### How many plant species are zoochorous?

Within the LK area, dispersal syndromes of a total of 735 species were analysed. These included 403 tree, 130 shrub and 202 liana species belonging to 77 plant families. Of these species, 85.0 % produce fleshy fruits and are primarily dispersed by animals (zoochory).

Zoochory is the dominant seed dispersal strategy among trees (83.9 %), shrubs (97.7 %) and lianas (79.2 %) Fig. 2. The proportion of zoochorous shrubs is significantly higher than for trees and lianas (test of proportion, $\chi^2 = 15.65$ and 21.51 respectively, df = 1, $p$ values <0.001; power analysis = 100 %). There was no significant difference in the proportion of trees and lianas dispersed by animals ($\chi^2 = 1.70$, df = 1, $p$ value = 0.2).

Herbaceous species were excluded from this study because it was difficult to distinguish species dispersed by multiple vectors (such as wind + ant, water + fish, etc.). Nevertheless, we identified 123 herbaceous species which may use animals as dispersal vectors (first or secondary).

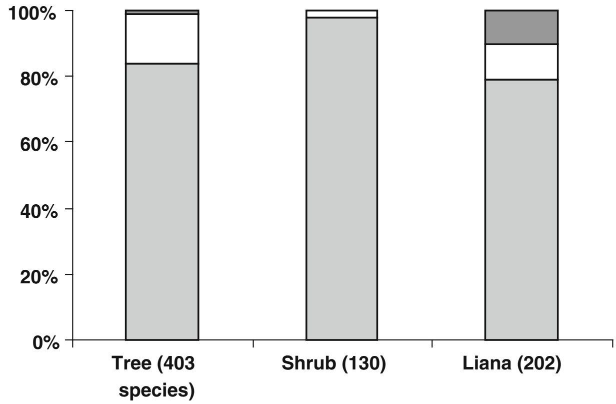


**Fig. 2** Proportions of species characterized by the different seed dispersal strategies among tree, shrub and liana species of LK. *Grey* animal-dispersed, *white* autochorous, *black* wind-dispersed

## Abundance and diversity of animal-dispersed trees

All 12 plots were similar in structure (size-class distribution: no significant difference in DBH class size: ANOVA, $F = 1.3$, $p$ value $= 0.25$; normal distribution of tree density: $W = 0.93$, $p$ value $= 0.43$). Within the 12 1 ha plots, zoochorous species accounted for a much greater proportion than did other dispersal strategies. Zoochorous species accounted for a mean of 88.1 %, ± SE 0.7, $CI_{95\ \%} = [86.6–89.6\ \%]$ of all species present in the plots. Autochorous species accounted for a mean of 10.6 %, ± 0.7, $CI_{95\ \%} = [9.0–12.1\ \%]$, while wind-dispersed species were nearly absent (0.5 %, ± 0.2, $CI_{95\ \%} = [0.0–1.0\ \%]$) Fig. 3. If tree species dispersed by different vectors tend to be equally abundant, then proportions of individual trees dispersed by different vectors should reflect the proportions of species dispersed by these vectors. However, trees belonging to zoochorous species accounted for a higher proportion of all individual trees than that expected under equal abundance of species with different dispersal strategies ($p$ value $<0.001$, power analysis = 100 %). A proportion of 95.1 % ± 0.7 of all individual trees in the plots belonged to animal-dispersed species ($CI_{95\ \%} = [93.5–96.6\ \%]$). Anemochorous and autochorous species account for smaller proportions of all individual trees present in the 12 1 ha plots compared to the proportion of all species that they account for ($p$ values $<0.001$, power analysis = 100 %). Among the 25 most dominant species (i.e. from the genera *Dialium*, *Polyalthia*, *Chaetocarpus*, *Drypetes*, *Strombosiopsis*, *Strombosia, Sorindeia*, etc.) representing +78 % of individual trees (4,098/5,234 trees), only one is autochorous: *Scorodophloeus zenkeri*, 23rd in rank with a total of 63 individual trees.

## Vertebrate seed dispersers and predators

Thirty eight non-aquatic vertebrates eating fruit were identified at LK. Some of these fruit-eating species, namely bushbuck (*Tragelaphus scriptus*), common genet (*Genetta genetta*), potto (*Perodicticus potto*), tree hyraxe (*Dendrohyrax dorsalis*), water chevrotain (*Hyemoschus aquaticus*), and west African linsang (*Poiana leightoni*), so far did not show evidence of seed dispersion, and thus were not classified as seed dispersers. Other

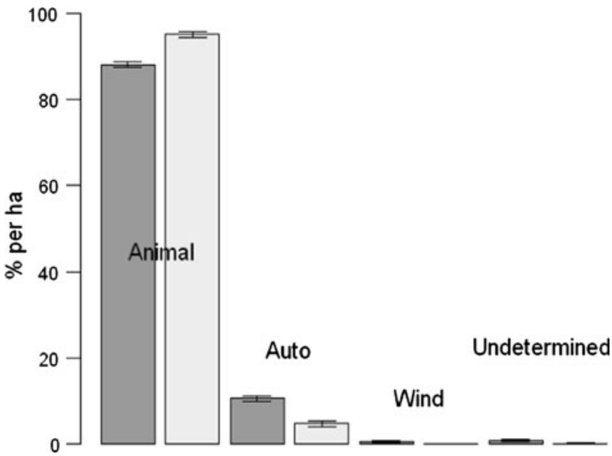


**Fig. 3** Proportion of different dispersal modes for all species (*dark bars*), and for all individuals (*light bars*) present in 12 × 1 ha plots. *Error bars* indicate SE

identified species, namely Afep pigeon (*Columba unicincta*), African green pigeon (*Treron calvus*), Congo peacock (*Afropavo congensis*), crested guineafowl (*Guttera pucherani*), grey parrot (*Psittacus erithacus*), streaky-throated barbet (*Tricholaema flavipunctata*), may both eat and disperse seeds of different plant species. Thus, it was not possible to assign a clear category to these animals. Finally, 31 fruit-eating species (including a non-exhaustive list of fishes) were identified as seed dispersers. All of them are exploited for meat (Table 1), including threatened species protected by law such as elephants and bonobos. Smaller frugivorous birds and bats which are usually not hunted are probably present but were not recorded. Five vernacular species of fish belonging to five genera (*Xenocharax*, *Distichodus*, *Clarias*, *Malapterurus*, *Schilbe*) were recorded to swallow fruits and seeds. Fruits from the forest gallery are used as bait by local people. Intact seeds of *Parinari congensis*, *Treculia africana*, *Uapaca* sp., etc. have been found in either stomach, intestines, or close to the anus of several fishes ($n = 23$ content analyses). The last three genera mentioned in Table 1 are catfishes (order Siluriformes) reaching +1 m. No amphibians or reptiles were observed to feed on fruits in LK but this cannot be excluded.

The seed predator guild comprises 19 identified species (Table 2). It is mainly comprised of seed-eater specialists such as rodents and birds (family Estrildidae with *Estrilda paludicola*, *Nigrita bicolour*, *N. canicapillus*, *Spermophaga haematina*). Snare trapping targets specifically the largest terrestrial rodents (Kingdon 1997), such as porcupines (*Atherurus africanus*, 1.5–4 kg) or giant pouched rats (*Cricetomys emini*, 1–1.4 kg). Squirrels (family Sciuridae) and anomalures (*Anomalurus derbianus*) are hunted with weapons when encountered, as are birds (francolin: *Francolinus lathami*). Bush pigs (*Potamochoerus porcus*) with their large body mass (45–115 kg) are among hunters' preferred prey (Wilkie and Carpenter 1999; Poulsen et al. 2009; Beaune unpublished data). The proportion of seed predator species hunted in their guild is with only 1/3$^{rd}$ as important of the seed disperser species significantly less important (37–100 %, $\chi^2 = 22.4$, df = 1, $p$ value <0.001, power analysis = 100 %). Yet, unlike the bonobos and the forest elephants, none of the seed predators are threatened by extinction (Table 2). According to hunters, seed predator species such rodents and passerines are not targeted preys of hunting expeditions, owing to their small size. Most seed predator species are opportunistically shot or trapped, except for *P. porcus*, the largest seed predator, favouring the hypothesis that frugivores are hunted more intensively than seed predators and by that the differential predation hypothesis.

## Discussion

Seeds of most plant species in tropical forests are dispersed by animals, rather than by wind, water or ballistic mechanisms (Jordano et al. 2003; Forget et al. 2006, 2011; Dennis 2007). In the LK forest systems of the Congo Basin, zoochorous species currently dominate plant communities (85 % of the referenced plant species in LK areas). More specifically, in the mixed tropical forest we sampled, the abundance of anemochorous and autochorous tree species (4.9 %) is lower than expected from the respective proportions of anemochorous and autochorous species in the tree community (11.1 %).

Zoochorous tree species are among the dominant trees in this Afrotropical forest, indicating the dominance of this dispersal strategy. However, adaptations for zoochory leads to dependence on animals, so zoochorous plants may become trapped in a coevolutionary dead-end if their partners become extinct (Jordano et al. 2003; Muller-Landau 2007; Muller-Landau et al. 2008). This is particularly important in tropical forests, where

**Table 1** List of fruit-eating vertebrates categorized as seed dispersers in the study site. IUCN status of each species was consulted in June 2011, indicating status of threat as follows: *LC*: Least Concern, *DD*: Deficient Data, *V*: Vulnerable, *NT*: Near Threatened, *E*: Endangered, ↕: stable population trends; ↓: decrease; ?: population trend unknown

| Class | Family | Species | Name | Status | Population trends | Threats |
|---|---|---|---|---|---|---|
| Mammalia | Bovidae | *Cephalophus callipygus* | Peter's duiker | LC | ↓ | Hunted |
| | | *Cephalophus dorsalis* | Bay duiker | LC | ↓ | Hunted |
| | | *Cephalophus monticola* | Blue duiker | LC | ↕ | Hunted |
| | | *Cephalophus nigrifrons* | Black-fronted duiker | LC | ↓ | Hunted |
| | | *Cephalophus silvicultor* | Yellow-backed duiker | LC | ↓ | Hunted |
| | Cercopithecidae | *Allenopithecus nigroviridis* | Allen's swamp monkey | LC | ? | Hunted |
| | | *Cercocebus chrysogaster* | Golden-bellied mangabey | DD | ↓ | Hunted |
| | | *Cercopithecus cephus ascanius* | Red-tailed monkey | LC | ? | Hunted |
| | | *Cercopithecus mona wolfi* | Wolf's monkey | LC | ? | Hunted |
| | | *Cercopithecus neglectus* | De Brazza's monkey | LC | ? | Hunted |
| | | *Lophocebus aterrimus* | Black mangabey | NT | ↓ | Hunted |
| | Hominidae | *Pan paniscus* | Bonobo | E | ↓ | Poached |
| | Elephantidae | *Loxodonta africana cyclotis* | Forest elephant | V | ↑ | Poached |
| | Pteropodidae | *Epomophorus grandis* | Epauletted fruit bat | DD | ? | Hunted |
| | | *Hypsignathus monstrosus* | Hammer-headed bat | LC | ? | Hunted |
| | | *Lissonycteris angolensis* | Angola fruit bat | LC | ↓ | Hunted |
| | Viverridae | *Civettictis civetta* | African civet | LC | ? | Hunted |
| | | *Nandinia binotata binota* | African palm civet | LC | ? | Hunted |
| Aves | Bucerotidae | *Bycanistes albotibialis* | White-thighed hornbill | LC | ? | Hunted |
| | | *Ceratogymna atrata* | Black-casqued hornbill | LC | ? | Hunted |
| | | *Tockus camurus* | Red-billed dwarf hornbill | LC | ? | Hunted |
| | | *Tockus fasciatus* | African pied hornbill | LC | ? | Hunted |
| | | *Tropicranus albocristatus* | White-crested hornbill | LC | ? | Hunted |
| | Musophagidae | *Musophaga rossae* | Ross's turaco | LC | ? | Hunted |
| | | *Tauraco schuettii* | Black-billed turaco | LC | ? | Hunted |
| | | *Corythaeola cristata* | Great blue turaco | LC | ? | Hunted |

**Table 1** continued

| Class | Family | Species | Name | Status | Population trends | Threats |
|---|---|---|---|---|---|---|
| Actinopterygii | Citharinidae | *Distichodus* sp | "Mboto" | | | Fished |
| | | *Xenocharax* sp | "Loboli" | | | Fished |
| | Clariidae | *Clarias* sp | "Ngolo" | | | Fished |
| | Malapteruridae | *Malapterurus* sp | "Nina" | | | Fished |
| | Schilbeidae | *Schilbe* sp | "Lolango" | | | Fished |

**Table 2** List of seed predators in the study site. IUCN status of each species was consulted in June 2011, indicating status of threat as follows: *LC*: Least Concern, *DD*: Deficient Data, ↕: stable population trends; ↓: decrease; ?: population trend unknown

| Class | Family | Species | Name | Status | Population trends | Threats |
|---|---|---|---|---|---|---|
| Mammalia | Anomaluridae | *Anomalurus derbianus* | Lord Derby's Anomalure | LC | ? | Hunted |
| | Hystricidae | *Atherurus africanus* | Brush tailed porcupine | LC | ? | Hunted |
| | Muridae | *Hylomyscus* sp | African wood mouse | LC | ? | |
| | | *Malacomys* sp | Long footed rat | LC | ? | |
| | | *Mus* sp | Common mouse | LC | ? | |
| | | *Praomys* sp | Soft-furred rat | LC | ? | |
| | | *Stochomys longicaudatus* | Target rat | LC | ? | |
| | Nesomydae | *Cricetomys emini* | Giant pouched rat | LC | ↕ | Hunted |
| | Sciuridae | *Funisciurus congicus* | Congo rope squirrel | LC | ↕ | Hunted |
| | | *Protoxerus aubinnii* | African giant squirrel | DD | ? | Hunted |
| | Suidae | *Potamochoerus porcus* | Bushpig | LC | ↓ | Hunted |
| | Estrildidae | *Estrilda paludicola* | Fawn-breasted waxbill | LC | ? | |
| | | *Nigrita bicolour* | Chestnut-breasted nigrita | LC | ? | |
| | | *Nigrita canicapillus* | Grey-headed nigrita | LC | ? | |
| | | *Spermophaga haematina* | Western bluebill | LC | ? | |
| | Phasianidae | *Francolinus lathami* | Forest francolin | LC | ? | Hunted |
| | Ploceidae | *Malimbus nitens* | Blue-billed malimbe | LC | ? | |
| | | *Malimbus cassini* | Cassin's malimbe | LC | ? | |
| | | *Malimbus rubricollis* | Red-headed malimbe | LC | ? | |

numerous animals, predominantly large vertebrates, are unsustainably overhunted (Wright et al. 2007). The importance of the largest seed dispersers in our study site, bonobos and elephants, has already been noted (Yumoto et al. 1995; Blake et al. 2009, 2007), and elephants have been described as the 'megagardeners' of the forest (Campos-Arceiz and Blake 2011). Some of the seed dispersers such as bonobos are endemic, rare, and threatened (Fruth et al. 2008) and others such as Allen's swamp monkeys, are insufficiently known (Oates and Groves 2008). Fruiting plants can have several consumers and seed dispersers with functional redundancy. However this does not help when all dispersal vectors are hunted. In the studied ecosystem all primary seed dispersers are hunted, trapped or fished; while seed predators are less impacted. Ecosystem resilience might be compromised.

Human pressure on animals providing seed dispersal services and large seed predators such as bush pigs should increase in the future with human demography and population increase (Brashares et al. 2001; Poulsen et al. 2009). In central Africa, consumption rates are estimated at 0.16 kg of bushmeat per person per year (Delvingt 1997) and extraction of bushmeat is estimated at 213–248 kg/(km$^2$ year) (Wilkie and Carpenter 1999). Bushmeat demand is increasing steadily as the population increases and cities expand (Poulsen et al. 2009). Many parks have failed to prevent poaching, including the adjacent Salonga National Park, where organized poaching is rife (Hart et al. 2008). Beyond the survival of animals, the entire ecosystem dominated by plants dependent on animal-mediated seed dispersal is also at risk.

This study also highlights the risk of the differential predation hypothesis (Mendoza and Dirzo 2007). While bush pigs are the biggest seed predators of the system, with dramatic effects on the mortality of large and hard protected seeds (Beaune et al. 2012b), they suffer greater hunting pressure than small seed predators eating small-seeded species. Large-seeded species such as (*Irvingia gabonensis*, *Mammea africana*, etc.) could benefit from reduced seed predation, This differential could modify plant reproduction and dominance in the forest. Similarly, the disappearance or decline of populations of large frugivores such as elephants and bonobos, which disperse large seeds, seems to alter recruitment of large-seeded plant species (Wang et al. 2007; Vanthomme et al. 2010). Of plant species with putative "megafaunal syndromes", many are ecologically disrupted by the loss of megafauna, but some show resilience (Janzen and Martin 1982; Guimarães et al. 2008; Johnson 2009).

If animal density decreases, animal-dependent plants could be replaced by autochorous and anemochorous species. Although this will be a slow and not immediately detectable process, ultimately a possible scenario in this forest is a radical change in the composition of the dominant species. With this inventory of seed disperser species and pressures on them, we can estimate the proportion of plants potentially affected by their loss as follows: 85 % of all plant species, and 88 % of tree species (but 95 % of individual trees). Thus, hunting is likely to trigger changes in forest structure and composition, as well as in population demography and genetics.

Tree density might stabilise, with autochorous and anemochorous trees occupying vacant space (Chapman and Onderdonk 1998) but biodiversity would decrease as a result (Muller-Landau 2007). More studies determining whether zoochorous plants can reproduce in the absence of animals are urgently required, as are conservation and management plans for these forests. Conservationists have focused on the direct consequences of habitat loss, animal species decline as well as consequences of habitat loss on animal species decline. However, a growing body of literature shows the increasing need to focus in addition on the reverse argument, the consequences of animal species' loss on habitat. In this respect, defaunation has to be considered as major conservation problem (Redford 1992; Terborgh et al. 2008). Its consideration is urgent in unprotected areas but even more in “protected” areas, where timber exploitation is banned but poaching still continues due to a lack of law enforcement (Hart et al. 2008; Canale et al. 2012).

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