The role of forest fragments in African conservation: A taxonomic and functional approach

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2. SUMMARY

2.1. Scientific public

2.1.1. English

The African human population size is expected to rise excessively within the coming decades, which will inevitably lead to an increase in demand for cropland and the coinciding largescale clearing of forests. Forest fragments will therefore become numerous in the African landscape and many forest species will depend on these remnants for their long-term survival. To unravel the diversity changes upon forest fragmentation/clearing, we conducted a largescale comparative study between Central African forests and forests fragments, primarily based upon differences in taxonomic and functional mammal diversity. Different aspects were discussed: changes of species identities (forest generalists versus forest specialists), vulnerable species/functions and consequences for the ecosystem, general diversity loss, protection of functional redundancy, the independent effects of fragmentation (isolation versus fragment reduction) and the influence of forest area size. Habitat specialists, larger herbivores, frugivorous ungulates and carnivores appeared to be the first (functional) groups to disappear when fragmentation occurred. The general depletion of diversity in forest fragments could not be overlooked but was not detected in the primate order that seems to tolerate extreme cases of fragmentation (when large-scale hunting is absent). As important seed-dispersers, their ecological role in potential forest regeneration keeps the plant community relatively viable. Furthermore, it was found that functional redundancy is almost non-existent, that isolated/larger forests exhibit lower diversities than non-isolated/smaller fragments and that diversity rises with forest area size until a diversity peak is reached around 2000-3000km². To achieve the highest conservation successes, we therefore recommend focusing African conservation measures towards forest fragments where primates are still present, the application of corridors and the prevention of continuous forests declining beneath 2000km².

2.1.1. Dutch

Er wordt verwacht dat de enorme toename in de Afrikaanse bevolkingsgroei de komende decennia onvermijdelijk zal leiden tot een grotere vraag naar landbouwgrond en daarmee grootschalige ontbossing zal veroorzaken. Gefragmenteerde bossen zullen hierdoor een belangrijke component van het Afrikaanse landschap gaan uitmaken en vele bos-specifieke

soorten zullen afhangen van deze habitatoverblijfselen voor hun langdurige overleving. Om te voorspellen welke diversiteitsveranderingen zullen plaatsvinden na bosfragmentatie/kap voerden we een grootschalige vergelijkende studie uit tussen nu reeds bestaande Centraal-Afrikaanse bossen en bosfragmenten, voornamelijk gebaseerd op hun verschillen in taxonomische en functionele zoogdierdiversiteit. Verscheidene aspecten werden onderzocht: verschil in soortidentiteit (bosgeneralisten tegen bosspecialisten), kwetsbare soorten/functies en de gevolgen voor het ecosysteem, algemeen diversiteitsverlies, bescherming van functionele redundantie, de onafhankelijke invloeden van fragmentatie (isolatie tegen oppervlakteverkleining) op diversiteit en de algemene invloed van bosoppervlak. Bosspecialisten, grote herbivoren, vrucht etende hoefdieren en carnivoren lijken de eerste (functionele) groepen om te verdwijnen in gefragmenteerd bos. De algemene achteruitgang van diversiteit in bosfragmenten is echter niet merkbaar bij primaten, die extreme fragmentatie lijken te tolereren (als grootschalige jacht afwezig is). Als zaadverspreiders spelen zij een belangrijke rol in potentiële bosregeneratie en houden zij de plantgemeenschap dus relatief levensvatbaar. Verder werd aangetoond dat functionele redundantie quasi onbestaand is, dat geïsoleerde/grotere bosfragmenten lagere diversiteit vertonen dan nietgeïsoleerde/kleinere bosfragmenten en dat een toename van het bosoppervlak samengaat met een stijging van de diversiteit, tot een piek wordt bereikt rond 2000-3000km². Om de hoogste slaagkansen in Afrikaanse conservatie te behalen, raden we aan om conservatiemaatregelen te concentreren op bosfragmenten waar primaten nog steeds aanwezig zijn, op de toepassing van corridors en op het voorkomen van boskap bij aaneensluitende bossen gelijk of kleiner aan 2000 km^2 .

2.2. Broad public

Due to African human population growth, many forests will be cut down to make room for agricultural lands. The remnants of these forests will be scattered all over the landscape and will serve as the only remaining habitat for many forest species. We tried to assess what will happen to general mammal diversity (amount of species and their functions) when their habitat forests would become fragmented or smaller. Therefore, we compared the diversities of now existing continuous forests and forest fragments in Central Africa to search for differences. Like expected, mammal diversity was much lower in forest fragments compared to continuous forests. A remarkable exception to the rule was the group of primates. Monkeys

and apes spread seeds while eating fruits and are thus very important for tree regeneration. Their presence in forest fragments makes that plants still have a relatively large chance to spread and grow so that the forest fragments could get larger. In the process of fragmentation, isolation from larger forests (i.e. animals in forest fragments cannot move to or from a large forest) is much more harmful for diversity than smaller forest area size per se. For the larger forests, diversity was found to decline beneath 2000km² forest area size. In light of Africa's future logging issues, the best protection for forest mammal species will be achieved by conserving forest fragments where primates are still present, by connecting forests and forest fragments (corridors) and by preventing continuous forests of declining beneath 2000km² forest area size.

3. INTRODUCTION

3.1. Potential environmental consequences of species loss

The Congo basin harbours the second largest contiguous expanse of forests worldwide (Haddad et al. 2015) and is part of one of the remaining centres for terrestrial mammal diversity (sub-Saharan Africa, Olson 2001; Tilman et al. 2017). So far, the region has suffered relatively little from the now ongoing global diversity extinction wave (Tilman et al. 2017) which is most probably linked to its rather low deforestation rate (FAO 2011, Mayaux et al. 2013). However, in the coming decades the African human population size is expected to rise tremendously (Tilman et al. 2017). This change will inevitably coincide with the increase in demand for cropland (Tilman et al. 2017) and bushmeat (Fa et al. 2003) and will so instigate the large-scale clearing of forests. Furthermore, it has been predicted that the most important increases in extinction risks will be experienced by animals living in formerly intact landscapes (Betts et al. 2017) with the mammals of the sub-Saharan region facing one of the highest elevated extinction risks of them all (Tilman et al. 2017). This upcoming diversity crisis together with lesser scientific studies conducted in the Congo Basin area (in comparison with other large forested areas, Malhi et al. 2013) makes it urgent to investigate how the region-specific reaction to forest loss will unfold.

In general, high rates of deforestation and forest degradation pose the greatest direct threat to the long-term viability of forests (Montoya 2008) and hence their specific biodiversity (Tilman et al. 2017). Forests under logging pressure will either lose their outer borders and diminish in overall size or will become fragmented over time whereby remnants can get isolated from the remaining continuous forest. These processes combined with an increased edge effect will force forest biodiversity to find a way to cope with these new environments, or to go extinct. Whereas the effects of habitat destruction and the coinciding increase of anthropogenic disturbance have already been shown to be detrimental towards sensitive animal species such as top-carnivores (Muench & Martinez-Ramos 2016), they could offer an ecological advantage towards the generalists (Ceballos and Ehrlich 2002; Fahrig 2003). Together with these taxonomic changes, the functional diversity of these faunas might alter as well whereby the ecological functioning of their ecosystem could become affected (Loreau et al. 2001). Especially the absence of trophic guilds such as pollinators and seed dispersers

could endanger the long-term existence of rain forests since the majority of plant species in tropical regions are zoochorous (Wunderle 1997, Beaune et al. 2012). So besides the survival of the animal species, the viability of the plant community and their natural provisioning of ecosystem services could also become under threat (Montoya 2008).

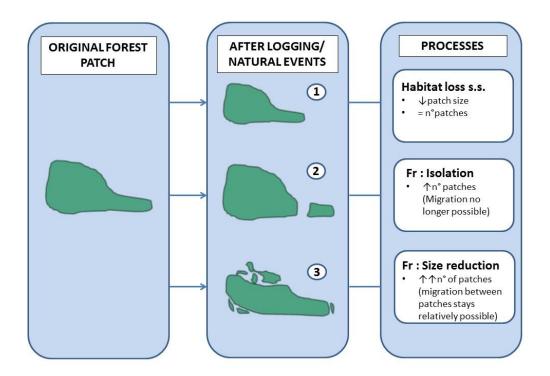


Figure 1| **Processes of forests loss:** Habitat loss per se (1) results in a smaller but still continuous forest patch; Fragmentation (Fr) can be seen as the product of both isolation (2) and size reduction (3). (2) results in relatively big patches excluded from migration between the source patch and (3) leads to (very) small patches constituting a non-continuous forest zone where migration between the patches and the source forest remains largely possible.

The overarching aim of this thesis was to distinguish between the consequences for biodiversity and ecosystem viability caused by the three independent processes affecting Central Africa's forests structure: the overall size reduction of continuous forests (Figure 1 (1)) and fragmentation (i.e. the division of habitat into smaller and more isolated fragments separated by a matrix of human-transformed land cover, Haddad et al. 2015). Both the isolation (Figure 1 (2)) as the size reduction component (Figure 1 (3)) could to some extent be independently investigated. We hereby used the mammalian species assemblage as a proxy for the complete forest animal community since this class consists of (large) vulnerable species that exists at lower average population densities (Damuth 1981), have low reproductive rates (Fenchel 1974), are often targets for subsistence hunters/poachers (Fa et al. 2003; Effiom et al. 2013) and are in general easy to detect or capture. The acquired overview

of these results can possibly contribute to fill the knowledge gap of how both taxonomic and functional biodiversity evolve in fragmented forest habitats and how this information may contribute to predicting the consequences of forest fragmentation in the light of the upcoming environmental issues.

3.2. Objectives

The highly fragmented forest study site located in the Democratic Republic of Congo (Relict Altitude Forest of the Albert Lake Escarpment (RAFALE), at the outer borders of the Congo basin) provided us with an ideal opportunity to investigate how species communities are affected by forest loss processes without being affected by large-scale poaching. By using data from mammal inventories from RAFALE and several other larger, continuous forests across Central Africa, we were able to conduct comparative biodiversity analyses with the use of RAFALE as proxy for isolated and fragmented forests. For the following executed analyses, the inventories of (subsets of) RAFALE, four continuous nature parks across Central Africa (inventories provided by M. Colyn) and the Lopé National Park (Gabon, Lopé NP) with its adjacent forest fragments (inventories copied from Tutin et al. 1997) were used.

Origin of the studied forest fragments (RAFALE)

To place the upcoming findings in the correct context, the chronology of habitat loss in our primary study area will first be explored by comparing the current forest status with the historical forest cover using remotely sensed information and old maps.

Presence forest generalists versus forest specialists (RAFALE)

A full mammalian inventory of RAFALE will be created to score the survival chances of generalists against specialists living in isolated forest remnants.

Loss of species and functional groups and the overall conservation value of forest fragments (RAFALE and 4 Nature Parks)

By comparing the inventories of forest fragments against larger continuous forest, we attempt to visualise what specific species and functions are more susceptible to be lost in the future if fragmentation would occur. We will try to explain the acquired trends and predict the most likely repercussions for ecosystem functioning.

• Relationship taxonomic and functional diversity (RAFALE and 4 Nature Parks) : General

By plotting all available mammalian taxonomic (Species richness) and functional indices (Functional richness, Functional entities, Functional redundancy) against each other, we can visualise how taxonomic and functional diversity behave in relation to one another. This will give us an idea on how much the concept of redundancy can protect the functioning of the environment.

• Taxonomic and functional dissimilarities of continuous forests against forest fragments (RAFALE and 4 Nature Parks)

By means of taxonomic and functional beta diversities, we will try to investigate how different forest fragments are in relation to contiguous forests. We will also gain additional information about the distinction of functional beta diversity into turnover and nestedness.

• Relationship taxonomic and functional diversity (RAFALE and 4 Nature Parks) : Impact of forest area size

By plotting the amount of species and functional entities against their analogous forest surface area, area size will be included as an explanatory factor. Both the full community (savannah animals were included) as the restricted forest community will be investigated to see if the reaction to forest area size differs.

• Relationship taxonomic and functional diversity (RAFALE & Lopé NP) : Distinction between impact of isolation and size reduction during fragmentation

The independent effects of size reduction and isolation on fragmented patches were distinguished by comparing the medium- and large mammal assemblage of RAFALE with fragments surrounding the Lopé Reserve. Both species richness and functional entities, as beta-diversities were compared.

Overall view of the importance of forest fragments in conservation

Our study will give an impression on how influential forest fragments can be in terms of mammal conservation and how resilient the ecosystem remains after a substantial amount of logging. Particularly the function of seed dispersal by mammals and hence the possible plant regeneration will be discussed.

4. MATERIAL & METHODS

4.1. Study sites

4.1.1. RAFALE

4.1.1.1. Today

We conducted the first studies on the biodiversity of the Relict Altitude Forests of the Albert Lake Escarpment (or RAFALE area). It is situated in the North-East part of the Democratic Republic of Congo (Ituri province), bordered by the Albert lake to the East and the Lendu plateau on its western side (Laudisoit et al. 2016, Figure 2). The RAFALE site is circa 40 kilometres (bird's eye, Google Earth Pro) removed from the nearest extensions of the continuous Ituri forest (Congo DR).

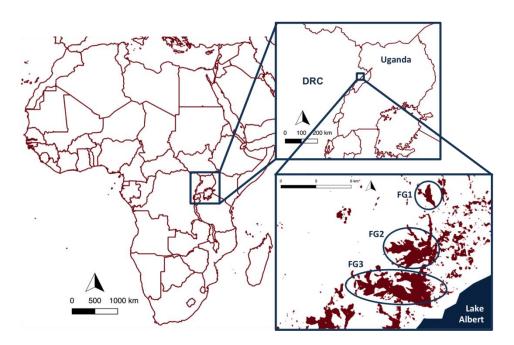


Figure 2 | Situation of the RAFALE study area (Huyghe 2017)

The Lendu plateau is nowadays deforested for the most parts, with agricultural fields and grasslands replacing the natural vegetation. The current forest fragments are most clustered around rapid flowing rivers forming dense riverine forest galleries (800-2000m) (Laudisoit et al. 2016). The forest closest to the small village of Kpandroma was arbitrarily subdivided in

separate blocks; FG1 (smallest fragment, estimated to be 0,96 km² (Huyghe 2017, Figure 2), FG2 and FG3 (both comprising the biggest fragment, estimated to be 17,19 km² (Huyghe 2017, Figure 2).

Between 2010 and 2015 FG1, FG2 and FG3 lost 4,70%, 12,44% and 2,88% respectively of their forest cover. Overall, the 3 forest blocks together lost 6,11% of forest cover over the course of 5 years (2010-2015, Huyghe 2017). By a simple extrapolation of the absolute logged forest surface area (Huyghe 2017) derived from the period 2012-2015, it was found that the three forest blocks of FG1, FG2 and FG3 will have disappeared completely within 89 (2106), 22 (2039) and 119 (2136) years respectively. Without the implementation of conservation measures, it is highly plausible that the logging pressures will keep increasing and that within less than a century RAFALE will no longer exist.

4.1.1.2. Past

Forest blocks FG2 and FG3 became separated between 1995 and 2005 whereas FG1 already became isolated before 1985 (Huyghe 2017, Google Earth Pro). Since the final loss of the corridors between FG2 and FG3 happened quite recent and the shortest distance between both fragments is estimated to be only around 142,29 meter (Huyghe 2017), we considered those two forest blocks as one (FG23).

The RAFALE zone was very well studied by geologists in 1953 what gave us a chance to go back further in time and investigate the original state of these forest fragment. Their priority was given to the area closest to the study site along a band between 2°00'7.55" and 1°50'33.31" north along the Lake Albert shoreline towards the west. These are the oldest available records of aerial pictures from the area. The photographs of the area were scanned for our convenience by the Geology Department of the Royal museum for Central Africa (Tervuren, Belgium).

Multiple small photographs were merged by repeatedly transferring distances between two maps (georeferencing) with the use of ArcGIS software. Since some photographs were not taken fully perpendicular to the earth surface, the final map was partly contorted.

4.1.2. Other used sites

We also used unpublished mammal species inventories of four Central African forests (Figure 3, coloured asterisks) provided by Marc Colyn (Université de Rennes, Paimpont, France). A medium- and large mammalian inventory of Lopé National Park (Figure 3, white asterisk) was taken from Tutin et al. (1997). All supplementary sites are situated within the dense Congolese forest belt which is visualised in Figure 3 (right).

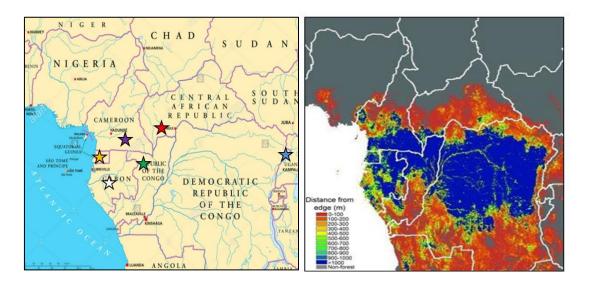


Figure 3| **Visual representation of the locations of the study sites (left):** RAFALE (Congo-Kinshasa, blue asterisk); Ngotto Forest (Central African Republic, red); Odzala-Kokoua National Park (Congo-Brazzaville, green); Dja Wild Reserve (Cameroon, purple); Monte Alén National Park (Equatorial Guinea, yellow); Lopé National Park (Gabon, white); blank map: alamy.com; **The size of forest fragmentation in the Congo basin (right):** Mean distances to forest edge (Haddad et al. 2015).

4.2. RAFALE's mammal inventory

To produce a comprehensive mammalian inventory of these forest fragments (Appendix 1 Table 1), we employed several complementary methods: (1) identification of animals through direct (visual) observation, (2) observations using camera traps and (3) DNA extracted from faeces and (4) tissue samples of small mammals (shrews, rodents, bats, ..).

4.2.1. Data collection during fieldwork

Fieldwork was primarily carried out using the transect methodology. A chosen straight line, containing as much biological variation as possible, was converted into real coordinates with the use of Google Earth Pro and GIS software (Laudisoit et al. 2016). In the field, this line was constructed by clearing the vegetation with machetes and setting identification points after every 50 meters using rope and sticks. With a GPS we identified the exact starting and end point of the transect while we used a compass to keep walking a straight line at all times. Next, we noted various indicators of the presence of animals (e.g. visual sightings, holes, prints, hairs, faeces ..) while walking the transect. In total there were five transects opened, two in FG1, two in FG2 and one in FG3 (visualised by Huyghe 2017).

Along each transect, observations and sampling was done with the assistance of local guides. By doing the data collection in a standardised manner, the observations could possibly be used in later studies for estimations of densities.

4.2.1.1. Direct visual observations

While walking along the transect, direct observations of mammals were recorded on field sheets enquiring the location along the transect, the animals' (local) name, number of individuals, distance and angle of observation, vegetation type, canopy/understory openness and visibility whereas the exact location was registered by GPS. In these and all other circumstances encountering mammals, efforts were made to obtain clear photographs and/or video recordings.

4.2.1.2. Camera traps

The Bushnell camera traps (27 pieces) were programmed in hybrid mode with different sensitivity settings depending on where they were placed (a number of consecutive images per trigger, 1080p video resolution, a picture resolution of 8 to 14 megapixels, with or without field scan) and systematic printing of the trap number, date and time (Laudisoit et al. 2016). These were installed from March-August 2016 plus April 2017 and had the primary aim to observe primates and other bigger mammal species. The camera traps were placed throughout the area in a opportunistically way, most of them in vicinity to the transects, both on the ground and up in the trees.

4.2.1.3. Indirect evidence

For indirect observations (e.g. holes, prints, hairs,...), the location along the transect, the animals' (local) name, vegetation type, canopy/understory openness and visibility were written down whereas the exact location was once again registered by GPS. For indirect observations other than hairs and faeces, there was a limit set to the animal traces that would be incorporated into the survey (10 meter on each side of the trail). This decision was made to still be able to calculate population densities if wanted. Photographs were taken whenever possible.

In contrast, faeces were always collected upon finding (both the faeces detected while walking on or off the transect). These were also photographed together with their identification number, measured and weighted if this was possible.

Furthermore, we also studied hunting trophies kept by the local people. Little tissue pieces were dissected and preserved. Occasionally hairs were also collected from chimpanzee nests after climbing up trees by one of the team members or local guides.

4.2.1.4. Captures of small ground dwelling mammals and bats

Two different traps were used to enhance our chances of capturing various kinds of species. Sherman traps (Figure 4, left) were primarily used to capture small rodents. These were set on a line every 5 meters in the forest (along the first 200m of the transect, +/- 40 pieces) and in the fallow lands at the ecotone between the cultivated fields and the forest (+/- 40 pieces). A second type of traps, Pitfall traps (i.e. buckets placed into the ground bordered by a plastic fence; Figure 4, right), were used to trap other species ranging from shrews to toads, other

amphibians or even reptiles. In all three forest blocks (FG1/FG2/FG3), 4 consecutive days of actual capturing was followed by checking the trap on the morning of the next day, preceding the dissections from that day. Sherman traps were therefore baited every other day with palm nut flakes or a mixture based on peanut butter. At every forest block, maximum one male and one female of each species (based upon field identifications) were euthanised.



Figure 4 | Methods trapping: Sherman traps (left); Pitfall traps (right)

The actual dissections involved making samples of the heart, lungs, kidneys, spleen and liver. We preserved the dissected organs in ethanol and all tissues were stored with their identification numbers. The same procedure was applied during other missions where bats were captured and dissected (Mande 2016).

Before the actual dissection, the collection of ectoparasites (mites, thicks, lice, flees) and the registration of the measurements of the total length, the tail, the ear, the foot and the weight of each animal were completed. Preservation of the organ samples and possible endoparasites were also done in RNA later (since this is better for the preservation of RNA viruses). Found ectoparasites and endoparasites were also stored in alcohol. A few tissue samples (spleen, lungs) were also stored in Cary Blair (most suitable for preservation of microbiological specimens) if there were pathological signs (i.e. white marks) visible. All these additional data and samples can possibly be used in later (disease-related) studies.

4.2.2. Species identification through expertise

The pictures and camera footage taken by one of the field team members or recorded on one of the camera traps, were later identified upon species level. Wherever possible, this was simply done by consulting the internet or African field guides (Kingdon 1977, Kingdon 1997). For the pangolin and carnivore footage however, Dr Marc Colyn (Station Biologique de Paimpont, Université de Rennes, France) was repeatedly consulted.

4.2.3. Species identification through DNA barcoding

The previously mentioned collected faeces, hunting trophies and organ samples (originating from the dissections) were processed in the laboratory in order to obtain DNA sequences that later were used to identify the particular (sub)species.

4.2.3.1. DNA extraction

Tissue samples were processed with the standard protocol for human or animal tissue and cultured cells (NucleoSpin® Tissue). With this method genomic DNA can be prepared from 25 mg animal tissue when it is cut into small pieces. Lysis is achieved by incubation of the sample material in a proteinase K / Buffer T1 solution. Appropriate conditions for DNA binding to the silica membrane in the NucleoSpin® Tissue Columns are achieved by the addition of chaotropic salts (B3 buffer) and ethanol to the lysate. The binding process is reversible and specific to nucleic acids. Contaminations are removed by subsequent washing with two different buffers, namely buffer BW and buffer B5. The silica membrane is dried with an additional spin in the centrifuge. Pure genomic DNA is finally eluted under low ionic strength conditions in RNAsefree water.

Faeces samples were processed with the extracting kit 'Genomic DNA from Soil (NucleoSpin® Soil)'. The sample material is resuspended in Lysis Buffer SL1 or SL2, supplemented with the Enhancer SX, and mechanically disrupted using ceramic beads. Proteins and PCR inhibitors are precipitated with Lysis Buffer SL3 and subsequently pelleted by centrifugation together with the ceramic beads and undissolved sample material. The supernatant is taken off and cleared by passing it through a NucleoSpin® Inhibitor Removal

Column. DNA binding conditions are then adjusted by addition of Binding Buffer SB to the flowthrough and the lysate is loaded onto a NucleoSpin® Soil Column. Residual humic substances, especially humic acids, and other PCR inhibitors are removed by efficient washing with Binding Buffer SB and Wash Buffers SW1 / SW2. After a drying step, ready-to-use DNA can be eluted with Elution Buffer SE (5 mM Tris/ HCl, pH 8.5).

4.2.3.2. Polymerase-chain reaction (PCR)

First, all needed liquids and DNA extractions had to be defrosted and needed to be vortexed vigorously (except Taqpolymerase). Then the PCR Mastermix was prepared according to the following applicable table (Table 1).

Table 1 PCR Mastermix	proportions for	the genes	Cytochrome B	and 16S riboso	mal RNA
-----------------------	-----------------	-----------	--------------	----------------	---------

1 reaction (μl)	Cyt B	16S
Buffer	3	1
$MgCl_2$	1,5	n/a
dNTPs 10mM	0,3	0,2
Primer 1	0,3	0,4
Primer 2	0,3	0,4
Taqpolymerase/Ferm	0,2	0,1
ddH_2O	7,9	6,9
Master Mix	13,5	9
DNA	1,5	1
PCR Mix	15	10

All species were identified based upon the amplification of the Cytochrome B (H15915 5'-ACCTCCGATCTYCGGATTACAAGAC-3' (10mM) and L14723 5'-ACCAATGACATGAAAAATCATCGTT-3', (10mM)) and/or the 16S ribosomal gen (Hm 5'-AGATCACGTAGGACTTTAAT-3' and ar-L 5'-CGCCTGTTTAACAAAAACAT-3' (New England Biolab)). Amplifications were performed with a Professional ThermoCycler machine by the following procedure: (CytB) a first cycle of an initial denaturation at 94°C for 5 min, then 35 cycles with denaturation at 94°C for 30", annealing at 52°C for 30", and extension at 72°C for 1 minute 30". These steps were followed by a 5 min extension at 72°C. For 16S, the two extension steps were changed to respectively 30 seconds and 10 minutes.

4.2.3.3. Gel electrophoresis

The gel was prepared with 1mg agarose, 75 ml TBE 1x and 1 µl redgel. PCR products with colouring (CytB) can directly be transferred into the solidified gel. Other PCR products (16S)

need to be mixed with bluegel before loading them. A ladder of 1000bp is needed to interpret the length of each DNA fragment. Subsequently, the gel is submerged in TBE 1x and the gel electrophoresis is run on 100 volts for 30 minutes. After this, the PCR products on the gel were visualised using a bio imaging system (Gene Flash, Syngene).

4.2.3.4. Preparation for VIB

All the bands visible in the previous step and thus showing proliferation of the DNA fragment, were send to the VIB (Vlaams Instituut voor Biotechnologie, Antwerp). Primers were diluted with RNAse free water (1:1) and PCR products were diluted according to the clarity of the visual bands with RNAse free water (1:1 or 3:7 or 1:0), so that the end volume was always $10 \, \mu l$.

4.2.3.5. Blasting of DNA sequences

The received ab1.- extensions files were loaded into Geneious (Kearse et al. 2012). This program is a powerful tool for viewing, managing and manipulating molecular sequence data. The forward and reverse sequences were first aligned where after the software highlights the bases that are not clearly distinct from each other. These uncertainties were manually selected based upon which colour signal was the strongest. The final sequence orders were all pasted into the blast application of NCBI (National Centre for Biotechnology Information). This site functions as a database of known genetic sequences and can search for the highest matching percentages with any input-sequence.

4.3. Biodiversity analyses based upon all available inventories

In total, six independent regions (4.1.2.) and nineteen different mammal (sub)inventories were used in this section.

- o The obtained RAFALE data gave rise to three complete mammal inventories (5.2.4.): one on the diversity of FG1, one on the diversity of the combined areas of FG2 and FG3 (treated as one continuous fragment, see Huyghe 2017 for arguments) and one with the combined diversity (union of FG1, FG2 and FG3).
 The three complete species inventories (used in 5.2.4.) were then confined to contain
 - The three complete species inventories (used in 5.2.4.) were then confined to contain only forest inhabitants (used in 5.2.2., 5.2.3 and 5.2.4.) and to contain only medium-and large-sized forest mammals (used in 5.2.5., so that the comparison with the data from Tutin et al. 1997 was feasible).
- o Four complete mammal inventories from independent Central African forests were provided by Dr M. Colyn. The four complete inventories (used in 5.2.4.) were then confined to contain only forest inhabitants (used in 5.2.2., 5.2.3 and 5.2.4.).
- Two mammal inventories were extracted from Tutin et al. 1997 (5.2.5): one of Lopé Natural Park and one of the adjacent forest fragments, containing only medium and large mammals.

4.3.1. Selection of functional traits

Five categorical traits - which we believe have a strong correlation with a species actual functional attribute in the ecosystem - were selected for each recorded species: body size, locomotion mode, primary food source, activity pattern (Magioli et al 2016) and sociality. Sociality was also included since behavioural traits may influence how species acquire resources from the environment (Flynn et al. 2009). For every present mammal species, the most relevant option for every category (i.e. related to foraging, Kingdon et al. 2003) was placed into a **trait matrix** (**Figure 7 (1)**, Appendix 2 Table 1, Appendix 3 Table 1). For the **assemblage matrix** (**Figure 7 (2)**, Appendix 2 Table 2, Appendix 3 Table 2), we only worked with presence/absence data since the accurate estimation of densities was not part of the focus of this thesis.

4.3.2. Functional diversity and the position in multidimensional space

The composed ecological trait matrix is converted into a distance matrix by means of the Gower's distance (i.e. method for working with categorical traits). This distance matrix will contain the computed functional distances between all possible species pairs. With the use of Principal Coordinates Analysis (PCoA, i.e. method for working with dissimilarities), this information is converted into several multiple functional spaces (Maire et al. 2015, 2 until 10 dimensions). For every dimension size, the mean squared-deviation between the initial functional distance and the standardised distance in functional space is calculated (Appendix 4 Figure 1). The amount of dimensions that has the lowest value for this calculation and thus fits best, should be selected. The corresponding species coordinates are then used in the following steps. That the distance matrix was based upon functional distances in the first place (Figure 7 (3)) leads to axes corresponding to relevant combinations of the selected ecological traits.

The species coordinates (Appendix 4 Table 1) extracted from the best suitable multidimensional space, can together with the trait matrix lead to the assessment of complementary functional diversity indices (Mouillot et al. 2013, **diversity matrix**, **Figure 7** (4)). As a result of not working with absolute density estimates, the only useful index that can be used for our research is functional richness (i.e. the proportion of functional space filled by species communities; Appendix 2 Table 3,4; Appendix 3 Table 3). The R output also illustrates how changes in species composition can modify the functional richness by depicting changes in the convex surface gathering all the species belonging to the community (Appendix 4 Table 2).

4.3.3. Comparison of taxonomic and functional β -diversity

Beta diversity is the ratio between regional (γ -diversity) and local (α -diversity) species diversity. This concept is based on the assumption that the total species diversity in a landscape (γ) is determined by two different things: the mean species diversity at the habitat level (α) and the differentiation among habitats (β). Beta diversity thus describes the variation in species composition between sites and can be used to infer why different species occupy different parts of habitat (Whittaker 1960). β -diversity can be investigated from either a **species identity or a functional-trait point of view**. We aim to investigate how these two

aspects of beta diversity vary between forest patches of different sizes. The results should be interpreted as a relative index of dissimilarity that go from 0 (all communities identical) to unity (all communities distinct) (Appendix 2 table 5; Appendix 3 table 4).

$$\mathbf{a}$$

$${}^{1}D_{\beta} = {}^{1}D_{\gamma}/{}^{1}D_{\alpha}$$

$${}^{1}D_{\alpha} = \exp\left[-w_{1}\sum_{i=1}^{S}\left(p_{i1}\ln p_{i1}\right) + -w_{2}\sum_{i=1}^{S}\left(p_{i2}\ln p_{i2}\right) + \cdots\right]$$

$$\mathbf{c}$$

$${}^{1}D_{\gamma} = \exp\left[\sum_{i=1}^{S}\left(-w_{1}p_{i1} + w_{2}p_{i2} + \cdots\right)\right]$$

$$\mathbf{d}$$

$${}^{1}D_{\gamma} = \exp\left[\sum_{i=1}^{S}\left(-w_{1}p_{i1} + w_{2}p_{i2} + \cdots\right)\right]$$

$$\mathbf{d}$$

$${}^{1}D_{\gamma} = \exp\left[\sum_{i=1}^{S}\left(-w_{1}p_{i1} + w_{2}p_{i2} + \cdots\right)\right]$$

$$\mathsf{d}$$

$$\mathsf{d$$

Figure 5| Formulas needed to compute the taxonomic beta-diversity where (a) and (b) are needed to compute (c) which then later can be transformed to (d). The used abbreviations are the proportion of individuals found in species i (p_i) , total number of species in the community (S) and the statistical weight of Community j (w_j , usually the number of individuals in Community j divided by the total number of individuals in the region). Copied from Jost (2007).

The taxonomic β-diversity (Figure 5, Figure 7 (2)) for every patch is obtained by the function to compute beta-diversity based on the *Shannon entropy diversity index* (proposed by Jost 2007; Villéger et al. 2012). The Shannon index is a diversity index, taking into account the number of individuals as well as number of taxa.

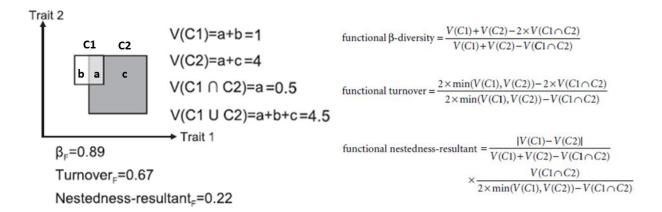


Figure 6 Conceptual framework for the decomposition of functional b-diversity: Classical representation of taxonomic b-diversity for a pair of two communities (C1 and C2) using a Venn diagram (for graphical simplicity, polygons instead of ellipses are used). a is the number of species shared by the two communities and b and c are the number of species present only in C1 and C2, respectively. This representation can be directly transposed to functional beta-diversity by considering the convex hull shaping the two communities in a functional space defined by functional axes (dashed arrows, only two for graphical convenience). Correspondences between a, b, c and the volumes of convex hulls, their intersection and union are given on the middle. The used formulas to compute the functional beta-diversity and its two components are given on the right. (copied from Villéger et al. 2013)

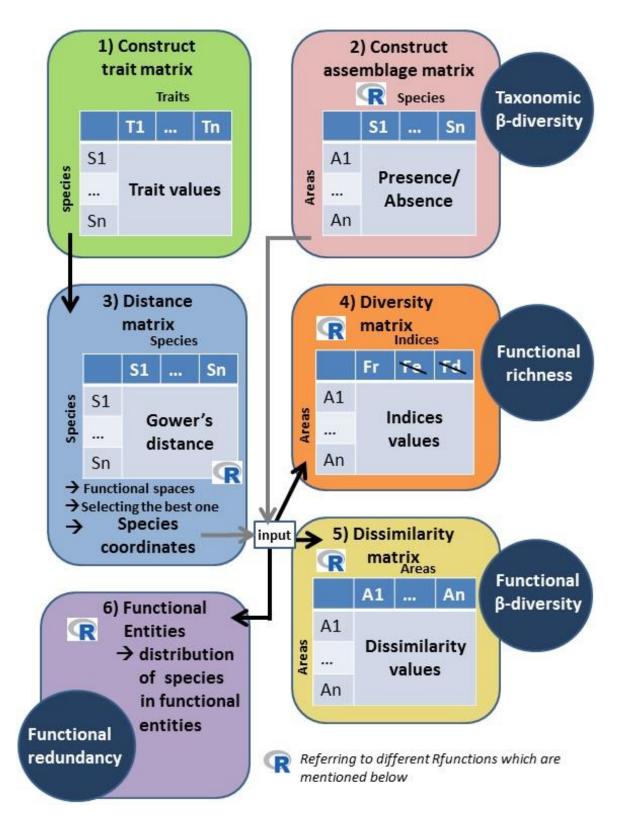


Figure 7| Schematic overview of the different steps taken in Rstudio to compute the different outputs (circles). Legend: black arrows: conversion process from one box to another; grey arrows: 2 boxes are needed as input for the last 3 boxes; circles: the output that can be extracted from the content of the adjacent box; R functions: betaH (2), quality_func_space (3), plot_func_space (3), multidimFD (4), multidimFbetaD (5), species_to_FE (6) and FE_metrics (6)

The species coordinates (only a maximum of 4 dimensions is used now) and the assemblage matrix can (Villéger et al. 2012) be converted into a **dissimilarity matrix** (**Figure 7 (5)**). This matrix leads to an assessment of the functional overlap of the different communities (**Functional \beta-diversity**) with the use of the above mentioned formulas (Figure 6). It can be partitioned into two distinct patterns (Villéger et. al 2013): turnover (traits differ from one another) and nestedness (present traits are a subset in comparison with the other patch) (Appendix 1 Table 5; Appendix 3 Table 5).

4.3.4. Functional entities, redundancy and vulnerability

First, the amount of traits per site (**Figure 7** (**2,3**)) are used to see how many different **functional entities** (**FE**, i.e. unique combinations of functional traits) in total are present in the landscape and how many species are grouped into each of them (n_i). With these values, the following ratios can then be calculated: **Functional redundancy** (FR), Functional vulnerability (FV) and Functional Over-redundancy (FOR) (**Figure 7** (**6**), Figure 8, Mouillot et al. 2014) (Appendix 2 Table 3,4; Appendix 3 Table 3).

$$FR = \frac{\sum_{i=1}^{FE} n_i}{FE} = \frac{S}{FE}$$

$$FV = \frac{FE - \sum_{i=1}^{FE} \min(n_i - 1, 1)}{FE}$$

$$FOR = \frac{\sum_{i=1}^{FE} \left[\max(n_i, FR) - FR \right]}{S}$$

Figure 8 Ratios used to calculate Functional redundancy (FR), Functional vulnerability (FV) and Functional Over-redundancy (FOR) with functional entities (FE), total species richness (S) and number of individuals or amount (e.g. biomass) of each species (the ith species) (n_i) (Copied from Mouillot et al. 2014)

Remark : I participated in the third and most intensive (in terms of collecting new material) mission to the area in Augustus 2016. Other missions were held in March 2016, June 2016 and April-May 2017. Tissue, skin and faeces samples and results from the camera traps were available and included in this study.

5. RESULTS

5.1. RAFALE

5.1.1. Historical habitat loss

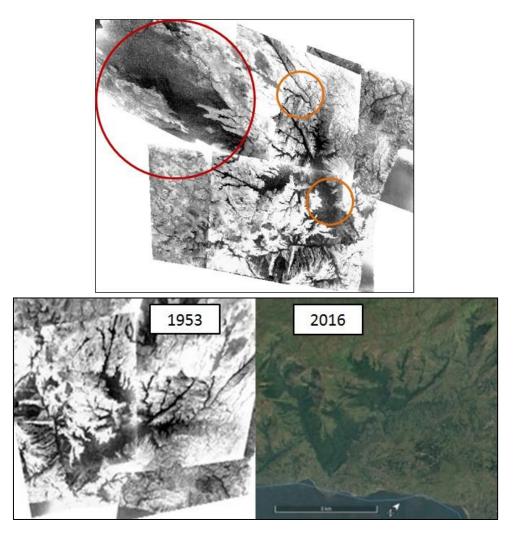


Figure 9| Close-up of the RAFALE are in 1953 (upper graph, individual maps from Royal Museum for Central Africa) with remarkable extra vegetation marked; Comparison of RAFALE's vegetation (lower graph): 1953 (left) vs 2016 (right, Huyghe 2017).

The maps clearly illustrates that the greatest part of RAFALE's isolation already occurred before 1953. Besides one large visible extra block of forest (Figure 9, red circle) and additional corridors between the forest blocks of FG1, FG2 and FG3 (Figure 9, orange circles), the site looked surprisingly similar to the current situation. Though, this does not

mean that the current deforestation rates are in any way negligible (Section 4.1.1.1. and 4.1.1.2.).

5.1.2. Mammal inventory and species identities

The provisional full mammalian inventory constitutes of 54 species with **9 Primates** (1 Hominidae, 7 Cercopithecidae, 1 Galagidae), **9 Carnivora** (1 Canidae, 1 Felidae, 5 Viverridae, 1 Nandiniidae, 1 Herpestidae), **1 Afrosoricida** (1 Tenrecidae), **1 Artiodactyla** (1 Bovidae), **1 Hyracoidea**, **2 Pholidota**, **18 Rodentia** (including *Hystrix cristata*, *Cricetomys emini*, *Thryonomys swinderianus*, 3 squirrels and 12 small rodent species), **6 Eulipotyphla** and **7 Chiroptera**. Every detected mammal species except the Johnston's mangabey (*Lophocebus johnstoni*; Blom et al. 2005; Kingdon et al. 2003) was found to be adapted to logging and/or artificial resources (Appendix 1 Table 1).

This enumeration includes forest mammals, savannah inhabitants and species that occur in a wide range of habitats. This distinction was however not always clear cut. If forests were not mentioned among a mammal's habitat preferences (Kingdon et al. 2003), the species was considered a savannah specialist and thus not incorporated in further forest-only inventories. An overview of the individual species names and used identification method(s) can be consulted in appendix 1 as well.

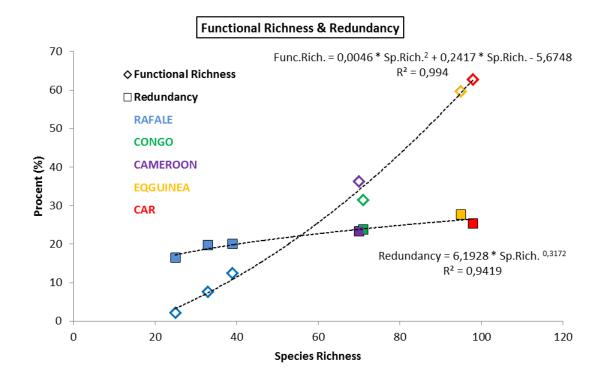
We also feel obliged to mention that the local population stated the current presence of a leopard and giant pangolins and the historical presence of the red river hog (unconfirmed tooth). We were however unable to confirm these claims so that none of these animals are included in the analyses.

5.2. Central African trends

5.2.1. Loss of species and functional groups in forest fragments

Based upon the comparison of the RAFALE inventory against the more continuous forests (Appendix 2 Table 2), it is reasonable to state that the functional groups of top predators and larger herbivores are the most prominent missing groups in the RAFALE area. Frugivorous mammals on the contrary are relatively well represented (i.e. presence of primates against almost complete absence of duikers).

5.2.2. General relationship between taxonomic and functional diversity



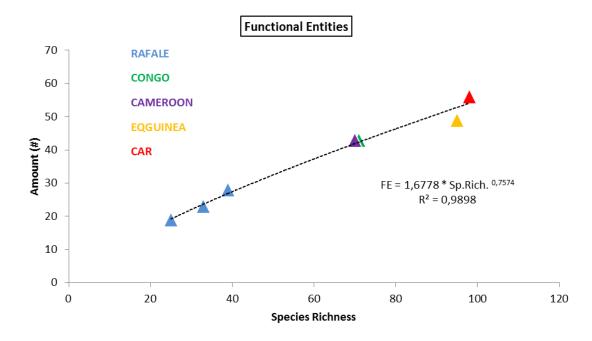


Figure 10| Relationship taxonomic and functional diversity of small forest fragments (RAFALE) and large continuous forests (situated in four West African countries): Functional richness and redundancy (upper graph); Amount of functional entities (lower Graph)

The two graphs above show that in general functional and taxonomic diversity follow the same trends: when species richness increases, the amount of unique functional entities will

too. However this does not happen in the same magnitude what makes that the increase of amount of FE is must higher than that of FR. When the initial species richness is very low, almost every additional species leads to a new functional role (i.e. unique set of functional traits). How higher the species richness, how less likely it becomes that a new species will add an entirely new function to the ecosystem and how more likely that it will contribute to species redundancy (Figure 10).

5.2.3. Beta-diversities **β-diversity** 100 Taxonomical 80 ■ Functional : Turn over Functional: Nestedness Percentage (%) 60 40 20 Ca-Co Ca-Car Co-Car Car-Eq Co-Eq Ca-Eq Car-Rf Eq-Rf Ca-Rf Co-Rf

Figure 11 β -diversity ranged according to increasing taxonomic beta-diversity values with Cameroon (Ca), Congo-Brazzaville (Co), Central African Republic (Car), Equatorial-Guinea (Eq), RAFALE (Rf, three patches summarised as one)

Comparison between different forests

The four highest values for taxonomic (74-82%) and functional (38-48%) beta-diversity are all obtained when the forest fragments of RAFALE are compared to the other continuous forests (Appendix 2 Table 5). The difference in available functions is here almost totally explained by the nestedness component (Appendix 2 Table 5; 80-100%). All larger forests seem to differ from one another in the same degree. However when the comparison between a large forest and a forest fragment is made, these values tend to (almost) double.

5.2.4. Species and Functional entity richness as a function of forest size

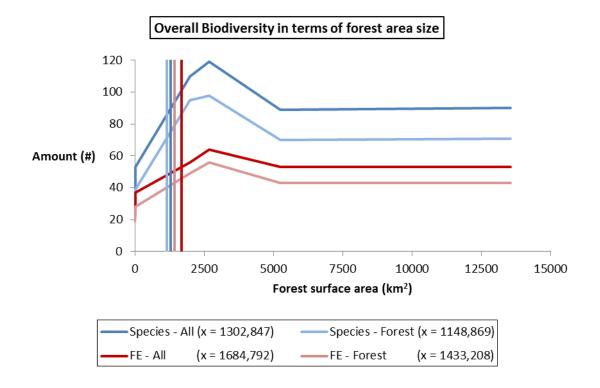


Figure 12 Species and Functional entity richness in function of the forest surface area of the used national parks/forest fragments: The vertical lines (estimated threshold values) show the minimal estimated forest surface areas that hold an equal diversity as the two largest forests of Cameroon and Congo (the beginning of the peak).

The graphs that represent the full mammalian assemblage (Figure 12 darker coloured, forest and savannah) and the subset of the forest assemblage (Figure 12 lighter coloured) show the same trends: i.e. an increase of species and functional entities (set of individual functions) with area size until the peak is reached around 2683 km² (Central African Republic) after which it declines to stabilise at a lower value for the largest forest area sizes. Medium-sized forests thus contain the highest value of biodiversity in terms of the total amount of present species/functions.

The number of species is always 32-94% higher than the sum of functional entities (Appendix 2 Table 3,4). The range between 1148,869 km² - 1433,208 km² (both for the forest species community only) and 2683 km² (the peak) holds the roughly estimated smallest possible area sizes with the same or a higher proportion of recorded species and functional entities as the two largest forest reserves in our study (values of Congo used to estimate the lowest mentioned value, calculated method in Appendix 2 Table 6).

5.2.5. RAFALE versus Lopé NP for medium- and large mammalian assemblages

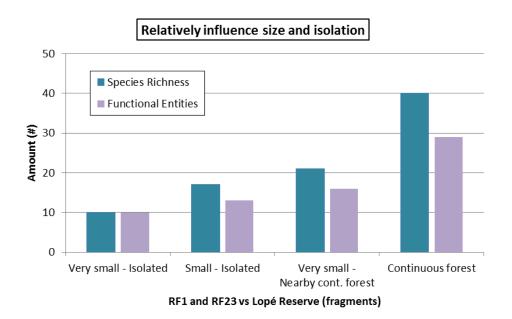


Figure 13 | Species and FE richness in terms of isolation and forest area size (the degree of fragmentation): with 'Very small - Isolated': fragment = 0,96 km² (RF1) and approx. 40 km away from continuous forest (Google Earth Pro), 'Small - Isolated': fragment = 17,19 km² (RF23) and approx. 40 km away from continuous forest (Google Earth Pro), 'Very small - Nearby continuous forest' fragments = 0,004-0,11 km² (Lopé forest fragments) and max. 450m away from continuous forest and 'Continuous forest' = 4200km² (Lopé forest Reserve) (Tutin et al. 1997).

The fragments surrounding the continuous forest are between 1 and 3 magnitudes smaller in size than the RAFALE fragments but still they perform better on diversity richness. Though, the difference in general richness between these fragments and RF23 becomes really small.

β-diversity with the Lopé Reserve

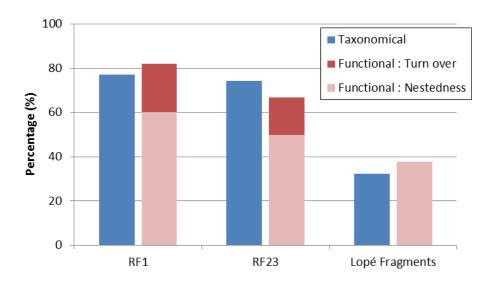


Figure 14| β-diversity of three areas compared to the Lopé Reserve with two independent isolated fragments (RF1: 0.96 km^2 , FG23: 17.19 km^2) and the fragments surrounding the continuous forest (0.004- 0.11 km^2).

Figure 14 clearly shows that the biodiversity of the continuous forest is much more similar to that of its adjacent fragments than to the richness of the independent forest fragments. The dissimilarity in functions is totally explained by nestedness in the Lopé fragments while turnover still explains a part of the functional beta-diversity with the RAFALE fragments.

6. DISCUSSION

6.1. RAFALE

6.1.1. Forest status

If we assume that the RAFALE forest area was once fully forested, our results suggest that the majority of its deforestation already occurred before 1953 (Figure 9). We however emphasise that the exact original state of the forest fragments could not be determined what makes that the RAFALE site could either have been a highly fragmented forest area all along or that severe fragmentation happened before 1953 (either by logging or natural events). Either way, a least one corridor must have existed between RAFALE and the nearest continuous forest (40 km away) to have enabled the animals to migrate towards these forest fragments.

Besides one large visible extra block of forest and additional corridors between the fragments, the site looks surprisingly similar to the current situation. The present forest fragments have thus already been isolated and fragmented for at least half a century what means that all species/populations in the current forest fragments must have survived at least several decades of increasing isolation.

The presence of vegetation corridors between the largest forest blocks in 1953 were probably used by many animals and so helped to enlarge their surviving chances. The relatively recent disappearance of these corridors (Huyghe 2017, Section 4.1.1.2.) together with the high current deforestation rates (Huyghe 2017, Section 4.1.1.1.) urges the need for good conservation measures in the RAFALE forest area.

6.1.2. Presence generalists versus specialists and overall conservation value of forest fragments

Almost all of the recorded mammal species are opportunistic generalists and thus capable of exploiting artificial food resources and/or adjusted to deforested habitats such as savannah, woodland, forest edge, cultivated and rural environments (Appendix 1 Table 1). The release

from interspecific competition for food resources with other, more heavily hunted/sensitive species or predation pressure (Rist et al. 2009) could contribute in explaining the presence of the relatively rich mammal fauna in these forest fragments. This indicates that the surrounding agricultural fields or grasslands made it impossible for forest specialists to survive in (or to migrate to) the RAFALE forests and favour the species that are capable to exploit the food resources from the surrounding area (agricultural crops). This leads to a human-wildlife conflict where the local people defend their crops against raiding while animals are trying to cope with the low availability of food sources in their small-scaled habitat. The effects of habitat destruction are thus selective and will have contrasting impacts on species with different ecological/habitat requirements (confirming previous statements of Ceballos & Ehrlich 2002 and Fahrig 2003). In conclusion, loss of forest will be detrimental to animals who are totally dependent upon the forest for their survival (forest specialists) while forests generalists experience an ecological advantage by benefitting from an additional food resource and the lack of competition with forest specialists.

Outside the true RAFALE forest, we also recorded several typical savannah species (*Canis adustus; Felis serval* (unconfirmed); *Xerus sp.* (unconfirmed); *Genetta angolensis* (unconfirmed); *Heterohyrax brucei* (unconfirmed), ..). Although we excluded these taxa from the majority of the analyses, these species contribute to the overall biodiversity of the RAFALE area.

6.1.2.1. Primates

The mammalian diversity of the RAFALE area is mainly noteworthy in terms of primate species (and pangolin species) presence. We confirmed 9 primate species in the whole RAFALE area (all sampling sites), including an endangered Chimpanzee and endangered Red Colobus monkey population (cfr: the Kibale National Park (KNP) harbours 13 (Onderdonk & Chapman 2000; Weisenseel et al. 1993), an extension of RAFALE's 9 species). The fact that the KNP comprises about 766 km² while the surface area of FG1 and FG23 are estimated to be 0,96 km² and 17,19 km² (Huyghe 2017) respectively, it is clear to say that these primate species can withstand severe habitat fragmentation. In order to live in fragments, it has been shown in some primates (Onderdonk & Chapman 2000, Tutin et al. 1997) that flexibility in group size, home size range and diet (artificial food resources and other plant species) can occur. In forest fragments, the advantage of living in large groups (i.e. protection against large predators) largely disappears (Onderdonk & Chapman 2000) since there are fewer predators

in these habitats. Therefore, it becomes more beneficial to roam in smaller groups whereby the individual foraging efficiency increases (the ecological constraints model) and large home ranges are no longer beneficial (Onderdonk & Chapman 2000). The minimum recorded home range sizes of our monkey species (except *P. anubis*) are indeed all lower than the area size of the smallest forest RAFALE fragment in which they occur (Onderdonk & Chapman 2000, Harrison 1983). The habitat size requirements of baboons and chimpanzees are not fulfilled (in the smallest fragment, Rowell 1966; Onderdonk & Chapman 2000) but these species probably solve this problem by exploiting the surrounding grasslands/croplands and (until quite recently, relates to FG1) by being able to move between patches (Onderdonk & Chapman 2000). Flexibility in primate diet can be seen as the fact that they do not necessarily depend on food from forest trees alone, but that they can supplement their diets by raiding crops in neighbouring farmlands (Naughton-Treves 1996). Being capable of using many different plant species also contributes to dietary flexibility (e.g. *Colobus guereza*, Onderdonk & Chapman 2000).

Blanco & Wallert (2013) suggested that in the absence of hunting, mixed agroforest systems may be important for primate conservation. Moreover, they highlighted that research of primate responses to different land-use systems are needed to make informed decisions on mixed landscape management and primate conservation. Our study not only confirms that disturbed forest fragments can be valuable for the survival of primate species but reinforces them in the way that our study area does not include any nearby continuous forest serving as a source patch (isolation confirmed since 1953). The presence of the crested mangabey (Lophocebus johnstonii, in the biggest fragment) is remarkable since this species rarely forages on open grasslands and swamps adjacent to closed canopy forest (Oluput 2000 personal observations). This may imply that they cannot rely on the abundant food sources outside the forest fragment. Additionally, mangabeys are also known to be sensitive to human disturbance (i.e. presence of villages, secondary roads, human passage and hunting pressure; Blom et al. 2005). Their presence in RAFALE could perhaps best be explained by the fact that this species has relatively little burden from the local people since traditional hunting techniques (i.e. absence of fire weapons) are not ideal for primate hunting and the possibility of extensive overlap between home ranges of multiple non-territorial groups (IUCN 2008). Some of their preferred fruit species (false nutmeg (Pycanthus) and dwarf dates (Phoenix) were also recorded for the RAFALE area (Huyghe 2017) what could help in clarifying their presence/survival (IUCN 2008).

6.1.2.2. Non-primates

The absence of non-primate forest specialists in the RAFALE forest fragments (Appendix 1) may again be best explained by their inability to exploit the food sources from the surrounding agricultural fields and their preference for intact forests. The impact of deforestation on non-primate mammals also differs according to the nature of the surrounding landscape. High densities of non-primate mammals in the patches around Lopé Reserve (Gabon, Tutin et al. 1997) stand in contrast to the virtual absence of non-primate mammals in the Kibale patches (Uganda, Onderdonk & Chapman 2000). This discrepancy between these two sites were ascribed (Onderdonk & Chapman 2000) to the intensive land use of the surrounding area in Kibale, while the surrounding area in Lopé is uninhabited. Species that are particularly sensitive to the presence of humans and their activities (grazing areas), are therefore absent from the forest fragments at Kibale. Furthermore, the fact that the process of forest fragmentation in Lopé is assumed to be the result of a gradual transformation due to climatic change (now maintained by fire, Onderdonk & Chapman 2000), may have allowed some primate and other mammal species to adapt to their current environment.

These two additional explanations could indicate that the landscape surrounding the RAFALE patches is characterised by human occupation (Huyghe 2017) which may have resulted in the disappearance of forest habitat specialists, and the persistence of opportunistic species (generalists). Although we are unable to confirm this evolutionary scenario, we presume that it is likely that the deforestation process that resulted in the current RAFALE forest fragments was not a result of a series of natural events. This assumption was based upon the many scattered forest fragments between RAFALE and Ituri forest, the proximity of many gold-mining companies, (globalforestwatch) and the fact that the main (gold) trade road between Bunia (biggest Congolese city nearby) and the neighbouring countries of Uganda and South-Sudan crosses in between RAFALE and the Ituri forest (Cuvelier 2010).

6.2. Biodiversity changes through forest loss

6.2.1. Species and function loss and their consequences for ecosystem functioning

The depletion of the mammalian species diversity is clearly visible throughout all orders except the primates and pangolins (Appendix 1, 2). In comparison with other Afrotropical forests, the most important functional groups that are absent from RAFALE, are the top predators, (large) herbivores and frugivorous ungulates. Frugivorous primates however are remarkably abundant (6.1.2.1.).

Carnivores as typical top predators seem to have a body size related response to habitat disturbance (Msuha et al. 2012) in comparison with non-carnivores. This can be explained by the fact that species of higher trophic levels have even lower population densities and larger home ranges than non-carnivore species of the same size (Jetz et al 2004, Carbone et al. 2005). This probably explains why (large) carnivores are among the first functional groups to disappear when forest become smaller. The disappearance of top predators in these habitats sets a series of changes in motion. Without niche competition with the bigger and more vulnerable carnivores, **smaller and/or more generalistic carnivores** (e.g. genet cats) can persist. The disappearance of large predators should normally cause **an increased abundance of herbivore species** (Huntly 1991), but our results in the RAFALE area do not underpin this hypothesis.

Herbivores most probably disappeared through the combined effect of selective traditional hunting (i.e. without firearms) which has resulted in the disappearance of the Red River Hog (*Potamochoerus porcus*, statements of the local people and unidentified tooth) and the inability of most herbivores to survive in a fragmented forest habitat. It must be kept in mind that herbivores who prefer swamps or giant lakes were most likely never present on the slopes of the RAFALE area and that their absence is thus not related to forest fragmentation. The missing ungulate folivores usually derive their food from either the subcanopy (e.g. pygmy antelope) or the gap areas (e.g. buffalo), while the primate folivores derive most of their food from the canopy (Cerling et al. 2004). While herbivory in the upper strata remained intact (*Colobus, Lophocebus, Cercopithecus, Papio, Pan*; Cerling et al. 2004), the observed absence of ungulate folivores in RAFALE could have an **negative effect on its future plant species**

diversity due to the ecological favouring of competitive species (Olff & Ritchie 1998 and references therein).

The almost complete extinction of ungulate frugivores (i.e. duikers), probably caused by the same factors that led to the disappearance of ungulate herbivores is counteracted by the prominent presence of primates who appear to cope very well with forest fragmentation (section 6.1.2.1.) in the absence of modern technique hunting (guns, rifles). Duikers, while living on the canopy floor, feed on fallen fruits and seeds that grow in the canopy (Cerling et al. 2004). Primate frugivores also derive the bulk of their food from the canopy (Cerling et al. 2004). This means that primates and duikers have a similar role towards **seed dispersal and forest regeneration** and so forth the still present monkey species can prevent the total disappearance of this crucial functional role.

6.2.2. Relationship between taxonomic and functional diversity

Both the amount of functional entities and redundancy increased at a constant rate in terms of species richness but with the first having an much more extensive effect (Figure 10). This implies that almost for every additional species a new unique ecological function is filled, leaving functional redundancy (i.e. multiple species performing similar functions) as an almost non-existing protection towards species loss (consistent with Loreau 2004). The absence of redundant species as guarantors of reliable and robust ecosystem functioning makes ecosystem processes very sensitive towards changes in species composition (Naeem 1998).

In addition, the complete ecological role of an organism in an ecosystem can simply not be summarised in a few categories. However, an oversimplified version of the complex living world is needed when it has to be quantified and incorporated into comparative and statistical analyses (like this thesis). Thus there will always be some (and often large) simplifications which not reflect an organism's actual role in the environment. This may lead to an even lower and probably non-existing functional redundancy in real species communities. (It can however still be used as an comparative tool between several study sites if everything is simplified in the same way (which was done in this study)). Without redundancy, almost every mammal species possesses an unique set of ecological traits in the environment and is therefore worth saving. Especially for ecosystems with low species richness, this means that

the functional diversity will be very vulnerable and with every species' extinction the chance of losing a unique ecological role is very high.

6.2.3. Degree of dissimilarity between forest fragments and contiguous forests

RAFALE has exceeded some kind of threshold (>>> 18,15km²) in that it now differs to a large extent with the continuous forests and contains a substantial lower amount of species and functions (nestedness). The exact value of the area size threshold could not be determined with the use of beta-diversities but is most probably much higher than 18,15km² but still smaller than 2000km² (Equatorial Guinea, the smallest continuous forest in this study). This means that the forest fragments of the RAFALE area are unable to hold the same amount of species and functions as continuous forests. Whether extinctions or impossible colonisations are at the basis of RAFALE's diversity impoverishment cannot be known for sure. The use of beta-diversities could thus probably be a future tool to identify 'healthy' from 'destructed' habitats.

We acknowledge the fact that the beta diversities were calculated in different ways (due to the convenience of available R scripts and due to time constraints not corrected) and that this is surely not the ideal method to acquire clear reliable comparisons. Furthermore, the taxonomic beta-diversity was based upon an index ideal for incorporating abundances which were unavailable in this study. Since our main conclusions are however based upon the difference between continuous forests versus forest fragments rather than on the relationship between the taxonomic and functional beta-diversity, this has only a minor impact on the validity of our findings. However, in order to be able to publish the results of this thesis the usage of identical computation methods will be required. We recommend using the calculation method of the functional diversity (Figure 6) for both diversities since the Shannon entropy diversity index (Figure 5, used computing method for taxonomic diversity) was intended to include species abundances which were not available in this study. Moreover, an additional estimation of the turnover and nestedness components of the taxonomic diversity could be interesting.

6.2.4. Impact of area size and the coinciding forest edge effect

Our results concerning the relationship between taxonomic/functional diversity and forest area size suggests that the largest forests do not necessarily contain the highest mammalian biodiversity (Figure 12). The medium-sized forests seem to contain the highest species and functional entities in both scenarios (i.e. inclusion and exclusion of savannah inhabitants). A possible explanation for the observed diversity peak in medium sized forests is that until this point forest specialists are still able to cope with the decline of their forest habitat size while generalists can benefit from disturbed forest habitat. This relationship is also discussed by Estavillo et al. (2013) for Atlantic forest small mammals. They discovered that the alleged forest specialists abruptly declined in abundance, alpha diversity and gamma diversity dropping from the 45 to the 25% forest cover landscape while the same indices for generalists responded positively to landscape heterogeneity. This led to a biodiversity threshold below 30% forest cover with a peak in species richness just above this threshold. Since we also worked on large, sometimes heavily poached mammals it is highly plausible that the biodiversity threshold for the full mammalian assemblage will already emerge at a higher forest cover in a matrix-context. The recorded lower species number for the two largest forests could also simply be an underestimation of the biodiversity during field work, as larger forests can be very heterogeneous and sampling stations are limited. Considering that our results only include a handful nature parks, we emphasise that the oversimplification or overgeneralization of our findings in practical conservation applications could be unwarranted (van der Hoek et al. 2015). We do however show that medium-sized African forests can be a valuable biodiversity hotspot and thus deserve an equal conservation interest as the more larger forests.

In addition, deforestation automatically creates forest edge and exposes forest to the conditions found within the surrounding landscape (Stevens & Husband 1998). The outermost portions of a forest adjacent to the edge become part of the zone of transition or ecotone and may undergo changes in composition of species (Harris, 1988). By becoming smaller and gaining relatively more forest edge, a forest automatically becomes less suitable for forest specialist and more suitable for ecotone species and generalists.

6.2.5. Isolation versus fragmentation

Figure 14 shows clearly that isolation of a forest fragment, rather than its size, is the most important factor to explain the observed differences in number of species and functional entities between distinct forest fragments. This confirms the suggestion made by Tutin et al. (1997) that fragmentation per se does not have to be catastrophic for most mammal species.

When the beta-diversities of independent forest fragments and adjacent forest fragments are compared with an continuous forests, we can draw the following conclusions: the biodiversity of a forest fragment will be more similar to the biodiversity of a neighbouring continuous forests than that of other, independent forest fragments (Appendix 3 Table 4). This pattern is probably best explained by the dispersal of species between neighbouring forests habitats. The functions of the Lopé fragments are an total subset from these occurring at the Lopé forest since this large continuous forest serves as a source for animal species and their functions towards the surrounding forest patches (Figure 14). The RAFALE patches contain different species (turnover) than the Lopé reserve since they are located in a different geographical zone and are naturally holding other (sub)species (Figure 14).

6.3. Implications for conservation

6.3.1. The role of isolated forest fragments in species conservation

Overall species and functional diversity of faunas in small forest fragments, isolated from continuous forests, will become impoverished over time (Figure 11, 12). The prevalence of generalists (ecologically versatile species) such as genets, confirms that the region is environmentally disturbed (Djagoun & Gaubert 2009). With the observation of medium-sized generalists being resilient towards forest fragmentation, the hypothesis that medium generalistic carnivores will become endangered in the coming 10 years (Cardillo et al., 2004) seem implausible. Magioli et al. 2016 even revealed high biodiversity levels and a meaningful amount of ecological functions for an agricultural and fragmented landscape in Brazil, indicating some resistance of species to pressure from the agricultural matrix and advancing urbanisation when they are not completely isolated.

Primates are shown to survive in patches and are thus more prone to large-scale poaching (which was not the case in our primary study area) and the shortage of their critical food sources (Marsh 2003) than to habitat fragmentation. Although with only six individual chimpanzees remaining in FG1 (Pers.Obs., assuming that migration between other forest patches is no longer occurring) and probable genetic consequences of inbreeding, it seems that an important area threshold has been reached in this fragment. Without the availability of abundance data of all the other mammals, the long-term existence of the present monkey populations could not be estimated but the relatively high population density of chimpanzees (Huyghe 2017) allows us to presume that the majority of the monkey species and populations in the RAFALE forest are healthy. Therefore, primates are an unsuitable group to examine the effects of habitat fragmentation on biodiversity (in conflict with Onderdonk & Chapman 2000) since they are clearly more adaptable than the others mammal orders (discussed in section 6.1.2.1. Primates).

Along with primates, pangolin species were also well represented in the forest fragments of RAFALE. There was an official confirmation of two species plus a third species *Manis gigantea* that could possibly be present as well (based on information of the local population). Pangolins who are worldwide targeted by commercial poaching and illegal trafficking, seem to be able to survive in small forest fragments. The global focus to conserve this specific order

of animals should thus stay on releasing them from the immense poaching pressures they are under, rather than on preventing forest fragmentation/reduction.

6.3.2. The impact of fragmentation on seed dispersers and forest regeneration

Mammals (primates, elephants, bats, ..) and birds (hornbills, ..) are the most important vertebrate groups responsible for seed dispersal in tropical regions worldwide (Jordano 2001; Stoner et al. 2007)

Omeja et al. (KNP Uganda, 2016) found that fallow land dominated by grassland and disturbed by fire can recover to closed canopy forest within 20 years over large spatial scales. Most of the early successional tree species were animal-dispersed, what confirms that frugivorous species play a major role in forest regeneration. In degraded African forests, members of the *Cercopithecidae* (Kaplin & Lambert 2002) and *Hominidae* families fulfil the most important roles towards (primary) seed dispersal (Stoner et al. 2007), while these mammals are usually among the most hunted species. In protected sites in Nigeria, seedlings dispersed by primates dominated while the other dispersal modes were more common in sites affected by hunting (Effiom et al. 2013). A forest lacking primates will likely undergo substantial changes in the tree community, principally characterised by a large-seeded plant species collapse. That our study indicates that primates are in general extremely adaptable towards forest fragmentation in the absence of large-scale hunting is promising for the long-term survival of the remaining forest (fragments) itself and for forest regeneration.

Since ungulate frugivores (i.e., duikers) have a similar food source as primates, their absence from these forests as seed dispersers may be compensated by the remaining monkey and ape species. This also applies to the giant pouched rat and porcupines that also contribute to maintain this function by including fallen canopy fruits and seeds as a significant proportion of their diet (Cerling 2004).

African frugivorous bats are principally dispersers of the seeds of later successional canopy fruits (hard, large-seeded fruits) and are considered less important as contributors to early plant succession (except if the propagules of *Ficus* are involved in this process, Muscarella & Fleming 2007).

Furthermore, the savannah mammal community (particularly rich in Sub-Saharan Africa, Omeja et al. 2016) and possibly rodents (Forget 1990) could play an important factor in forest restoration as well, although the role of this last group is under-studied (Evrard et al. 2017).

6.3.3. Long-term conservation of forests

With a healthy primate community, the frugivorous guild is robust and forest regeneration remains possible (even in extreme isolated forest remnants as RAFALE). The same study that stated that forest regeneration is achievable (Omeja et al. 2016) emphasised that the presence of a nearby continuous old-growth forest is a major factor to ensure there is a species pool available to support the regeneration of a new forest. Our results confirm that the depletion of mammalian species and their functions in forest remnants appears to be more influenced by the absence of a nearby forest rather than by its size (Figure 12). Thus even under optimal conditions and with a full complement of animal seed dispersers and a nearby seed source, large-seeded species (because of their relative immobility) should be planted if a full return to primary forest is desired (Wunderle 1997). This sets a limit to the positive effect that primates can have for restoring healthy forest communities, notwithstanding their indispensable role in converting the degraded landscape surrounding primary and degraded forests.

Many conservationists are also being confronted with the conservation triage, where a priority in species protection need to be made due to limited resources. Primates, with their general vulnerable IUCN-status and their essential role in seed dispersal, often serve as the ideal guide. Lambert (2011) proposed an alternative mixed strategy where *Cercopithecus* could serve as an ideal umbrella species (i.e. species whose conservation confers protection to a large number of naturally co-occurring species and the important mutualisms among them, after Roberge & Angelstam (2003)) while other charismatic species such as the Chimpanzee can serve as an ideal flagship species (i.e. often large, 'popular' species serving as symbols and rallying points to stimulate conservation awareness and action, after Heywood (1995)).

We therefore recommend focusing protection measures towards forests that still contain healthy primate communities which are essential for passive forest regeneration. These include either extended continuous forests and adjacent fragments (where many mammals and their ecological functions are still present) and/or towards small forests where reintroduction of species is possible after passive regeneration has occurred.

7. CONCLUSION

We found that **redundancy hardly exists** in real communities what implies that ecosystem processes are very sensitive towards changes in species composition. Almost all mammal species need to be saved in order to guarantee reliable unchanged ecosystem functioning.

When parts of forests become isolated and smaller in size, they tend to lose the majority of their species and hence important functions.

Habitat specialists, larger herbivores (terrestrial herbivory), frugivorous ungulates (terrestrial frugivory) carnivores (top-down control) appear to disappear first. An important ray of hope is that (in the absence of large-scale hunting) primates, the primary seed dispersers in the tropics, seem to withstand an extended amount of forest fragmentation and can still partly guarantee (i.e. not fully compensating for the removal of other mammal frugivores) potential forest regeneration and hence the long-term viability of the plant communities. Together with their ecological function, primates are very charismatic and can serve both as umbrella and flagship species. Their double role in conservation makes it valid to **focus conservation measures towards forest fragments that still contain primates.**

It also has been found that in the process of forest fragmentation, geographic isolation from the large forest is more detrimental than size reduction of the fragments per se. Thus implementation of **corridors** should already help protecting forest biodiversity on larger scales.

The largest forests do not necessarily contain the highest conservation value since the biodiversity peak is probably already reached around 2000-3000km². Larger forests probably contain distinct species and function assemblages and as a result deserve an equal conservation interest. Until better estimations are found, we recommend focusing on preventing forests area sizes from declining below 2000 km².

Our study case was quite a severe case of forest fragmentation. For that reason, we emphasise that the same kind of research needs to be done on forest fragments with other historical forest loss and hunting scenarios to see if the same conclusions can be drawn and if an exact threshold for isolation and forest patch size can be determined.

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Table 1| **Mammalian RAFALE inventory**, confirmed by direct observations (D), footage on camera traps (CT) and/or genetic analyses on tissue (G¹) or faeces (G¹) samples. The 'literature' column summarises the adaptability of every mammal towards logging and agriculture lands that can be found in scientific literature. Yellow marked species are species not used in the majority of the statistical analyses since they are not known to occur in forests (general species were still included). Green marked species are exceptional in the sense that they are not known to be adapted to degraded forests. ¹Naughton-Treves et al. 1996 ²Onderdonk & Chapman 2000 ³Struhsaker 1997, ⁴Johns & Skorupa 1987, ⁵Blom et al. 2005, ⁶Vanthomme et al. 2013; ⁷Djagoun & Gaubert 2009; ⁸Waterman et al. 2014; ⁹Angelici et al. 1999; ¹⁰Kingdon et al. 2003

RAFALE mammal	ia	n i	n۱	/e	ntory including adaptability Part 1
Species	1	Met	ho	d	Literature
PRIMATES	D	СТ	G ^t	G ^f	
Cercopithecus ascanius schmidti	х				Known to raid crops ^{1,2}
Cercopithecus mitis stuhlmanni	х				Known to raid crops ¹
Chlorocebus pygerythrus/aethiops	х				Known to raid crops ² ; Inhabitant of forest edge, cultivated and rural environments ¹⁰
Colobus guereza (occidentalis)	х				Known to raid crops ² ; respond positively to logging ³ ; leafy diet ⁴
Galagoides thomasi		х			Inhabitant of savannah, woodland and forest edge ¹⁰
Lophocebus johnstoni	х				Sensitive to logging and hunting 5,10
Pan Tradadutas sehwainfurthii		,		,	Known to raid crops ² ; not poached;
Pan Troglodytes schweinfurthii		X		X	natural defenders agaist baboons Pers.Obs
Pania anuhis		.,			Curious and extremely adaptable species;
Papio anubis	Х	X			able to survive on grass ¹⁰
Pilicolobus tephrosceles / oustaleti	Х				Thrive in disturbed forest habitat ² ; leafy diet ⁴
CARNIVORA	D	СТ	Ğ	G ^f	
Canis adustus		,,			Savannah inhabitant; Opportunistic behaviour and
cums adustus		Х			morphology ¹⁰ ; Tolerates human disturbance ⁶
Civettictis civetta		x			Found on agricultural land and near houses; Thrives in
Civetticus civetta		<i>x</i>			degraded/deforested areas, opportunistic forager IUCN2015
Crossarchus alexandri		Х			Persist despite heavy anthropogenic pressures ⁷
Leptailurus serval			?		Savannah inhabitant; tolerates farming practices
Leptullarus servul			:		if cover and food is available ¹⁰
Genetta angolensis			?		Savannah inhabitant ¹⁰
Genetta maculata		х			Wide spectrum of habitats ; crop field and feeding on poultry 7
Genetta servalina (bettoni)		х			Wide spectrum of habitats; crop field and feeding on poultry 7
Genetta victoriae		х			Wide spectrum of habitats ; crop field and feeding on poultry ⁷
Nandinia binotata					Occurs in logged and second-growth forests; known to visit
Nanaina binotata		Х			cultivated fields bordering forest edge IUCN2015

RAFALE mammal	ia	n i	'n۱	/e	ntory including adaptability Part 2
Species	ı	Vlet	tho	d	Literature
AFROSORICIDA	D	СТ	G ^t	G ^f	
Potamogale (velox)			х		Not threatened by logging per se, more threatened by indirect soil logging and increased poaching IUCN 2016
EULIPOTYPHLA	D	СТ	ct	of	Very high reproduction rates; small home ranges;
EULIPUTTPHLA	Ľ		G	G	easy accessibility to food resources
Crocidura denti	ļ		х		Crocidura species respond positively to edge effects 10
Crocidura luna			Х		Crocidura species respond positively to edge effects ¹⁰
Crocidura olivieri			Х		Crocidura species respond positively to edge effects 10
Crocidura poensis			х		Crocidura species respond positively to edge effects 10
Scutisosex somereni			х		Forest obligate species? ¹⁰
Suncus infinitesimus			х		Ocurrence of forest edge confirmed 10
HYRACOIDEA	D	СТ	G ^t	G ^f	
Heterohyrax brucei	?	?			Savannah inhabitant ¹⁰
ARTIODACTYLA	D	СТ	G^{t}	\mathbf{G}^{f}	Forest-dependent duikers and large herbivores are absent
Cephalophus rufilatus		x			Unusual duiker species in being an inhabitant of i.a.
	L	_			savannas and degraded forests; flexibility in diet ¹⁰
PHOLIDOTA	D	СТ	G^{t}	G ^f	Mostly Vulnerable IUCN due to extensive poaching levels
Manis tricuspis		х	х		Can survive in human-modified habitats ⁸
Phataginus tetradactyla		х			Has been recorded in i.a. altered forest and farm lands ⁹
				4	Very high reproduction rates; small home ranges;
RODENTIA	P	СТ	G,	G ^f	easy accessibility to food resources
Aethomys (hindei)			х		Grassland inhabitant ¹⁰
Arvicanthus niloticus			Х		Grassland inhabitant ¹⁰
Cricetomys emini		х	X		Can become a pest species IUCN2016
Gerbilliscus (kempi)			Х		Grassland inhabitant 10
Grammomys sp.			х		
Heliosciurus rufobranchium		х	Х	*******	Grassland inhabitant ¹⁰
Hylomyscus stella			Х		
Hystrix cristrata		,			Found in both woodland savannah and
mystrix cristrata		X			forest formations; can become a pest species IUCN2016
Lemniscomys sp.	?				Grassland inhabitant ¹⁰
Lophurumys sikapus			х		Grassland inhabitant ¹⁰
Malacomys longipes			Х		
Mus bufo			Х		Inhabitant of a wide range of habitat: grassland and forest 10
Mus musculoides			Х		HICKNOM C
Paraxerus (alexandri)			Х		Recorded from fallow plantations IUCN2016
Praomys jacksoni	ļ		X		
Praomys misonnei Thryonomys sp.	?		X		Swamp inhabitant ¹⁰
	· ·		?		Grassland inhabitant ¹⁰
Xerus sp.			ŗ		Wide-spread in Africa and a wide range of habitats
CHIROPTERA	D	СТ	G ^t	G ^f	suggest it to be an adaptable species 10,1UCN
Chaerophon (pumilis)			х		IUCN2014
Hipposideros ruber		ļ	X	-	IUCN2008
Micropteropus pusillus	 		X	-	IUCN2016
Myonycteris (torquata)			X		IUCN2016
Myonycteris angolensis ruwenzori			X		IUCN2008
Neoromicia nanus		ļ	X	-	IUCN2014
					IUCN2016
Rousettus aegypticus (leachii)			Х		

Table 1| **Trait matrix : Input for statistics : masscode** (mean weight) : xxl(>1000kg), xl(>100kg), l(>10kg), m(>1kg), s(>100g), xs(<100g); **loco** (locomotion when foraging) : TE(terrestrial), AR(arboreal), TA(terrestrial and arboreal), AE(aerial), AQ(aquatic); **primfood** (primary food source) : FR(frugivorous), HE(herbivorous), IN(invertebrates), CA(carnivorous); **act** (activity when foraging): D(day), N(night), DN(day and night); **social** (sociality when foraging) : S(social), NS(solitary); Yellow marked species were not included in analyses solely regarding forest communities; generalists were not excluded (information extracted from Kingdon et al. 2003).

Trait Matri	x Part 1					
Species Full name	species	masscode	loco	primfood	act	socia
PRIMA	ΓES					
Arctocebus areus	artare	s	AR	IN	N	ns
Arctocebus calabarensis	artcal	m	AR	IN	N	ns
Cercocebus galeritus	cergal	1	TA	FR	D	S
Cercocebus torquatus	certor	i	TE	FR	D	S
Cercopithecus ascanius (schmidti)	cerasc	l i l	AR	FR	D	S
Cercopithecus cephus	cercep	i	AR	FR	D	S
Cercopithecus mitis stuhlmanni	cermit	i i	AR	FR	D	S
Cercopithecus neglectus	cerneg	i	TA	FR	D	S
Cercopithecus nictitans	cernic	i	AR	FR	D	S
Cercopithecus pogonias	cerpog	i	AR	FR	D	S
Chlorocebus pygerythrus/aethiops	chlaet	 '	TA	FR	D	S
Colobus quereza (occidentalis)	colgue	i	AR	HE	D	S
Colobus satanas	colsat	i	AR	FR	D	S
		<u> </u>	AR	HE	N N	
Euoticus elegantulus Galaqo alleni	euoele galall	m m	TA	FR	N N	ns ns
Galago alieni Galago demidovii	galdem	m	AR	IN	N N	1
3		†			N	ns
Galago gabonensis / Sciurocheirus gabonensis	galgab	m	AR	FR		ns
Galago thomasi	galtho	m	AR	IN	N D	ns
Gorilla gorilla	gorgor	xl	TA	HE		S
Lophocebus albigena (johnstoni)	lopalb	!	AR	FR	D	S
Mandrillus sphinx	mansph	I	TE	FR	D	S
Miopithecus talapoin - similar to ogouensis	miotal	m	AR	FR	D	S
Pan troglodytes (schweinfurthii)	pantro	xl	TA	FR	D	S
Papio anubis	papanu	I	TA	HE	D	S
Perodicticus potto	perpot	m	AR	FR	N	ns
Pilicolobus rufoitratus (tephrosceles?)ellioti/oustaleti	pilruf		AR	HE	D	S
CARNIV	ORA					
Aonyx congica	aoncon	1	AQ	IN	N	ns
Atilax paludinosus (swamps)	atipal	- 1	AQ	IN	N	ns
Bdeogale nigripes	bdenig	- 1	TE	CA	N	ns
Canis adustus	canadu	1	TE	CA	N	S
Civettictis civetta	civciv		TE	CA	N	ns
Crocuta corcuta	crocor	xl	TE	CA	N	S
Crossarchus alexandri	croale	m	TE	IN	DN	S
Crossarchus platycephalus	cropla	m	TE	IN	D	S
Felis aurata /Profelis	felaur	I	TA	CA	N	ns
Felis serval	felser	ı	TE	CA	DN	ns
Galerella sanguinea / Herpestes (general)	galsan	m	TA	IN	D	ns
Genetta angolensis	genang	m	TE	IN	N	ns
Genetta maculata	genmac	m	TA	CA	N	ns
Genetta servalina (bettoni)	genser	ı	TA	CA	N	ns
Genetta victoriae	genvic	I	TA	CA	N	ns
Herpestes ichneumon	herich	ı	TE	CA	D	ns
Herpestes naso /Xenogale nase	hernas	ı	TE	CA	D	ns
Hydrictis maculicollis	hydmac	i	AQ	CA	D	ns
Ichneumia albicauda	ichalb	i	TE	IN	N	ns
Mellivora capensis (general)	melcap	l i	TE	CA	N	ns
Nandinia binotata	nanbin	m	AR	FR	N	ns
Panthera leo	panleo	xl	TE	CA	N	S
Panthera pardus (general)		xI xI	TA	CA	DN	ns
Poiana richardsonii	panpar	m xi	AR	CA	N N	ns
PROBOSC PROBOSC			AR	CA	IN	115

Trait Matrix	Part 2					
Species Full name	species	masscode	loco	primfood	act	social
AFROSORICI				,,		
Chrisochloris leucorhina / Calcochloris leucorhinus based on C.stuhlmanni	chrleu	S	TE	IN	N	ns
Potamogale velox	potvel	m	AQ	IN	N	ns
EULIPOTYPH	ILA					
Crocidura denti	croden	xs	TE	IN	N	ns
Crocidura dolichura	crodol	xs	TE	IN	N	ns
Crocidura flavescens	crofla	S	TE	IN	N	ns
Crocidura grassei	crogra	xs	TE	IN	N	ns
Crocidura luna	crolun	xs	TE	IN	N	ns
Crocidura olivieri	crooli	S	TE	IN	N	ns
Crocidura poensis	cropoe	XS	TE	IN	N	ns
Crocidura sp	crosp	S	TE	IN	N	ns
Paracrocidura schoutedeni	parsch	XS	TE	IN	N	ns
Scutisosex somereni	scusom	S	TE	IN	N	ns
Soricidae sp	sorsp	S	TE	IN	N	ns
Suncus infinitesimus	suninf	xs	TE	IN	N	ns
Sylvisorex johnstoni	syljoh	XS	TE	IN	N	ns
Sylvisorex ollula	suyloll	XS	TE	IN	N	ns
Sylvisorex sp	sylsp	XS	TE	IN	N	ns
HYRACOID	EA					
Dendrohyrax arboreus/dorsalis	dendor	1	AR	HE	N	ns
Heterohyrax brucei	hetbru	1	TA	HE	D	S
ARTIODACT	/LA					
Cephalophus calliphygus	cepcal	ı	TE	FR	D	ns
Cephalophus dorsalis (general)	cepdor	ı	TE	FR	N	ns
Cephalophus leucogaster	cepleu	1	TE	FR	D	ns
Cephalophus monticola /Philantomba	cepmon	ı	TE	FR	D	s
Cephalophus nigrifrons	cepnig	ı	TE	FR	D	ns
Cephalophus ogilbyi	cepogi	ı	TE	FR	D	ns
Cephalophus rufilatus	cepruf	ı	TE	FR	D	ns
Cephalophus sylvicultor	cepsyl	хl	TE	FR	D	ns
Hippopotamus amphibius	hipamp	xxl	TE	HE	N	ns
Hyemmoschus aquaticus	hyeaqu	ı	TE	FR	N	ns
Hylocherus meinertzhageni	hylmei	хl	TE	HE	D	S
Neotragus batesi	neobat	ı	TE	HE	DN	ns
Potamocherus porcus	potpor	хl	TE	HE	N	S
Syncerus caffer nanus	syncaf	xxl	TE	HE	DN	S
Tragelaphus euryceros	traeur	xxl	TE	HE	N	S
Tragelaphus scriptus (bush land)	trascr	хl	TE	HE	DN	ns
Tragelaphus spekii (swamp)	traspe	хl	TE	HE	D	S
PHOLIDOT	Α					
Manis tricuspis	mantri	1	TA	IN	N	ns
Manis tetradactyla	mantet	ı	TA	IN	DN	ns
Manis gigantea	mangig	хl	TE	IN	N	ns
TUBULIDENT	ATA					
Orycteropus afer (general : savanna to forest)	oryafe	xl	TE	IN	N	ns

Trait Matrix	Part 3			<u>, </u>		
Species Full name	species	masscode	loco	primfood	act	social
RODENT		masscoae	1000	primodu	ucc	300101
Aethomys (hindei)	aethin	s	TE	FR	DN	ns
Anomalurus beecrofti	anobee	m	AR	FR	N	ns
Anomalurus derbianus	anoder	m	AR	HE	N	ns
Anomalurus pusillus	anopus	s	AR	FR	N	ns
Arvicanthus niloticus	arvnil	s	TE	HE	D	s
Atherurus africanus	athafr	i	TE	HE	N	ns
Cricetomys emini	criemi	s	TE	FR	N	ns
Dasymys sp (based on incomtus)	dassp	s	AQ	HE	D	ns
Dendromus messorius	denmes	xs	TA	HE	N	ns
Dendromus sp1	densp1	xs	TA	HE	N	ns
Dendromus sp2	densp2	xs	TA	HE	N	ns
Deomys ferrugineus	deoferr	S	TE	IN	N	ns
Epixerus wilsoni /ebii	epiwil	m	TE	FR	D	ns
Funisciurus anerythrus	funleu	m	TA	FR	D	S
Funisciurus isabella	funane	s	TA	FR	D	ns
Funisciurus lemniscatus	funisa	S	TA	FR	D	ns
Funisciurus leucogenys	funlem	m	AR	FR	D	ns
Funisciurus pyrrhopus	funpyr	m	TE	FR	D	ns
Gerbilliscus kempi	gerkem	s	TE	HE	N	ns
Grammomys rutilans / kuru	grarut	S	AR	FR	N	ns
Grammomys sp.	gramsp	S	AR	FR	N	ns
Graphiurus sp> Lorraineus as example	grapsp	XS	AR	FR	N	ns
Heimyscus fumosus	heifum	XS	TE	IN	N	ns
Heliosciurius gambianus	helgam	m	AR	FR	D	ns
Heliosciurius rufobrachium	helruf	m	AR	FR	D	ns
Hybomys univittatus	hybuni	S	TE	IN	DN	ns
Hylomyscus alleni	hylall	xs	AR	HE	N	ns
Hylomyscus parvus	hylpar	xs	TA	FR	N	ns
Hylomyscus sp	hylsp	XS	TA	FR	N	ns
Hylomyscus stella	hylste	XS	TA	FR	N	ns
Hystrix cristrata	hyscri	I	TE	HE	N	S
Idiurus macrotis	idimac	S	AR	FR	N	ns
Idiurus zenkeri - similar to macrotis	idizen	XS	AR	FR	N	ns
Lemniscomys striatus	leggsp	S	TE	HE	N	ns
Lophuromys nudicaudus	lemstr	S	TE	IN	N	ns
Lophuromys sp	lopnud	S	TE	IN	N	ns
Lophurumys sikapus	lophsp	S	TE	IN	N	ns
Malacomys longipes	lopsik	S	TE	IN	N	ns
Mastomys sp (natalensis)	mallon	S	TE	HE	N	ns
Mus bufo (grassland-forest)	mastsp	XS	TE	HE	N	ns
Mus musculoides (1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.	musbut	XS	IE	HE	N	ns
Mus setulosus - similar mus muscul.(grassland-forest)	musmus	XS	TE	HE	N	ns
Mus sp	musset	XS	TE	HE	N	ns
Myoscirius pumilio	myopum	XS	AR	HE	D	ns
Oenomys hypoxanthus	oenhyp	S	TE	HE	DN	ns
Paraxerus (alexandri)	parale	S	AR	IN	D	ns
Paraxerus poensis	parpoe	S	AR	FR	D	ns
Praomys Jukololae	prajac	S	TE	FR	N	ns
Praomys lukolelae Praomys misonnei	praluk	S	TE	FR	N	ns
,	pramis	S	TA	FR	N N	ns
Praomys sp Praomys tullberahi	praosp	S	TE TE	FR FR	N N	ns
, ,	pratull	S		+ +		ns
Prionomys batesi Protoxerus strangeri	pribat	XS m	TA AR	IN FR	N D	ns
Rattus rattus	prostr	m		1 -		ns
Stochomys longicaudatus	ratrat stolon	S S	TA TA	HE FR	DN N	S ns
Thryonomys swinderianus	thrswi	S	AQ	HE	N N	ns
Xerus erythropus		m	TE	HE	D	S ns
, ,	xerery			1 -	D	ns ns
Zenkerella insignis	zenins	m	TA	HE	υ	ns

Trait Matrix	Part 4					
Species Full name	species	masscode	loco	primfood	act	social
CHIROPTER	RA					
Casynicteris argynnis	casarg	S	AE	FR	N	ns
Chaerephon aloysiisabaudiae /Tadarida	chaalo	S	ΑE	IN	N	ns
Chaerophon / Tadarida nigeriae	tadnig	xs	AE	IN	N	s
Chaerephon pumilus /Tadarida	chapum	xs	AE	IN	N	ns
Eidolon helvum	eidhul	S	ΑE	FR	N	S
Epomophorus gambianus	epogam	S	AE	FR	N	S
Epomophorus sp	eposp	S	AE	FR	N	s
Epomops franqueti	epofra	S	AE	FR	N	S
Eptesicus tenuipinnis /Pipistrellus	eptten	xs	AE	IN	N	ns
Glauconycteris poensis	glapoe	XS	AE	IN	N	ns
Hipposideros beatus	hipbea	xs	AE	IN	N	S
Hipposideros caffer	hipcaf	xs	AE	IN	N	S
Hipposideros commersonni> probably. H. gigas	hipcom	S	AE	IN	N	ns
Hipposideros cyclops	hipcyc	S	AE	IN	N	ns
Hipposideros ruber	hiprub	XS	AE	IN	N	ns
Hypsignatus monstrosus	hypmon	S	AE	FR	N	ns
Kerivulla harrisoni / lanosa	kerhar	xs	AE	IN	N	ns
Megaloglossus woermanni	megwoe	xs	AE	FR	N	S
Micropteropus pusillus	micpus	s	AE	FR	N	s
Mimetillus moloneyi	mimmol	XS	AE	IN	N	ns
Miniopterus inflatus	mininf	xs	AE	IN	N	ns
Miniopterus schreibersii	minsch	xs	AE	IN	N	ns
Mops brachypterus /Tadarida	mopbra	xs	AE	IN	N	ns
Mops nanulus	mopnan	xs	AE	IN	N	ns
Mops spurrelli	mopspu	xs	AE	IN	N	ns
Mops thersites	mopthe	xs	AE	IN	N	ns
Myonycteris angolensis ruwenzori / Lissonycteris	myoang	S	AE	FR	N	ns
Myonysteris torquata	myotor	s	AE	FR	N	ns
Myotis bocagei	myoboc	xs	AE	IN	N	ns
Neoromicia capensis / Pipistrellus	neocap	xs	AE	IN	N	ns
Neoromicia nanus / Pipistrellus	neonan	xs	AE	IN	N	S
Nycteris arge	nycarg	xs	AE	IN	N	ns
Nycteris grandis	nycgra	s	AE	IN	N	ns
Nycteris hispida	nychis	xs	AE	IN	N	ns
Nycteris sp	nycsp	xs	AE	IN	N	ns
Pipistrellus nanulus	pipnan	xs	AE	IN	N	s
Rhinolophus alcyone	rhialc	xs	AE	IN	N	ns
Rhinolophus landeri	rhilan	XS	AE	IN	N	ns
Rousettus aegypticus (leachii)	rouaeg	S	AE	FR	N	S
Scotonycteris zenkeri	scozen	xs	AE	FR	N	ns
Scotophilus nigrita	sconig	S	AE	IN	N	ns

Table 2| **Assemblage Matrix**: **Input for statistics**: absence (0) and presence (1) with the full RAFALE zone (RF), only FG1 (RF1), only FG23 (RF23), Central African Republic (CAR), Congo-Brazzaville (CO), Cameroon (CAM) and Equatorial-Guinea (EQG). Yellow marked species were not included in analyses solely regarding forest communities; generalists were not excluded (Information extracted from unpublished inventories of M. Colyn).

	trix Pa	rτı						
Species Full name	Species	RF	RF1	RF23	CAR	СО	CAM	EQG
PRIMATE	S							
Arctocebus areus	artare	0	0	0	0	1	1	0
Arctocebus calabarensis	artcal	0	0	0	1	0	0	1
Cercocebus galeritus	cergal	0	0	0	1	1	1	0
Cercocebus torquatus	certor	0	0	0	0	0	0	1
Cercopithecus ascanius (schmidti)	cerasc	1	1	1	1	0	0	0
Cercopithecus cephus	cercep	0	0	0	1	1	1	1
Cercopithecus mitis stuhlmanni	cermit	1	1	1	0	0	0	0
Cercopithecus neglectus	cerneg	0	0	0	1	1	1	1
Cercopithecus nictitans	cernic	0	0	0	1	1	1	1
Cercopithecus pogonias	cerpog	0	0	0	1	1	1	1
Chlorocebus pygerythrus/aethiops	chlaet	1	1	0	0	0	0	0
Colobus guereza (occidentalis)	colgue	1	0	1	1	1	1	0
Colobus satanas	colsat	0	0	0	0	1	1	1
Euoticus elegantulus	euoele	0	0	0	1	1	1	1
Galago alleni	galall	0	0	0	1	0	0	1
Galago demidovii	galdem	0	0	0	1	1	1	1
Galago gabonensis / Sciurocheirus gabonensis	galgab	0	0	0	0	1	1	0
Galago thomasi	galtho	1	1	0	0	0	0	0
Gorilla gorilla	gorgor	0	0	0	1	1	1	1
Lophocebus albigena (johnstoni)	lopalb	1	0	1	1	1	1	1
Mandrillus sphinx	mansph	0	0	0	0	0	0	1
Miopithecus talapoin - similar to ogouensis	miotal	0	0	0	0	1	0	1
Pan troglodytes (schweinfurthii)	pantro	1	1	1	1	1	1	1
Papio anubis	papanu	1	1	1	1	0	0	0
Perodicticus potto	perpot	0	0	0	1	1	1	1
Pilicolobus rufoitratus (tephrosceles?)ellioti/oustaleti CARNIVOF	pilruf	1	1	1	1	0	0	0
		0	0	0	1	1	1	1
Aonyx congica Atilax paludinosus (swamps)	aoncon atipal	0	0	0	1	1	1	1
Bdeogale nigripes	bdenig	0	0	0	1	1	1	1
Canis adustus	canadu	1	0	1	0	0	0	0
Civettictis civetta	civciv	1	1	0	1	1	1	1
Crocuta corcuta	crocor	0	0	0	0	1	1	0
Crossarchus alexandri	croale	1	0	1	1	0	0	0
Crossarchus platycephalus	cropla	0	0	0	0	0	1	1
Felis aurata /Profelis	felaur	0	0	0	1	1	1	1
Felis serval	felser	1	0	1	1	1	1	0
Galerella sanguinea / Herpestes (general)	galsan	0	0	0	0	0	0	1
Genetta angolensis	genang	1	0	1	0	0	0	С
Genetta maculata	genmac	1	0	1	1	0	0	1
Genetta servalina (bettoni)	genser	1	0	1	1	1	1	1
Genetta victoriae	genvic	1	0	1	0	0	0	0
Herpestes ichneumon	herich	0	0	0	1	1	1	C
Herpestes naso /Xenogale nase	hernas	0	0	0	1	1	1	0
Hydrictis maculicollis	hydmac	0	0	0	1	1	1	1
Ichneumia albicauda	ichalb	0	0	0	1	0	0	0
Mellivora capensis (general)	melcap	0	0	0	1	1	1	0
Nandinia binotata	nanbin	1	0	1	1	1	1	1
Panthera leo	panleo	0	0	0	0	1	1	0
Panthera pardus (general)	panpar	0	0	0	1	1	1	1
Poiana richardsonii	poiric	0	0	0	1	1	1	1
PROBOSCIE	AE							
i noboscie								

Assemblage Ma	trix Pa	rt 2										
Species Full name	Species	RF	RF1	RF23	CAR	СО	CAM	EQG				
AFROSORIC			=	25	G, III		0,	200				
Chrisochloris leucorhina / Calcochloris leucorhinus based on C.stuhlmanni	chrleu	0	0	0	1	1	1	0				
Potamogale velox	potvel	1	1	1	1	1	1	1				
EULIPOTYPI	HLA											
Crocidura denti	croden	1	0	1	0	0	0	0				
Crocidura dolichura	crodol	0	0	0	0	0	0	1				
Crocidura flavescens	crofla	0	0	0	0	0	0	1				
Crocidura grassei	crogra	0	0	0	0	0	0	1				
Crocidura luna	crolun	1	1	0	0	0	0	0				
Crocidura olivieri	crooli	1	1	1	0	0	0	0				
Crocidura poensis	cropoe	1	1	1	0	0	0	1				
Crocidura sp	crosp	0	0	0	1	0	0	1				
Paracrocidura schoutedeni	parsch	0	0	0	0	0	0	1				
Scutisosex somereni	scusom	1	1	1	0	0	0	0				
Soricidae sp	sorsp	0	0	0	0	1	1	0				
Suncus infinitesimus	suninf	1	0	1	0	0	0	0				
Sylvisorex johnstoni	syljoh	0	0	0	0	0	0	1				
Sylvisorex ollula	suyloll	0	0	0	0	0	0	1				
Sylvisorex sp	sylsp	0	0	0	1	0	0	0				
HYRACOIDEA												
Dendrohyrax dorsalis	dendor	0	0	0	1	1	1	1				
Heterohyrax brucei	hetbru	1	0	1	0	0	0	0				
ARTIODACT	YLA						•					
Cephalophus calliphygus	cepcal	0	0	0	1	1	1	1				
Cephalophus dorsalis (general)	cepdor	0	0	0	1	1	1	1				
Cephalophus leucogaster	cepleu	0	0	0	1	1	1	1				
Cephalophus monticola /Philantomba	cepmon	0	0	0	1	1	1	1				
Cephalophus nigrifrons	cepnig	0	0	0	1	1	1	1				
Cephalophus ogilbyi	cepogi	0	0	0	0	1	0	0				
Cephalophus rufilatus	cepruf	1	0	1	0	0	0	0				
Cephalophus sylvicultor	cepsyl	0	0	0	1	1	1	1				
Hippopotamus amphibius	hipamp	0	0	0	1	1	1	0				
Hyemmoschus aquaticus	hyeaqu	0	0	0	1	1	1	1				
Hylocherus meinertzhageni	hylmei	0	0	0	1	1	1	0				
Neotragus batesi	neobat	0	0	0	1	1	1	1				
Potamocherus porcus	potpor	0	0	0	1	1	1	1				
Syncerus caffer nanus	syncaf	0	0	0	1	1	1	1				
Tragelaphus euryceros	traeur	0	0	0	1	0	0	0				
Tragelaphus scriptus (bush land)	trascr	0	0	0	1	1	1	0				
Tragelaphus spekii (swamp)	traspe	0	0	0	1	1	1	1				
PHOLIDOT	ГА											
Manis tricuspis	mantri	1	1	1	1	1	1	1				
Manis tetradactyla	mantet	1	0	1	1	0	0	1				
Manis gigantea	mangig	0	0	0	1	1	1	1				
TUBULIDENT	TATA											
Orycteropus afer (general : savanna to forest)	oryafe	0	0	0	1	0	0	1				

Assemblage Ma	trix Pa	rt 3						
Species Full name	Species	RF	RF1	RF23	CAR	СО	CAM	EQG
RODENTIA	Δ		l					
Aethomys (hindei)	aethin	1	1	1	0	0	0	0
Anomalurus beecrofti	anobee	0	0	0	0	0	0	1
Anomalurus derbianus	anoder	0	0	0	1	1	1	1
Anomalarus pusillus	anopus	0	0	0	1	0	0	0
Arvicanthus niloticus	arvnil	1	1	0	0	0	0	0
Atherurus africanus	athafr	0	0	0	1	1	1	1
Cricetomys emini	criemi	1	1	1	1	1	1	1
Dasymys sp (based on incomtus)	dassp	0	0	0	0	1	1	0
Dendromus messorius	denmes	0	0	0	0	0	0	1
Dendromus sp1	densp1	0	0	0	0	1	1	0
Dendromus sp2	densp2	0	0	0	0	1	1	0
Deomys ferrugineus	deoferr	0	0	0	1	1	1	1
Epixerus wilsoni /ebii	epiwil	0	0	0	0	0	0	1
Funisciurus anerythrus	funleu	0	0	0	1	0	0	0
Funisciurus isabella	funane	0	0	0	1	0	0	0
Funisciurus lemniscatus	funisa	0	0	0	1	0	0	1
Funisciurus leucogenys	funlem	0	0	0	1	1	1	1
Funisciurus pyrrhopus	funpyr	0	0	0	1	1	1	1
Gerbilliscus kempi	gerkem	1	0	1	0	0	0	0
Grammomys rutilans / kuru	grarut	0	0	0	1	1	1	1
Grammomys sp.	gramsp	1	1	0	0	0	0	0
Graphiurus sp> Lorraineus as example	grapsp	0	0	0	1	0	0	0
Heimyscus fumosus	heifum	0	0	0	0	0	0	1
Heliosciurius gambianus	helgam	0	0	0	0	1	1	0
Heliosciurius rufobrachium	helruf	1	1	1	1	0	0	1
Hybomys univittatus	hybuni	0	0	0	1	1	1	1
Hylomyscus alleni	hylall	0	0	0	0	0	0	1
Hylomyscus parvus	hylpar	0	0	0	0	1	1	0
Hylomyscus sp	hylsp	0	0	0	1	1	1	0
Hylomyscus stella	hylste	1	1	1	0	0	0	0
Hystrix cristrata	hyscri	1	0	1	0	0	0	0
Idiurus macrotis	idimac	0	0	0	1	0	0	1
Idiurus zenkeri - similar to macrotis	idizen	0	0	0	1	0	0	0
Lemniscomys striatus	leggsp	0	0	0	0	1	1	0
Lophuromys nudicaudus	lemstr	0	0	0	1	1	1	0
Lophuromys sp	lopnud	0	0	0	0	0	0	1
Lophurumys sikapus	lophsp	0	0	0	1	0	0	0
Malacomys longipes	lopsik	1	1	1	0	1	1	0
Mastomys sp (natalensis)	mallon	1	1	0	1	1	1	1
Mus bufo (grassland-forest)	mastsp	0	0	0	1	0	0	0
Mus musculoides	musbuf	1	0	1	0	0	0	0
Mus setulosus - similar mus muscul.(grassland-forest)	musmus	1	0	1	0	0	0	0
Mus sp	musset	0	0	0	1	0	0	1
Myoscirius pumilio	myopum	0	0	0	0	0	0	1
Oenomys hypoxanthus	oenhyp	0	0	0	1	1	1	1
Paraxerus (alexandri)	parale	1	1	0	0	0	0	0
Paraxerus poensis	parpoe	0	0	0	1	1	1	1
Praomys jacksoni	prajac	1	1	1	0	0	0	0
Praomys lukolelae	praluk	0	0	0	0	0	0	1
Praomys misonnei	pramis	1	0	1	0	0	0	0
Praomys sp	praosp	0	0	0	1	1	1	0
Praomys tullberghi	pratull	0	0	0	0	0	0	1
Prionomys batesi	pribat	0	0	0	1	0	0	0
Protoxerus strangeri	prostr	0	0	0	1	1	1	1
Rattus rattus	ratrat	0	0	0	0	1	1	1
		0	0	0	1	1	1	1
	stolon							
Stochomys longicaudatus Thryonomys swinderianus	thrswi	1	0	1	1	1	1	1
Stochomys longicaudatus							_	

Assemblage Ma	trix Pa	rt 4						
Species Full name	Species	RF	RF1	RF23	CAR	СО	CAM	EQG
CHIROPTEI	RA							
Casynicteris argynnis	casarg	0	0	0	1	0	0	0
Chaerephon aloysiisabaudiae /Tadarida	chaalo	0	0	0	1	0	0	0
Chaerophon / Tadarida nigeriae	tadnig	0	0	0	1	0	0	0
Chaerephon pumilus /Tadarida	chapum	1	1	1	1	0	0	0
Eidolon helvum	eidhul	0	0	0	1	1	1	1
Epomophorus gambianus	epogam	0	0	0	1	0	0	0
Epomophorus sp	eposp	0	0	0	1	0	0	0
Epomops franqueti	epofra	0	0	0	1	1	1	1
Eptesicus tenuipinnis /Pipistrellus	eptten	0	0	0	1	0	0	1
Glauconycteris poensis	glapoe	0	0	0	0	0	0	1
Hipposideros beatus	hipbea	0	0	0	1	0	0	0
Hipposideros caffer	hipcaf	0	0	0	1	0	0	0
Hipposideros commersonni> probably. H. gigas	hipcom	0	0	0	1	0	0	0
Hipposideros cyclops	hipcyc	0	0	0	1	1	1	1
Hipposideros ruber	hiprub	1	1	1	1	1	1	1
Hypsignatus monstrosus	hypmon	0	0	0	1	1	1	0
Kerivulla harrisoni / lanosa	kerhar	0	0	0	1	0	0	0
Megaloglossus woermanni	megwoe	0	0	0	1	1	1	1
Micropteropus pusillus	micpus	1	1	1	1	1	1	1
Mimetillus moloneyi	mimmol	0	0	0	1	0	0	1
Miniopterus inflatus	mininf	0	0	0	0	0	0	1
Miniopterus schreibersii	minsch	0	0	0	0	0	0	1
Mops brachypterus /Tadarida	mopbra	0	0	0	1	0	0	1
Mops nanulus	mopnan	0	0	0	0	0	0	1
Mops spurrelli	mopspu	0	0	0	1	0	0	1
Mops thersites	mopthe	0	0	0	1	0	0	1
Myonycteris angolensis ruwenzori / Lissonycteris	myoang	1	1	1	0	0	0	1
Myonysteris torquata	myotor	1	1	1	1	1	1	1
Myotis bocagei	myoboc	0	0	0	1	0	0	1
Neoromicia capensis / Pipistrellus	neocap	0	0	0	0	0	0	1
Neoromicia nanus / Pipistrellus	neonan	1	1	1	1	0	0	1
Nycteris arge	nycarg	0	0	0	0	1	1	0
Nycteris grandis	nycgra	0	0	0	0	1	1	1
Nycteris hispida	nychis	0	0	0	1	0	0	1
Nycteris sp	nycsp	0	0	0	0	1	1	0
Pipistrellus nanulus	pipnan	0	0	0	1	0	0	1
Rhinolophus alcyone	rhialc	0	0	0	0	0	0	1
Rhinolophus landeri	rhilan	0	0	0	0	0	0	1
Rousettus aegypticus (leachii)	rouaeg	1	1	1	0	0	0	1
Scotonycteris zenkeri	scozen	0	0	0	1	0	0	1
Scotophilus nigrita	sconig	0	0	0	1	0	0	0

Table 3| Forest mammal community: Output from statistics used in 5.2.2. and 5.2.4. with forest area size (A), Amount of species (SP) and functional entities (FE), Functional Richness (F.Rich), Redundancy (Red), Over redundancy (OvRed: 1= number, 2= percentage) and Vulnerability (Vuln)

	Sum	mary	statist	ical re	sults				
Area	Parc name	A(km²)	#SP	#FE	F.Rich.	Red	OvRed1	OvRed2	Vuln
RAFALE1	na	0,96	25	19	2,2	1,316	0,164	16,4	0,684
RAFALE23	na	17,19	33	23	7,6	1,435	0,198	19,8	0,652
RAFALE	na	18,15	39	28	12,4	1,393	0,201	20,1	0,714
CAR	Ngotto	2683	98	56	62,8	1,75	0,253	25,3	0,589
CONGO	Odzala	13546	71	43	31,4	1,651	0,238	23,8	0,605
CAMEROON	Dja	5260	70	43	36,3	1,628	0,233	23,3	0,605
EQGUINEA	Monte Alén National Park (PNMA)	2000	95	49	59,6	1,939	0,277	27,7	0,571

Table 4 | Complete mammal community: Output from statistics used in 5.2.4. with forest area size (A), Amount of species (SP) and functional entities (FE), Functional Richness (F.Rich), Redundancy (Red), Over redundancy (OvRed: 1= number, 2= percentage) and Vulnerability (Vuln)

	Sum	mary	statist	ical res	sults		•		
Area	Parc name	A(km²)	#SP	#FE	F.Rich.	Red	OvRed1	OvRed2	Vuln
RAFALE1	na	0,96	31	23	1,8	1,348	0,18	18	0,696
RAFALE23	na	17,19	45	31	8,7	1,452	0,201	20,1	0,645
RAFALE	na	18,15	53	37	16,3	1,432	0,204	20,4	0,676
CAR	Ngotto	2683	119	64	40,1	1,859	0,267	26,7	0,578
CONGO	Odzala	13546	90	53	29,4	1,698	0,233	23,3	0,566
CAMEROON	Dja	5260	89	53	34,5	1,679	0,229	22,9	0,566
EQGUINEA	Monte Alén National Park (PNMA)	2000	110	56	51,5	1,964	0,289	28,9	0,589

Table 5| **Beta-diversities: Output from statistics used in 5.2.3. with** Cameroon (Ca), Congo-Brazzaville (Co), Central African Republic (Car), Equatorial-Guinea (Eq), RAFALE (Rf, three patches summarised as one)

Output β-diversity (%)								
Comparisons Taxonomic Functional Turn over Nested								
Ca - Co	2,9	6,9	3,6	3,3				
Ca - Car	32,7	19,4	0,2	19,2				
Co - Car	33,4	21,4	6,5	14,9				
Car - Eq	35,8	14,5	10,6	3,9				
Ca - Eq	41,2	25,2	12,5	12,7				
Co - Eq	41,2	22,5	12,3	10,2				
Car - Rf	74,1	47,6	0	47,6				
Eq - Rf	76,8	47,8	6,3	41,5				
Ca - Rf	82,1	37,8	4,9	32,9				
Co - Rf	82,2	41,5	8	33,5				

Table 6 Area size thresholds: Output from Excel used in 5.2.4.

Method estimation threshold values							
Category Congo value (x) Equation RAF - EQG Threshold value (y)							
Forest - SP	71	y = 0,0283x + 38,487	1148,869				
All - SP	90	y = 0,0288x + 52,478	1302,847				
Forest - FE	43	y = 0,0106x + 27,808	1433,208				
All - FE	53	y = 0,0096x + 36,826	1684,792				

Table 1| **Trait matrix medium and large mammals : Input for statistics** : masscode (mean weight) : xl(>50kg), l(>15kg), m(>5kg), s(>1kg), xs(<1kg); loco (locomotion when foraging) : TE(terrestrial), AR(arboreal), TA(terrestrial and arboreal), AE(aerial), AQ(aquatic); primfood (primary food source) : FR(frugivorous), HE(herbivorous), IN(invertebrates), CA(carnivorous); act (activity when foraging): D(day), N(night), DN(day and night); social (sociality when foraging) : S(social), NS(solitary); Yellow marked species were not included in analyses regarding solely forest communities; generalists were not excluded (information extracted from Kingdon et al. 2003).

Trait matrix M & L assemblage Part 1								
Species full name	species	bodymass	loco	primfood	act	social		
PRIMAT	ES							
Arctocebus calabarensis	arccal	XS	AR	IN	N	ns		
Cercopithecus ascanius	cerasc	s	AR	FR	D	s		
Cercopithecus cephus	cercep	S	AR	FR	D	S		
Cercopithecus mitis	cermit	m	AR	FR	D	s		
Cercopithecus nictitans	cernic	m	AR	FR	D	s		
Cercopithecus pogonias	cerpog	S	AR	FR	D	S		
Chlorocebus aethiops	chlaet	s	TA	FR	D	S		
Colobus quereza	colgue	m	AR	HE	D	S		
Colobus satanas	colsat	m	AR	FR	D	s		
Euoticus elegantulus	euoele	xs	AR	HE	N	ns		
Galago alleni	galall	xs	TA	FR	N	ns		
Galago demidoff	galdem	XS	AR	IN	N	ns		
Galago thomasi	galtho	XS	AR	IN	N	ns		
Gorilla gorilla	gorgor	xl	TA	HE	D	S S		
Lophocebus albigena	lopalb		AR	FR	D			
Mandrillus sphinx		m I	TE	FR	D D	S		
	mansph	<u> </u>	TA	+		S		
Pan troglodytes	pantro	<u> </u>		FR	D	S		
Papio anubis	papanu	1	TA	HE	D	S		
Perodictius potto	perpot	S	AR	FR	N	ns		
Pilicolobus rufilatus	pilruf	m	AR	HE	D	S		
CARNIVO	RA			, ,		<u>, </u>		
Aonyx capensis	aoncap	m	AQ	IN	N	ns		
Aonyx congica	aoncon	m	AQ	IN	N	ns		
Atilax paludinosus	atipal	s	AQ	IN	N	ns		
Bdeogale nigripes	bdenig	S	TE	CA	N	ns		
Canis adustus	canadu	m	TE	CA	N	S		
Civettictis civetta	civciv	m	TE	CA	N	ns		
Crossarchus alexandri	croale	S	TE	IN	DN	S		
Felis aurata	felaur	m	TA	CA	N	ns		
Felis serval	felser	m	TE	CA	DN	ns		
Genetta angolensis	genang	S	TE	IN	N	ns		
Genetta maculata	genmac	S	TA	CA	N	ns		
Genetta servalina	genser	S	TA	CA	N	ns		
Genetta victoriae	genvic	S	TA	CA	N	ns		
Herpestes sanguineus	hersan	xs	TA	IN	D	ns		
Mellivora capensis	melcap	m	TE	CA	N	ns		
Nandinia binotata	nanbin	S	AR	FR	N	ns		
Panthera pardus	panpar	xl	TA	CA	DN	ns		
PROBOSCI				<u> </u>				
Loxodonta africana	loxafr	xl	TE	HE	DN	s		

Trait matrix M & L ass	embla	ge Part	2			
Species full name	`	bodymass		primfood	act	social
AFROSORIO	IDA					
Potamogale velox	potvel	xs	AQ	IN	N	ns
HYRACOID	EA					
Dendrohyrax dorsalis	dendor	S	TA	HE	N	ns
Heterohyrax brucei	hetbru	S	TA	HE	D	S
ARTIODACT	YLA					
Cephalophus callipgus	cepcal	I	TE	FR	D	ns
Cephalophus dorsalis	cepdor	ı	TE	FR	N	ns
Cephalophus leucogaster	cepleu	ı	TE	FR	D	ns
Cephalophus monticola	cepmon	s	TE	FR	D	S
Cephalophus ogilbyi	cepogi	I	TE	FR	D	ns
Cephalophus rufilatus	cepruf	m	TE	FR	D	ns
Cephalophus silvicultor	cepsil	хl	TE	FR	D	ns
Hippotamus amphibius	hipamp	хl	TE	HE	N	ns
Hyemoschus aquaticus	hyeaqu	m	TE	FR	N	ns
Neotragus batesi	neobat	S	TE	HE	DN	ns
Potamochoerus porcus	potpor	xl	TE	HE	N	S
Syncerus caffer nanus	syncaf	xl	TE	HE	DN	S
Tragelaphus scriptus	trascr	- 1	TE	HE	DN	ns
Tragelaphus spekei	traspe	xl	AQ	HE	D	S
PHOLIDOTA						
Manis gigantea	mangig	- 1	TE	IN	N	ns
Manis tetradactyla	mantet	s	TA	IN	DN	ns
Manis tricuspis	mantri	S	TA	IN	N	ns
RODENTIA						
Hystrix cristata	hyscri	m	TE	HE	N	S
Thyronomys swinderianus	thyswi	S	AQ	HE	N	S

Table 2| **Assemblage Matrix medium and large mammals : Input for statistics:** absence (0) and presence (1) with only FG1 (RF1), only FG23 (RF23), The Lopé Reserve (Lope) and the fragments surrounding the reserve (Lopefr). Yellow marked species were not included in analyses solely regarding forest communities; generalists were not excluded (Information extracted from Tutin et al. 1997).

Assemblage Matrix M & L assemblage Part 1								
Species Full name	Species	RF1	RF23	Lope	Lopefr			
PRIMATES								
Arctocebus calabarensis	arccal	0	0	1	0			
Cercopithecus ascanius	cerasc	1	1	0	0			
Cercopithecus cephus	cercep	0	0	1	1			
Cercopithecus mitis	cermit	1	1	0	0			
Cercopithecus nictitans	cernic	0	0	1	1			
Cercopithecus pogonias	cerpog	0	0	1	1			
Chlorocebus aethiops	chlaet	1	0	0	0			
Colobus guereza	colgue	0	1	0	0			
Colobus satanas	colsat	0	0	1	1			
Euoticus elegantulus	euoele	0	0	1	0			
Galago alleni	galall	0	0	1	0			
Galago demidoff	galdem	0	0	1	1			
Galago thomasi	galtho	1	0	1	0			
Gorilla gorilla	gorgor	0	0	1	1			
Lophocebus albigena	lopalb	0	1	1	1			
Mandrillus sphinx	mansph	0	0	1	1			
Pan troglodytes	pantro	1	1	1	1			
Papio anubis	papanu	1	1	0	0			
Perodictius potto	perpot	0	0	1	0			
Pilicolobus rufilatus	pilruf	1	1	0	0			
CARNIVORA	\							
Aonyx capensis	aoncap	0	0	1	0			
Aonyx congica	aoncon	0	0	1	0			
Atilax paludinosus	atipal	0	0	1	0			
Bdeogale nigripes	bdenig	0	0	1	0			
Canis adustus	canadu	0	1	0	0			
Civettictis civetta	civciv	1	0	1	0			
Crossarchus alexandri	croale	0	1	0	0			
Felis aurata	felaur	0	0	1	0			
Felis serval	felser	0	1	0	0			
Genetta angolensis	genang	0	1	0	0			
Genetta maculata	genmac	0	1	1	0			
Genetta servalina	genser	0	1	1	1			
Genetta victoriae	genvic	0	1	0	0			
Herpestes sanguineus	hersan	0	0	1	0			
Mellivora capensis	melcap	0	0	1	0			
Nandinia binotata	nanbin	0	1	1	1			
Panthera pardus	panpar	0	0	1	1			
PROBOSCIDA	E							
Loxodonta africana	loxafr	0	0	1	1			

Assemblage Matrix M & L assemblage Part 2								
Species Full name	Species	RF1	RF23	Lope	Lopefr			
AFROSORICIDA				·				
Potamogale velox	potvel	1	1	1	0			
HYRACOIDEA								
Dendrohyrax dorsalis	dendor	0	0	1	1			
Heterohyrax (brucei)	hetbru	0	?	0	0			
ARTIODACTYLA								
Cephalophus callipgus	cepcal	0	0	1	1			
Cephalophus dorsalis	cepdor	0	0	1	1			
Cephalophus leucogaster	cepleu	0	0	1	1			
Cephalophus monticola	cepmon	0	0	1	1			
Cephalophus ogilbyi	cepogi	0	0	1	1			
Cephalophus rufilatus	cepruf	0	1	0	0			
Cephalophus silvicultor	cepsil	0	0	1	1			
Hippotamus amphibius	hipamp	0	0	1	0			
Hyemoschus aquaticus	hyeaqu	0	0	1	0			
Neotragus batesi	neobat	0	0	1	0			
Potamochoerus porcus	potpor	0	0	1	0			
Syncerus caffer nanus	syncaf	0	0	1	0			
Tragelaphus scriptus	trascr	0	0	1	1			
Tragelaphus spekei	traspe	0	0	1	1			
PHOLIDOTA								
Manis gigantea	mangig	0	0	1	0			
Manis tetradactyla	mantet	0	1	1	0			
Manis tricuspis	mantri	1	1	1	1			
RODENTIA								
Hystrix cristata	hyscri	0	1	0	0			
Thyronomys swinderianus	thyswi	0	?	0	0			

Table 3 Medium and large mammal community: Output from statistics used in 5.2.5. with area size (A), Amount of species (SP) and functional entities (FE), Functional Richness (F.Rich), Redundancy (Red), Over redundancy (OvRed: 1= number, 2= percentage) and Vulnerability (Vuln)

Summary statistical results									
Area	Area Forest state A(km²) #SP #FE F.Rich. Red OvRed1 OvRed2 Vul								Vuln
RAFALE1	Isolated 0,96 10 10 0,001 1 0 0								1
RAFALE23	B Isolated 17,19 17 13 5,1 1,308 0,181 18,1 0,7							0,769	
Lopefr Nearby cont. Forest max. 0,11 21 16 6,6 1,312 0,193 19,3							0,812		
Lope	Continuous Forest	4200	40	29	57,7	1,379	0,199	19,9	0,724

Table 4| Beta-diversities medium and large mammals: Output from statistics used in 5.2.5.

Output β-diversity (%)									
Comparisons Taxonomic Functional Turn over Nested									
FG1 - FG23	53,7	61,9	36,9	25					
FG1 - Lope	77,1	82,1	22	60,1					
FG1 - Lopefr	89,3	79,3	48,2	31,1					
FG23 - Lope	74,4	66,9	17,1	49,8					
FG23 - Lopefr	79,8	60,2	39,5	20,7					
Lope - Lopefr	32,3	37,7	0	37,7					

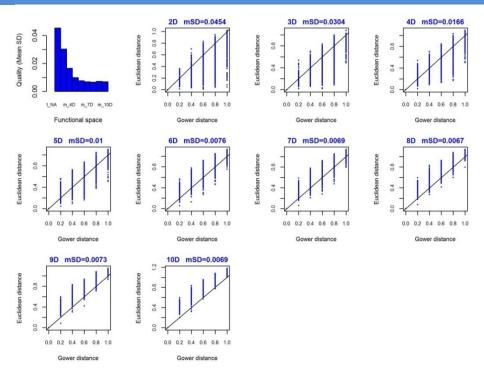


Figure 1| **Example R output** (forest only): results with the use of qual_funct_space measures the quality (i.e. mean squared-deviation between initial functional distance and standardised distance in the functional space) for the best functional space. In this example, eight dimensions would be the best choice (Maire et al. 2015).

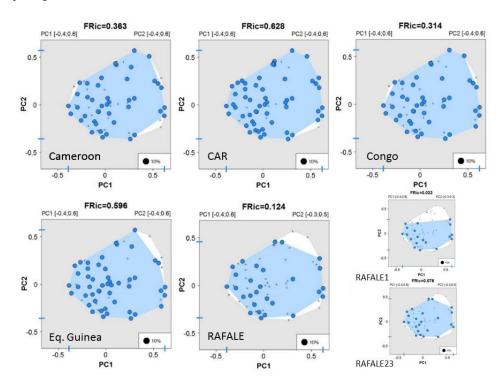


Figure 2 Example R output (forest only): illustration how changes in species composition can modify the functional richness (FRic) by depicting changes in the convex surface gathering all the species belonging to the community. Other axispairs display different shapes of convex surfaces but all of them lead to the same value of FRic, with multidimFD' function to compute and illustrate multidimensional functional diversity indices for a set of species assemblages (Mouillot et al. 2013).

Table 1| **Example R output** (forest only): After the axes are constructed of relevant combinations of the selected ecological traits, every species gets its own coordinates alongside every one of those axes (Mouillot et al. 2013, eight dimensions, 8 axes in this example).

artare		PC1	PC2	PC3	PC4	PC5
arctacl -0.214258004 -0.118646073 0.0736771733 0.316189607 -0.200018217 cerator 0.555401993 0.221737804 -0.0310263803 -0.263205747 -0.014365056 cercep 0.618555954 -0.116082320 -0.1056094948 0.052157848 -0.092254356 cerneq 0.618555954 -0.116082320 -0.1056094948 0.052157848 -0.092254356 cerneq 0.618555954 -0.116082320 -0.1056094948 0.052157848 -0.092254356 cerpog 0.618555954 -0.116082320 -0.1056094948 0.052157848 -0.092254356 cerpog 0.618555954 -0.116082320 -0.1056094948 0.052157848 -0.092254356 cerpog 0.618555954 -0.116082320 -0.1056094948 0.052157848 -0.092254356 colsat 0.618555954 -0.116082320 -0.1056094948 0.052157848 -0.092254356 colsat 0.618555954 -0.116082320 -0.1056094948 0.052157848 -0.092254356 colsat 0.05609362 -0.126609586 -0.03136663	artaro		-			
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