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Agro-Bio Tech

Distribution and determinants of mammal assemblages across central African forests

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DISTRIBUTION AND DETERMINANTS OF MAMMAL ASSEMBLAGES ACROSS CENTRAL AFRICAN FORESTS

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Dissertation originale présentée en vue de l'obtention du grade de docteur en sciences
agronomiques et ingénierie biologique

Promoteur(s) : Dr Adeline FAYOLLE ; Pr. Cédric VERMEULEN
Année civile : 2022

This work benefitted from a FRIA grant of the Fonds de la Recherche Scientifique (FNRS) in Belgium and also received support from the “Programme de Promotion de l’Exploitation Certifiée des Forêts” (PPECF) (contract C132) and the “Commission des Forêts d’Afrique Centrale” (COMIFAC) through the project “De l’Inventaire au Plan de Gestion de la Faune, développement d’outils pour rencontrer les exigences des référentiels de certification” (IPGF).

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Abstract

Central Africa is one of the last parts of the world where large mammal assemblages can be regarded as nearly intact in comparison to the Late Pleistocene levels. Yet the tropical forests of the region face significant threats, including overhunting, which could trigger rapid and widespread wildlife depletion even in the most remote areas. In this context of unprecedent defaunation, the aim of this thesis is to identify the distribution patterns of mammal assemblages and their determinants across central African forests at both regional and local scales.

Firstly, as a preliminary step to the local assessment of mammal assemblage alteration, I explored the biogeography of central African forests (**Chapter 2**). Using species lists from wildlife and bushmeat-related surveys, I classified the region into zoogeographic districts. Then, random forest classification models were used to identify the environmental and spatial determinants of the districts' distribution as well as to produce a wall-to-wall zoogeographic map critical for assessing the district's conservation status and ongoing threats. While carnivores do not present a clear spatial structure across central African forests, our findings highlighted the congruence between primate and artiodactyl assemblages and the structuring role of rivers on their distribution. Priority districts, threatened and poorly represented in the protected area network, were pinpointed and implications for further conservation were proposed.

Secondly, I determined the most appropriate sampling strategy for surveying terrestrial mammals in tropical forests using camera traps (**Chapter 3**), a non-invasive technique widely used to monitor wildlife populations worldwide. I specifically tested the impact of the camera orientation on the remotely sensed mammal diversity within a responsibly managed logged forest in eastern Gabon. Using a pairwise design composed of systematically placed and wildlife-trail-oriented camera traps, I showed that both orientations provide a comparable picture of the particularly rich and well-preserved ground-dwelling mammal assemblages in the area. Species richness, detectability and capture rates, and the species composition of the assemblages were barely influenced by the camera orientation, paving the way for multi-site analyses combining both types of camera trap data.

Thirdly, relying on standardized camera trap surveys, I identified the main determinants of the species composition of mammal assemblages along a gradient of increasing anthropogenic pressure in two distinct zoogeographic districts, in southeastern Cameroon (**Chapter 4**) and in eastern Gabon (**Chapter 5**). Responsibly managed production forests were found to be of varying conservation value, supporting similar species richness and composition to nearby protected areas but also more depleted assemblages. Rather than forest management, it is mainly forest accessibility that determines the alteration state of mammal assemblages in these areas. Village hunting territories, for their part, exhibit altered assemblages, dominated by rodents and small-size species, but the degree of alteration strongly varied between villages, likely related to local history of hunting pressure.

In this thesis, I evidenced the diverse and unique mammal assemblages found across central African forests and the dramatic level of pressure they face, highlighting urgent need for coordinated conservation strategies. I reasserted the conservation potential of responsibly managed production forests and the buffer role they can play around protected areas, as long as integrated wildlife management is safeguarded and coupled with a strict control of forest access. Generally depleted, village forests still contribute to people livelihoods and can maintain populations of species resistant to hunting if offtake pressure does not recklessly soar. Moving towards a model of sustainable use of game species in these forests is a priority to ensure the long-term persistence of the region's wildlife but may be hampered by the lack of monitoring and management tools that can be easily appropriated by local communities, as well as the limited ecological knowledge of even the most hunted mammal species. In this perspective, I paved the way for a conceptual framework describing the differential response of species to hunting and applied it on hunting offtake and camera trap data obtained from eastern Gabon to discern which species would be unlikely to withstand low and moderate harvesting pressure from those that might thrive while being hunted. Finally, I highlighted the research outputs and products generated in this work of interest to forest managers and, more broadly, to wildlife ecologists, and the ancillary but critical ecological information that can be gleaned from camera trap surveys, notably the evidence of range extension of two primate species in Gabon.

Résumé

L'Afrique centrale est l'une des dernières régions du monde où les assemblages de grands mammifères peuvent être considérés comme quasiment intacts par rapport aux niveaux de la fin du Pléistocène. Les forêts tropicales de la région restent toutefois confrontées à d'importantes menaces, notamment la chasse excessive, qui pourrait entraîner un appauvrissement rapide et généralisé de la faune, même dans les zones les plus reculées. Dans ce contexte, l'objectif de cette thèse est d'identifier les patrons de distribution des assemblages de mammifères et leurs déterminants dans les forêts d'Afrique centrale aux échelles régionale et locale.

Premièrement, comme étape préliminaire à l'évaluation locale du degré d'altération des assemblages de mammifères, j'ai étudié la biogéographie des forêts d'Afrique centrale (**Chapitre 2**). Sur base de listes d'espèces provenant d'inventaires fauniques et d'enquêtes sur la viande de brousse, j'ai proposé une division de la région en districts zoogéographiques. Ensuite, j'ai utilisé des modèles de classification par forêt aléatoire pour identifier les déterminants environnementaux et spatiaux expliquant la distribution de ces districts, ainsi que pour dresser une carte zoogéographique continue de la région, essentielle pour évaluer l'état de conservation et les menaces encourues pour chaque district. Alors que la distribution des carnivores ne présente pas de structuration spatiale claire au sein des forêts d'Afrique centrale, nos résultats ont mis en évidence des patrons de distribution convergents entre les assemblages de primates et d'artiodactyles et le rôle structurant des rivières. Les districts prioritaires, menacés et mal représentés dans l'actuel réseau d'aires protégées, ont été identifiés et des orientations pour une meilleure conservation ont été proposées.

Dans un second temps, j'ai déterminé la stratégie d'échantillonnage la plus appropriée pour étudier les mammifères terrestres dans les forêts tropicales à l'aide de pièges photographiques (**Chapitre 3**), une technique peu intrusive largement utilisée pour recenser les populations d'animaux sauvages dans le monde entier. J'ai plus spécifiquement testé l'impact de l'orientation du piège photographique sur l'évaluation de la diversité mammalienne détectée au sein d'une forêt exploitée de manière responsable dans l'est du Gabon. À l'aide d'un dispositif d'échantillonnage par paires composées d'un piège photographique orienté de manière systématique et d'un autre orienté vers une piste animale, j'ai mis en évidence que les deux orientations dressent un portrait comparable des assemblages de mammifères terrestres, particulièrement riches et bien préservés dans cette zone d'étude. La richesse en espèces, la détectabilité et les taux de capture individuels, ainsi que la composition spécifique des assemblages sont peu influencés par l'orientation du piège photographique, ouvrant la voie à des analyses multi-sites combinant les deux types de données.

Troisièmement, j'ai identifié par le biais d'inventaires par pièges photographiques standardisés les principaux déterminants de la composition spécifique des assemblages de mammifères le long d'un gradient de pression anthropique croissant dans deux districts zoogéographiques distincts : le sud-est du Cameroun (**Chapitre 4**) et l'est du Gabon (**Chapitre 5**). Les forêts de production de bois d'œuvre exploitées de manière responsable se sont avérées posséder une valeur conservatoire variable, abritant tantôt une richesse et une composition spécifique similaires à celles des zones protégées voisines, tantôt des assemblages plus appauvris. Plutôt que la gestion

forestière, c’est surtout l'accessibilité des forêts qui détermine l'état d'altération des assemblages de mammifères dans ces massifs. Les terroirs de chasse villageois présentent quant à eux des assemblages altérés, dominés par les rongeurs et les espèces de petite taille, mais le degré d'altération varie fortement entre les villages, probablement en lien avec l'histoire locale de la pression de chasse.

Dans cette thèse, j'ai fait le point sur la diversité et la singularité des assemblages de mammifères présents dans les forêts d'Afrique centrale et le niveau de pression considérable auquel ils sont confrontés localement, soulignant le besoin urgent de stratégies de conservation coordonnées. J'ai réaffirmé le potentiel de conservation des forêts de production gérées de manière responsable et le rôle tampon qu'elles peuvent jouer autour des aires protégées, à condition qu’une gestion intégrée de la faune soit maintenue et combinée à un contrôle strict des accès à la forêt. Généralement appauvries en faune, les forêts villageoises contribuent toujours aux moyens de subsistance des populations rurales et peuvent assurer le maintien de populations d'espèces résistantes à la chasse tant que la pression des prélèvements ne croît pas de façon inconsidérée. L'évolution vers un modèle de prélèvement durable du gibier dans ces forêts constitue une priorité pour assurer la survie à long terme de la faune de la région, mais elle peut être compromise par le manque d'outils de suivi et de gestion facilement appropriables par les communautés locales, ainsi que par les connaissances écologiques limitées des espèces de mammifères, même les plus couramment chassées. Dans cette perspective, j'ai posé les premières bases d'un cadre conceptuel décrivant la réponse différenciée des espèces à la chasse et je l'ai transposé aux données de prélèvements de chasse et aux données issues des pièges photographiques obtenues dans l'est du Gabon afin de discerner les espèces qui seraient peu susceptibles de résister à une pression de prélèvement faible à modérée de celles qui pourraient prospérer tout en étant chassées. Pour finir, j'ai présenté les réalisations et les produits générés dans le cadre de ce travail qui présentent un intérêt particulier pour les gestionnaires forestiers et, plus largement, pour les écologues de la faune, ainsi que les informations écologiques secondaires mais néanmoins capitales qui peuvent être obtenues à partir d’inventaires par pièges photographiques, et notamment la preuve de l'extension de l'aire de distribution de deux espèces de primates au Gabon.

Une thèse qui s'achève c'est aussi le moment de lancer un petit coup d'œil dans le rétroviseur. L'occasion de se rappeler que malgré ses apparences solitaires et austères, la thèse est une aventure certes complexe mais enrichissante et que l'on vit et que l'on partage avec un très grand nombre de personnes que je veux remercier ici dans les quelques lignes qui suivent. Chacune de ces personnes m'a apporté une aide, un soutien et des encouragements, qu'ils aient été ponctuels ou bien continus, qui ont permis à cette thèse de voir le jour et je remercie chacune d'entre elles pour cela.

Je tiens avant tout à remercier mes deux promoteurs, Adeline et Cédric, sans qui rien de tout ça n'aurait été possible.

De mes premiers pas dans l'analyse de données quelque part à Yaoundé jusqu'à la rédaction d'un projet bien ficelé en un temps record, tu as toujours cru en moi **Adeline**. Ton soutien et tes conseils mais aussi ton empathie et ton enthousiasme tout au long de ces années ont permis à ce bonhomme à l'esprit « un peu tordu », comme tu aimes à le décrire, de se former et de grandir. Au détour de quelques gin'to et soirées improvisées, tu es devenue bien plus qu'une « simple » promotrice : une oreille attentive, prête à rigoler ou à recadrer quand il le faut, et un soutien sans faille. Alors je te dis Merci ! Merci de répondre « Of course ! » à mes innombrables messages Skype « Tu as 2 secondes ? » alors que tu sais bien que cela durera des minutes, voire des heures. Merci d'encadrer tes doctorants comme des collègues en qui tu crois. Merci de veiller à mettre de l'humain quand il le faut et de la rigueur quand il y en a besoin. Et Merci aussi pour tous ces petits souvenirs que je n'ai pas l'occasion d'évoquer ici mais qui font que je me remémorerai cette thèse comme une chouette aventure plus qu'une épreuve de longue haleine.

La première impression n'est pas toujours la bonne, dit-on. Je suis bien heureux de l'avoir constaté avec toi **Cédric** ! Derrière ce gabarit impressionnant et cette éloquence naturelle qui m'intimidait lors de nos premières rencontres se cache un encadrant à l'écoute qui aime challenger les chercheurs qu'il encadre, toujours à la recherche de ce petit plus qui rendra notre travail le plus utile possible. Des histoires de terrain en passant par ton rire inimitable et un « coin coin » glissé comme un bonjour en ouvrant la porte du bureau, c'est aussi ce qui me vient à l'esprit quand je repense à ces années. Je suis sûr que la faune, la conservation ou bien l'humain nous feront nous recroiser encore de nombreuses fois au détour d'un vocal WhatsApp ou d'une bière à l'*alma mater*.

Derrière le duo qui a mis en musique cette thèse se cache en fait un trio ! Et je ne pouvais pas ne pas évoquer ici le rôle de promoteur de l'ombre que tu as joué **Jean-Louis**. Tu as en fait endossé un peu tous les rôles dans cette thèse : professeur quand il a fallu me former, directeur de labo quand il a fallu m'intégrer à l'équipe , encadrant quand il a fallu s'attaquer aux aspects pratico-pratiques du terrain, et enfin collègue et ami lors des nombreux moments que nous avons pu partager dans et hors du bureau. Merci pour tout !

Je tiens également à remercier l'ensemble du comité de thèse qui a suivi mon évolution et m'a subtilement conseillé au gré de nos réunions annuelles.

Je tiens plus particulièrement à remercier **Philippe Lejeune** qui a joué à merveille le rôle de garde-fou aussi bien dans le comité d'accompagnement qu'en acceptant de présider le jury de cette thèse. Je tiens à remercier aussi **Daniel Cornélis**. De nos premiers échanges de début de thèse à Montpellier s'est construit au fur et à mesure des mois une collaboration étroite et complice, parsemée de multiples discussions et anecdotes partagées jusqu'aux bouis-bouis de Lastoursville. Merci de m'avoir fait confiance durant ces années et de le faire pour encore quelque temps. Je tiens aussi à remercier chaleureusement, **Roseline Beudels** pour son inépuisable enthousiasme pour ma thèse et son soutien lors de la rédaction du projet initial et **Marc Dufrêne** pour son regard acéré et ses conseils avisés sur les diverses analyses et thématiques abordées dans ce travail. I would also like to thank **John Poulsen** for taking part in this thesis in the shadow of some papers for some time but more formally in recent weeks for his critical and constructive proofreading.

Cette thèse aura aussi été l'occasion d'apprendre à défendre son propre projet face à de multiples bailleurs que je tiens à remercier. Merci au jury FRIA d'avoir cru en un projet un peu ambitieux il faut se l'avouer. Merci au PPECF et à **Romain Lorent** d'avoir soutenu et insufflé à ce projet ses aspects les plus pratiques. L'argent ne fait pas une thèse pour paraphraser un dicton célèbre mais il y contribue tout de même pas mal !

Cette thèse qui a commencé dans les bons vieux murs de Gembloux et qui se clôture entre la Belgique et Montpellier m'a permis de rencontrer et travailler avec un tas de personnes que j'aimerais évoquer et remercier ici.

Au commencement, tu étais déjà là **Simon**. Un encadrant de mémoire du tonnerre, un ami de longue date maintenant qui a su trouver les mots et la motivation pour lancer ce projet de thèse avec moi et me soutenir tout du long. Merci pour ces moments partagés et ton inaltérable envie d'aider dans toutes les occasions !

Merci aussi à toi **Anaïs** ! Pour ces pétages de plomb qui débouchent en fou rire incontrôlé, pour tes conseils et ton aide tant appréciés qui m'ont aidé à garder la tête hors de l'eau plus d'une fois et pour ton soutien infaillible dans tous les moments forts de cette thèse.

Merci aux très nombreuses personnes du labo, de l'axe forestier ou même de la faculté qui ont croisé ma route tantôt en y amenant de la gaieté dans le train-train quotidien de la thèse tantôt en y apportant une aide et des conseils avertis. Je pense plus particulièrement à tous les doctorants, post-docs et autres collègues : **Leslie**, **Steeve**, **Chauvelin**, **Julie**, **Barbara**, **Fructueux**, **Romaric**, **Grace**, **Quentin G**., **Quentin E**., **Gaël**, **Robin**, **Donatien**, **Nassim**, **Gyslene**, **Sarah**, **Pedro**, **Modestine**, **Lisette**, **Romain**, **Alexandre**, **Capucine**, **Chloé**, **Gauthier**, **Nicolas**, **Jérôme**, **Estelle**, **Clotilde**, **Clément**, **Stéphanie**, **Sébastien, Héloïse, Mathilde, Victor**, **Yves**, **Blandine**, **Marie-Pierre**, **Hugues**, **Andyne**, **Lucie**, **Adrien**, **Peter**, **Corentin**, **Jeff**, **Jo**, **Aurore**, **Axel**, **Marie-Ange**, **Marie**, **Samuel**, **Alain**, **Cédric**, **Hassan**. Une pensée particulière va à mon binôme de choc, **Jean-Yves** mon paternel comme j'aime à l'appeler et **Marie-Alice**. Merci aussi aux employés de Nature +, passés et actuels, avec qui j'ai pu partager du temps de réflexion, des idées et de très bons moments. Je pense particulièrement à **Félicien**, **Charles**, **Kasso**, **Cécilia**, **Franck**, **Vincent**,

Adrien et **Sarah**. Ces derniers mois au CIRAD m'ont également permis de rencontrer une nouvelle équipe de recherche riche d'expériences, de soutien et de conseils dans la finalisation de ce travail. Je pense plus particulièrement à **Philippe**, **Sébastien**, **Noëmie**, **Plinio**, **Clarisse**, **Marie-Jo**, **Guillaume**, **Christophe**, **Hadrien**, **Marion, Stéphane, Benoît, Audrey, Guido, Salman**.

Cette thèse fut aussi l'occasion d'encadrer quelques personnes, de près ou de loin, qui m'ont fait et à qui j'ai fait confiance aussi et que je tiens à remercier. Je pense à **Florine**, **Justin**, **Manon**, **Cindy**, **Robin**, **Rémi**, **Mexan**, **Ulrich**, **Guy-Landry**, **Jeff, Harold**.

Une thèse en milieu tropical c'est beaucoup de temps sur un pc mais c'est aussi de belles aventures et rencontres lors de la collecte de données sur le terrain. De nombreuses personnes ont rendu ces missions de terrain faisables, agréables et productives et je voudrais ici les remercier toutes. Je pense plus particulièrement à **Phillipe Jeanmart**, **Paul Lagoute**, **Vincent Pasquet**, **Markus Pfannkuch**, **Nicolas Zurcher**, **Yanick Nkoulou**, **Frédéric Ober**, **Vincent Monnet**, **Herman Azambou**, **Belphégor Ngali**, **Paulin Nsonka**, **David Zakamdi**, **Samuel Pereira Dias**, **Martin Hega, Nicolas Deflandre, Toussaint Ogombet, Stéphane Kehou**, **Katharine Abernethy**, **Christopher Orbell**.

J'aimerais aussi remercier ma famille et mes amis car on est toujours le reflet quelque part de ceux qui nous entourent et nous aiment. Merci à mes parents de m'avoir bâti un cocon qui m'a protégé un temps mais qui s'est ouvert sur le monde une fois les armes de la vie bien acquises. Merci aussi à mes amis d'enfance (**Wen**, **Maud**, **Meg**), d'adolescence (**Lilou**, **Dono**, **Alex**) et de fac (**Flo**, **Pix**, **Loulou**, **Mickey**, **Charly**, **Adri**, **Lisou**, **Quentin**, **Eme**, la team forestier 2017, la team CenoBeats et tant d'autres…) qui par leurs mots, leur soutien et les moments partagés ont été les meilleurs compagnons de voyage qui soient !

Pour finir, mes derniers mots vont à toi **Morgane**, ma petite Mo... Un tempérament de feu mais plein d'empathie, une bouffé d'oxygène et de rire quand le besoin s'en fait ressentir et une force d'une fébrilité touchante. En somme une combinaison parfaitement parfaite qui dure depuis de nombreuses années et qui m'a permis de tenir le coup ces derniers mois. Merci pour ce soutien sans faille, pour ta patience et pour tes nombreux encouragements ! Merci pour tout !

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Figure 5.1 Location of the camera traps (black dots), the villages (black triangles), the national road (black line) and the Ogooué (blue line) across the study area as well as zoom on the utilization distribution (UD) within the hunting territory of each surveyed village (Ndambi, Doumé & Bembicani). UD was computed using a movement-based kernel method with a minimum smoothing parameter of 30 m and a diffusion coefficient of 500 m^2/sec on a 50m x 50m quadrat grid (see Benhamou & Cornélis, 2010, for a complete description of the method). The grey contour corresponds to the 95% UD isopleth provided by the classical kernel method using the ad hoc smoothing parameter.

Figure 5.2 *Main graph*: Faunistic similarity (Bray-Curtis index, from no similarity "0" to similar composition "1") between camera traps (1 camera trap = 1 point) along the studied gradient displayed on a non-metric multidimensional scaling, from the most hunted village (Bembicani) to the "intact" Ivindo National Park. *Histograms*: Mean detection rates in each site (three villages, the PWG-CEB logging company and the Ivindo National Park) of five species showing a contrasted trend along the gradient. *Bottom left*: the Bray-Curtis similarity of each camera trap compared to each camera trap in the Ivindo National Park, *i.e.*, the compositional alteration, presented in the form of smoothed histograms.

Chapter 6: General discussion

Figure 6.10 An example of an identification sheet for the white-bellied duiker (*Cephalophus leucogaster*) from the FAUNEFAC toolbox.

Figure 6.11 New camera trap records for *Cercocebus agilis* (a) and *Mandrillus sphinx* (b) in eastern Gabon. The background map corresponds to tree cover (Hansen *et al.* 2013). Species range (cross-hatched) from the International Union for Conservation of Nature (IUCN) and occurrence (cross) from the Global Biodiversity Information Facility (GBIF) repository (occurrence dataset: https://doi.org/10.15468/dl.d47asp, https://doi.org/10.15468/dl.p5qf62 accessed via GBIF.org on 2021-03-31) are also shown. The Minkébé National Park (NP) (1), Ivindo NP (2), Mwagna NP (3), Batéké Plateau NP (4) and Lopé NP (5) are highlighted in green.

Chapter 2: Mammal regionalization

Table 2.1 Conservation status and anthropogenic threats faced by the zoogeographical districts. Total coverage and proportion of areas under protection status, mean defaunation index ($\overline{\mathrm{DI}}$) (0 virtually represents a completely defaunated mammal community and 1 an intact community) (Benítez-López *et al.* 2019) and mean forest landscape integrity index ($\overline{\mathrm{FLI}}$) ranging from no forest integrity (0) up to a complete forest integrity (1) (Grantham *et al.* 2020) is provided for each zoogeographical district.

Chapter 3: Appropriate sampling

Table 3.1 List of detected species with the identifier (ID) used in the figures, IUCN status (listed as 'Least Concern' [LC], 'Near Threatened' [NT], 'Vulnerable' [VU], 'Endangered' [EN], or 'Critically Endangered' [CR]), and mean adult body mass following Mittermeier *et al.* (2013) for primates, Wilson *et al.* (2016) for rodents, and Wilson & Mittermeier (2009, 2011) for carnivores and hoofed mammals. The species average relative abundance index (RAI) and species site association (SSA) are given for each species and for each placement ('Syst' for systematic placement and 'Trail' for wildlife trail placement).

Table 3.2 (a) Multi-method occupancy model likelihood selection based on $\mathrm{AIC_c}$ for the 13 species with more than 10 detection events in both placements. Four occupancy models were compared: model (1), $\psi()\theta()p()$, model (2) considering p different between placements $\psi()\theta()p(\text{placement})$, model (3) considering p different between grids $\psi()\theta()p(\text{grid})$, and model (4) considering p different between placements and grids $\psi()\theta()p(\text{placement + grid})$. $\Delta\mathrm{AIC_c}$ corresponds to the $\mathrm{AIC_c}$ difference between the given occupancy model and the reference occupancy model $\psi()\theta()p()$ and bold values represent a significant difference ($\Delta\mathrm{AIC_c} > 2$). (b) Estimated p and associated 95% confidence interval of *Cephalophus silvicultor* for each grid and placement when considering the occupancy model $\psi()\theta()p(\text{placement + grid})$, and for each placement when considering the occupancy model $\psi()\theta()p(\text{placement})$.

Chapter 4: Conservation value

Table 4.1 Values of VIP (Variable Importance in Projection) obtained from the sPLS explaining mammal and dung beetle species richness with correlates of biodiversity. The two highest VIP values are shown in bold for each taxonomic group. The sign in brackets indicate the direction of the effect of each predictor variable on species richness.

Chapter 5: Response to hunting

Abbreviations

AFD: Agence française de développement
AIC: Akaike information criterion
ANCOVA: Analysis of Covariance
ANOSIM: Analysis of similarity
B. P.: Before Present
CARPE: Central Africa Regional Program for the Environment
CIFOR: Center for International Forestry Research
CIRAD: Centre de coopération internationale en recherche agronomique pour le développement
COMIFAC: Commission des Forêts d'Afrique Centrale
COP: Conference of the parties
CPUE: Catch per unit effort
CSA: Community Site Association
CT: Camera trap
DRC: Democratic Republic of Congo
DI: Defaunation Index
EU: European Union
ESRI: Environmental Systems Research Institute
FAO: Food and Agriculture Organization
FFEM: Fonds français pour l'environnement mondial
FLI: Forest Landscape Integrity
FPIC: Free, Prior and Informed Consent
FSC: Forest Stewardship Council
GBIF: Global Biodiversity Information Facility
GPS: Global Positioning System
IF: Impact factor
IPBES: Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IPGF: Project acronym « de l'Iventaire au Plan de Gestion de la Faune »
IUCN: International Union for the Conservation of Nature (IUCN)
K: Carrying capacity
MBK: movement-based kernel
MSc: Master of Science
MSY: maximum sustained yield
NMDS: Nonmetric Multidimensional Scaling

NP: National Park
NTFP: Non Timber Forest Product
OEACP: Organisation des États d’Afrique, des Caraïbes et du Pacifique
OECMs: Other effective area-based conservation measures
PEFC: Programme for the Endorsement of Forest Certification
PPECF: Programme de Promotion de l'Exploitation Certifiée des Forêts
PWG-CEB: Precious Woods Gabon - Compagnie Equatoriale des Bois
RAI: Relative Abundance Index
REDD / REDD+: Reducing Emissions from Deforestation and Forest Degradation
REM: Random Encounter Model
RIL: Reduced Impact Logging
TEAM: Tropical Ecology Assessment and Monitoring
sPLS: sparse Partial Least Squares
SSA: Species Site Association
SWM: Sustainable Wildlife Management Programme
UD: Utilization Distribution
USAID: United States Agency for International Development
VIP: Variable Importance in the Projection
WCS: Wildlife Conservation Society

1

General introduction

1 Vanishing wildlife

Human societies have been shaping the Earth's biosphere for at least 12,000 years (Ellis *et al.* 2021), and the synchrony between late Quaternary megafaunal extinctions and the arrival of humans in many parts of the world seems to suggest a much older influence (Koch & Barnosky 2006, Prates & Perez 2021). It has led some authors to agree that a new human-dominated geological epoch, the Anthropocene, has started (Steffen *et al.* 2007, Lewis & Maslin 2015). This epoch typifies the increasing extent and intensity of human activities, which have already profoundly altered the functioning of Earth system and are causing most contemporary environmental changes, though the beginning of the Anthropocene epoch is still subject to some controversy (Malhi *et al.* 2014, Lewis & Maslin 2015, Zalasiewicz *et al.* 2015).

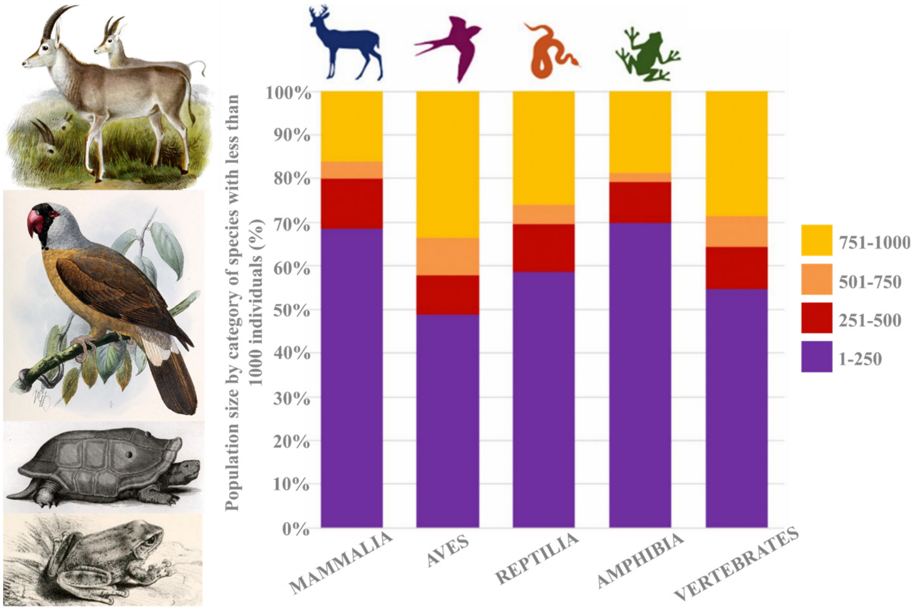


Figure 1.1 Illustrations of recently extinct species on the left. From top to bottom: the bluebuck (*Hippotragus leucophaeus*) by Smit and Wolf (1899) and the mascarin (*Mascarinus mascarinus*) by John Gerrard Keulemans (1893), both supposed to have become extinct around 1800; the Reunion giant tortoise (*Cylindraspis indica*) by Johann David Schoepf (1792) extinct around 1840; *Pseudophilautus variabilis* by Albert Charles Lewis Günther (1858) last seen in 1858. The stacked bar chart represents the number and estimated population size of terrestrial vertebrate species on the brink of extinction (*i.e.*, with under 1,000 individuals) by Ceballos *et al.* (2020).

In the last 500 years a radical shift in the interaction between humans and their environment has been however observed. Over this period, the International Union for the Conservation of Nature (IUCN) reports the extinction of around 900 species (www.iucnredlist.org) and more than 500 vertebrate species are on the brink of an immediate extinction with less than 1,000 individuals recorded in the wild (Ceballos *et al.* 2020, **Figure 1.1**). The situation is probably much more critical since the IUCN assessment covers only 5.6% of the world's estimated plant and animal diversity (estimated at ~ 2.14 millions of species), focusing on taxa that have received most conservation efforts and fundings in the past decades, namely mammals and birds (Cowie *et al.* 2022). Moreover, the rate of extinction tends to accelerate and already exceeds the background extinction rate of the previous five mass extinction events by 100 to 1,000 times (Pimm & Raven 2000, Ceballos *et al.* 2015, 2020).

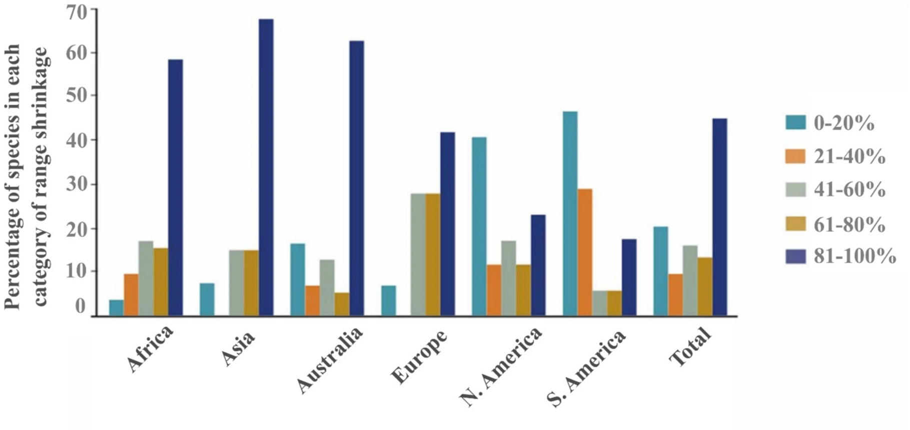


Figure 1.2 Species range reduction for land mammals for the five major continents/ subcontinents and the entire globe between ~1900 and 2015 by Ceballos *et al.* (2017).

In addition to species extinctions, human activities are also inducing dramatic declines of wildlife populations driving thousands of other species towards extinction, ~ 40,000 according to the IUCN. The latest report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) suggests, for instance, that a quarter of all species are currently facing extinction risk (IPBES 2019). The last century has also seen the severe contraction in species range and population size of more than 8,000 vertebrate species (Ceballos *et al.* 2017, **Figure 1.2**). Even greater loss has been depicted by the Living Planet Index which has tracked population trends of vertebrate species from terrestrial, freshwater and marine habitats for 50 years (WWF 2020). In addition, a similar fate seems to be shared by other groups as shown by the massive declines observed for invertebrates (Sánchez-Bayo & Wyckhuys 2019, Wagner 2020) and plants (Pimm & Raven 2017).

Beyond species loss, another hallmark of global human influence on the Earth's ecosystems lies in the biotic homogenization of previously distinct natural assemblages, *i.e.*, a drastic reduction in β-diversity across all taxonomic orders (Baiser *et al.* 2012, see **Box 1**). Indeed, not all species are equally affected and threatened by human activity, and some may even benefit from ongoing changes and thrive in human-altered environments, the so-called winners of global changes (McKinney & Lockwood 1999). Once extirpated, the most vulnerable native species might be replaced by less sensitive native clades (*e.g.* in amphibians, Nowakowski *et al.* 2018) or even by non-indigenous invasive species that easily spread (*e.g.* in plants, Daru *et al.* 2021), a species turnover that has been well observed in both marine and terrestrial habitats during the past 150 years (Dornelas *et al.* 2014). This simplification process is often spatially scattered, following hotspots of anthropogenic activities (Allan *et al.* 2019, Grantham *et al.* 2020), and generally results in a human-dominated landscape matrix where areas with impoverished and simplified species assemblages co-exist with remote and nearly intact areas.

Box 1: The β-diversity approach or how to assess variation in species composition along anthropogenic gradients

The diversity of ecological communities can be characterized at both local (α-diversity, **Figure 1.3**) and regional (γ-diversity) scales using a variety of metrics including species richness, species abundance/density, species occupancy as well as trait structure and phylogenetic diversity (Díaz *et al.* 2006). How species composition and species abundance structure change between these ecological communities is however related to beta(β)-diversity. Navigating towards the multiple meanings of β-diversity analysis can be complicated (Anderson *et al.* 2011) but allows to better grasp complex ecological responses along disturbance gradients, such as the impoverishment of animal communities as a result of habitat degradation (*i.e.*, nestedness) or the substitution of some species by others as a result of differential pressure and resistance between species (*i.e.*, turnover, Baselga 2010, Ulrich & Almeida-Neto 2012).

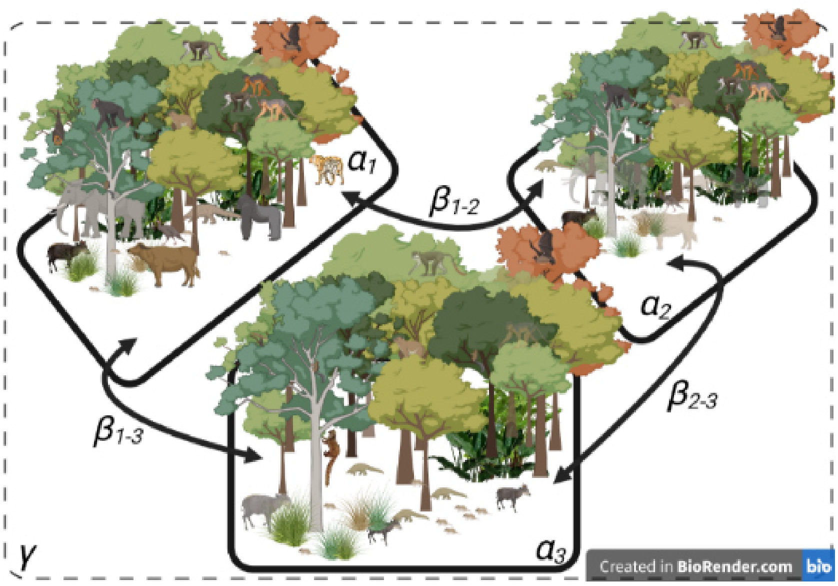
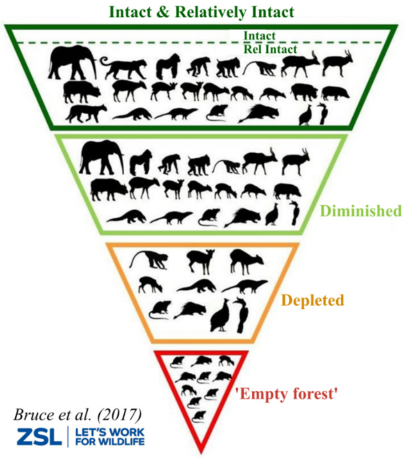


Figure 1.3 Spatial scales of biodiversity measurement initially introduced by Whittaker (1972). Alpha (α) diversity refers to the diversity, usually the number of species, within a particular sampling unit, area, or ecosystem. Beta(β)-diversity informs the change in species diversity between the α-units and encompasses two processes: the spatial replacement of species (*i.e.*, turnover) and the ordered loss of species (*i.e.*, nestedness) along environmental or ecological gradients (Baselga 2010, Ulrich & Almeida-Neto 2012). Gamma (γ) diversity clusters the overall diversity of the different α-units within a region.

All together, these results suggest that a world-wide defaunation process is ongoing (Dirzo *et al.* 2014, see **Box 2**). The resilience to future global changes of these modified and depleted ecosystems will be profoundly altered and the large range of services that human societies derive from their environment is already impacted (Chapin III *et al.* 2000). The causes of this Anthropocene defaunation are well identified, all being underlying consequences of human population growth and unsustainable use of resources (Young *et al.* 2016, IPBES 2019, Ripple *et al.* 2019). Of all recognized drivers, species overexploitation and habitat destruction due to the expansion and intensification of agricultural productions and urbanization, are by far considered as the most prevalent threats for the vast majority of threatened and near-threatened species (Maxwell *et al.* 2016). Land use change has long been recognized as a major threat to biodiversity in the tropics (Sala *et al.* 2000). In addition, the release and establishment of invasive alien species, pollution, climate change, human disturbance and transport and energy infrastructures are other direct threats to biodiversity (Maxwell *et al.* 2016).

Box 2: What do we mean by defaunation?



Bruce et al. (2017)

Figure 1.4 A conceptual framework of defaunation status categories of the large fauna of tropical forests in the northwest tropical forest of the Congo Basin from Bruce *et al.* (2017).

The concept of “defaunation” reflects the ongoing biological impoverishment of ecological communities, including both the complete extirpation of species and the decline in abundance of their populations (Dirzo *et al.* 2014), leading to functionally extinct environments. Although the global extent of the phenomenon is no longer in question, the continuum of alteration from an intact (or almost intact) environment to a severely depleted habitat, generally described under the term "empty habitat", albeit somewhat abusive, remains difficult to generalize and largely dependent on the local socio-ecological context (Bruce *et al.* 2017, **Figure 1.4**).

2 Threats in tropical forests

Tropical forests harbor more than half of Earth's biodiversity while only covering 7-10% of the land surface (Pianka 1966, Pimm & Raven 2000, Lewis *et al.* 2015). Anthropogenic disturbances in these speciose ecosystems are many and diverse, and generally grouped into three main categories: forest conversion, forest degradation (including hunting, logging and fire impacts) and forest fragmentation (Malhi *et al.* 2014). Because of the key role of tropical forests for the global carbon cycle (Xu *et al.* 2021), many actions including economic incentives such as the REDD and the following REDD+ mechanisms have been implemented to curb forest conversion and degradation over the past decades (Phelps *et al.* 2012). A recent study covering three decades has shown that deforestation and forest degradation are both slowing down in most tropical regions but central Africa (Vancutsem *et al.* 2021). Concerning wildlife, it is clear that unsustainable hunting is now the most pervasive and extended driver of the current extinction crisis in tropical forests (Fa & Brown 2009, Wilkie *et al.* 2011, Harfoot *et al.* 2021). As a consequence, many tropical biodiversity hotspots (Myers *et al.* 2000) are now considered as depauperated Edens (Benítez-López *et al.* 2017).The rapid expansion of these “empty forests” (Redford 1992, see **Box 2**) is not predicted to decrease since human population density is still increasing in many tropical forest areas (United Nations 2019).

Hunting wildlife for food is deeply rooted in human evolutionary history (Coimbra *et al.* 2020) and part of the culture of most indigenous communities across the tropics. Traditional low-impact subsistence hunting that has long been a source of nutrients and income for the poorest populations is now largely replaced by unsustainable extraction levels to supply the increasing urban demand and the local, national and international wildmeat markets (Fa *et al.* 2002). Among all hunted taxa, mammals face the greatest pressure and threats, especially the largest species which are typically preferred by hunters and highly sensitive to hunting, even at moderate pressure (Ripple *et al.* 2015, 2016, 2019). They are the first to be extirpated and the last to recover, particularly because of their long generation times and their low population growth rates (Cardillo *et al.* 2005). By focusing on the largest individuals and species, hunters exert a directional evolutive pressure. This size-selective behavior induces a general downsizing of hunted mammal communities (Young *et al.* 2016) which echoes to past megafaunal extinctions (Hansen & Galetti 2009, Malhi *et al.* 2016) and explains the skewed distribution of body mass between extinct, threatened, and non-threatened species (Dirzo *et al.* 2014, **Figure 1.5**). The mass extirpation of most megaherbivores and megacarnivores has already weakened and simplified interspecific interactions and trophic structure in present-day wild ecosystems (Malhi *et al.* 2016, Cooke *et al.* 2022). The depletion of the last remaining large forest mammals (Maisels, Strindberg, *et al.* 2013, Strindberg *et al.* 2018) will have tremendous direct consequences and ripple effects on all animal-mediated ecological processes going from seed dispersal to carbon stock and nutrient cycling (Terborgh *et al.* 2008, Abernethy *et al.* 2013).

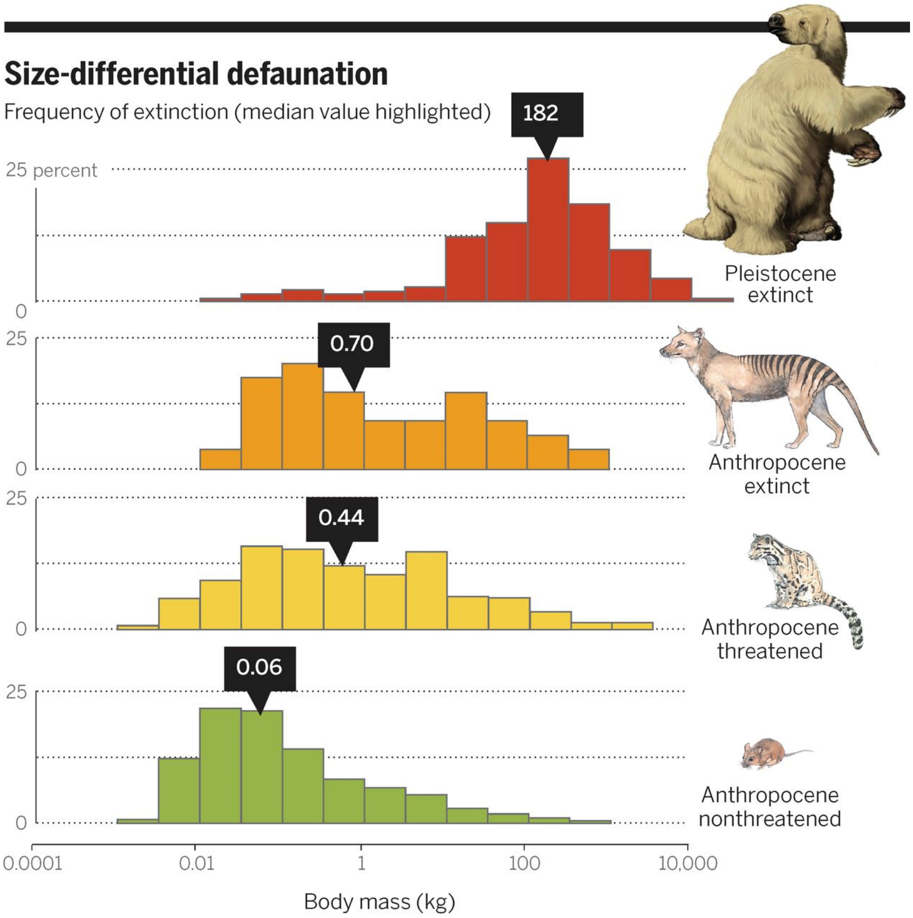


Figure 1.5 Comparing data on body size of all animals that are known to have gone extinct in Pleistocene or are recently extinct (<5000 years B.P.) with the body mass distributions of currently threatened and nonthreatened species suggesting a size-differential defaunation (extracted from Dirzo *et al.* 2014).

3 Defaunation in central African forests

The tropical rainforest of central Africa is one of the last remaining parts of the world where large faunal assemblages can be regarded as nearly intact when comparing to the Late Pleistocene levels (Hempson *et al.* 2015, Malhi *et al.* 2016), harboring some of the most iconic mammal species in the world such as lowland gorillas (*Gorilla gorilla*) and forest elephants (*Loxodonta cyclotis*). Beyond its intrinsic biological value, central Africa is also playing a key role in the regulation of the global climate acting as a massive carbon sink at the global scale (Hubau *et al.* 2020). Alike the rest of the rainforest biome, the region is however subject to substantial threats and is now at a social, economic and environmental crossroad (Abernethy *et al.* 2016). Mostly driven by shifting agriculture (Curtis *et al.* 2018), forest conversion in the region has been gradually increasing over the past 30 years and new deforestation hotspots are now emerging, particularly in the Democratic Republic of the Congo (Harris *et al.* 2017, Vancutsem *et al.* 2021). Though highly detrimental to forest-dependent species, forest cover losses remain low in comparison to the other tropical basins and subregions that experienced massive deforestation in the last decades (Pan *et al.* 2011, Vancutsem *et al.* 2021). Extractive activities such as unsustainable logging, mining, and most importantly hunting, are however thriving across the region driving unprecedent degradation of the second largest block of continuous tropical forest after the Amazon (Fa & Brown 2009, Abernethy *et al.* 2013, 2016). Compared to other tropical basins, the annual rate of species harvesting in central Africa is massive, estimated to be at least 1 and up to 11 million tonnes a year and deemed largely unsustainable (Fa *et al.* 2002, 2016, Ingram 2018). Wildmeat harvests are also expected to increase in the coming years due to population growth (especially in urban centers), facilitated access in once remote and undisturbed areas *via* new road infrastructures, and extensive use of more efficient modern hunting techniques such as wire traps and guns (Fa *et al.* 2005, Fa & Brown 2009, Coad *et al.* 2018).

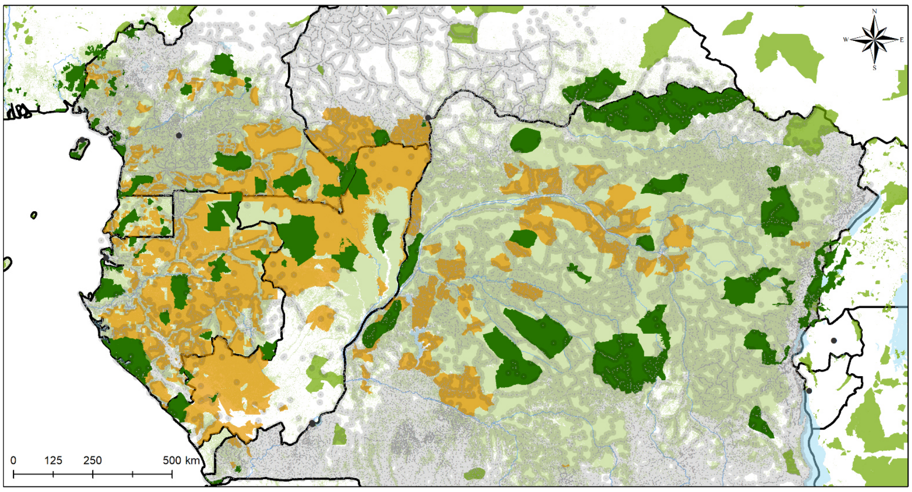


Figure 1.6 Forest allocations in central African moist forest derived from the Copernicus Global Land Cover classification (Buchhorn *et al.* 2020). Protected areas and logging permits are displayed in green (dark green for forest protected areas) and orange respectively. Grey halo represents a 10 km buffer around rural villages, showing the large overlap between forests potentially used by local communities, logging companies, and protected areas.

Only a concerted regional strategy, including all parties involved in forest management, can prevent the complete conversion of central African forests into altered and highly depleted forests, *i.e.*, the "empty forest syndrome" (Wilkie *et al.* 2011). While protected areas remain central for conservation (Chen *et al.* 2022), chronic underfunding has drastically limited their resources to tackle the many threats including poaching of emblematic species, illegal mining and logging activities and widespread commercial bushmeat hunting that have emerged in the context of high poverty that prevails in central Africa (Tranquilli *et al.* 2014). The forest elephant case is illustrative of this unequal fight. Once widespread in the forests of central Africa, populations of this iconic species have been wiped out by ivory poaching despite international concern and regulations (Maisels, Strindberg, *et al.* 2013). Even in the last sanctuaries (Laguardia *et al.* 2021), drastic declines have been recorded in recent years instigated by organized criminal groups that rely on a network of poachers, transporters and many other intermediaries whose numbers far outnumber those of ecoguards (Maisels, De Wachter, *et al.* 2013). This worrying trend also affects other iconic species such as great apes (Walsh *et al.* 2003, Strindberg *et al.* 2018).

As most forest areas outside protected areas have been or will be selectively logged at some point (Putz *et al.* 2012, **Figure 1.6**), the integration of the private forest operators into national and transnational conservation strategies must also be considered (Nasi *et al.* 2012). Forest permits already largely exceed the protected area coverage in the region (~ 55 Mha *versus* ~ 35 Mha, **Figure 1.6**). Though changes in species composition are inevitable in exploited environments, responsibly managed forests where selective and reduced impact logging (RIL) is applied, have shown to still sustain a large number of species as well as a non-negligible carbon stock with lower opportunity costs than strictly protected forests (Putz *et al.* 2012, Edwards *et al.* 2014, Shapiro *et al.* 2021). This buffering role is however largely dependent on the use of RIL practices and the control of forest access and must be confirmed on a case-by-case basis as neighboring units have been shown to influence the state of the forest up to 50 km (Shapiro *et al.* 2021). Supporting the wider adoption of such responsible practices, for example by encouraging forest certification (see the PPECF initiative in **Box 3**), should foster better governance of the region's forests and undoubtedly increase their resilience to future change, but many challenges and uncertainties remain, not least in relation to how wildlife recovers from logging interventions, questioning the ability of selectively logged forests to maintain relatively undisturbed mammal assemblages.

Box 3: Fostering responsible management of central African forests through certification

Given the lack of knowledge regarding the environmental impact of logging operations and the limited expertise of private operators in forest biodiversity management, the German Development Bank and the Central African Forest Commission (COMIFAC) have agreed on a funding deal to promote certified forestry in the Congo Basin countries and to support private operators in their efforts to meet the requirements of certification standards such as FSC®, through the PPEFC initiative (http://www.ppecf-comifac.com/accueil.html). This work is part of an intervention supported by the Programme, the IPGF project, which led to the production of a technical guide to help forest managers improve their wildlife management practices.

Customary territories where bushmeat hunting is extensively practiced often extend deep into the forest (usually around 10 km but up to 50 km, Abernethy *et al.* 2013, **Figure 1.6)** and overlap with other forest allocations which can be a source of much tension between private and public actors and local communities (Karsenty & Vermeulen 2017). The role of these areas, currently neglected in landscape-level conservation policies, is not well understood. They are sometimes identified as uncontrolled pumps that empty the surrounding forests, undermining all conservation efforts at larger scales, and sometimes as key areas for rural communities' livelihoods which can maintain populations of species that are moderately sensitive or even resistant to hunting. The truth is undoubtedly more nuanced, but these areas represent a real conservation concern (Coad *et al.* 2019, Ingram *et al.* 2021, see **Box 4**) and detailed assessment of their alteration patterns and determinants is still missing (Wilkie *et al.* 2019).

Despite the adoption of increasingly ambitious global conservation targets, one cannot but notice that central African forests are still insufficiently protected (~11% according to Eba'a Atyi *et al.* 2022), falling far short of the 17% threshold by 2020 established under Aichi Target 11 (UN CBD 2010) and the 30% pledged by most countries ahead of the 15th Conference of Parties (COP) of the Convention on Biological Diversity for the post-2020 agenda ("30 by 30" target - protect at least ~30% of world's land and oceans by 2030). Achieving these conservation efforts will require the development of alternative and complementary conservation models to the more restrictive and protective classical approach, especially as new areas available for protection are not limitless in the region. The previous COP in 2018 has however agreed on a new conservation model, distinct from protected areas, where conservation is carried out mainly as a by-product of other governance and management regimes under the concept of Other Effective area-based Conservation Measures (OECMs). Supported by the IUCN, this status offers a chance to better acknowledge the conservation that takes place beyond strictly protected areas in places that "may be managed with conservation as a primary or secondary objective or [where] long-term conservation may simply be the ancillary result of management activities" (IUCN-WCPA Task Force on OECMs 2019). Recognizing the effective long-term conservation that can be achieved by a range of actors as diverse as indigenous peoples and local communities, the private sector and government agencies is a significant advance in the conservation paradigm. In central Africa, this "conservation by use" model could potentially be applied to responsibly managed certified forests as well as to customary territories where sustainable hunting management is carried out, but providing the human expertise and financial support to accurately identify and report on potential OECMs and to properly assess progress towards conservation goals remains a major concern for most developing countries of the region.

Box 4: Improving conservation and sustainable use of wildlife outside protected areas, the SWM project

The Sustainable Wildlife Management (SWM) Program is an initiative of the Organisation of African, Caribbean and Pacific States (OEACP) funded by the European Union (EU) and co-financed by the French Global Environment Facility (FFEM) and the French Development Agency (AFD). This seven-year program (2017-2024) is implemented in 15 OEACP member countries by a consortium of partners including the Food and Agriculture Organization of the United Nations (FAO), the Centre de coopération internationale en recherche agronomique pour le développement (CIRAD), the Center for International Forestry Research (CIFOR) and the Wildlife Conservation Society (WCS).

The program ambitions to address wildlife conservation and food security through the development of innovative, collaborative, and scalable new approaches to conserve wild animals and protect ecosystems, whilst at the same time improving the livelihoods of indigenous peoples and rural communities who depend on these resources (https://swm-programme.info/).

In Gabon, the project operates in the department of Mulundu in a context of low human density, and where the exploitation of wildlife contributes significantly to the food and economic security of rural populations.

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4 Research strategy

While the threats and pressures affecting the rainforest of central Africa are multiple and intensifying, the state of knowledge on the faunal assemblages roaming these forests remains scarce, highly patchy and generally based on expert opinion. As a result, the underlying patterns governing the distribution of these species assemblages are poorly understood and the few studies which do exist are frequently restricted to a few, albeit emblematic, species, obscuring the more complex response that the whole species assemblage may exhibit. In this context of ongoing and unprecedent forest defaunation, the general objective of the thesis was to identify the distribution patterns of large mammal assemblages and their determinants across central African forests at the regional and local scales. To do so, I developed a research strategy based on four research axes (**Figure 1.7**) including a prior regionalization of mammal assemblage to integrate biogeographic variation in future assessment of defaunation (**Chapter 2**), a methodological contribution implemented in eastern Gabon to determine the appropriate sampling strategy for camera trap surveys (**Chapter 3**), and two local studies to characterize the main determinants of the composition of mammal assemblages in two distinct zoogeographic districts, southeastern Cameroon (**Chapter 4**) and eastern Gabon (**Chapter 5**). A beta-diversity approach (see **Box 1**) was implemented in all these chapters, in which the composition of mammal assemblage was first described and then related to a set of spatial and environmental determinants, both patterns and determinants being of increasing precision, from **Chapter 2** to **Chapter 5**.

While few studies examined the distribution of very specific groups (herpetofauna by Chifundera 2019; primates by Colyn *et al.* 1991; guenons by Colyn & Deleporte 2004; and birds by De Klerk *et al.* 2002), the diversity, distribution, and determinants of large mammal assemblages across central African forests still remains barely known. In **Chapter 2**, I addressed this knowledge gap using an original dataset of published species lists from wildlife and bushmeat-related surveys, aggregating much needed information for conservation from a highly diverse yet data-deficient region. This study has been resubmitted to Diversity and Distributions (IF = 5.71) in September 2022 after a first review cycle. These results can be directly used by forest managers to describe the biogeographic context of newly surveyed areas as well as to provide information on the potential species pool and the defaunation level. At the regional scale, our zoogeographic map also informs conservation practitioners on the species and areas of interest that can be targeted for further sampling, and conservation and rewilding efforts.

Despite the rapid increase in the use of camera traps for wildlife monitoring, there is still a lack of standardized reporting and harmonized study design and data collection protocol (Meek *et al.* 2014). In **Chapter 3**, I specifically tested the impact of camera trap orientation on the remotely sensed mammal diversity using a pairwise design composed of systematically placed and wildlife-trail-oriented camera traps and provided recommendations for further camera trap surveys. I am the first author of this study that was published in Remote Sensing in Ecology and Conservation (IF=5.78) in December 2020, in an article entitled ‘Wildlife trail or systematic? Camera trap placement has little effect on estimates of mammal diversity in a tropical forest in Gabon'. These results are particularly useful for wildlife managers to determine the appropriate camera trap sampling strategy for field studies. They also provide a four-step approach to characterize the diversity of terrestrial mammal assemblages using camera traps and pave the way for multi-site analyses combining both types of camera trap data.

The continuum of alteration that mammal assemblages might experience under increasing anthropogenic pressure remains poorly documented as refine species composition data are hardly obtainable in remote areas as complex and diversified as the rainforests of central Africa (Bruce *et al.* 2017). In **Chapter 4** and **Chapter 5**, I addressed this knowledge gap using a standardized camera trap survey protocol and identified the main determinants explaining the alteration state of mammal assemblages in two distinct zoogeographic districts, in southeastern Cameroon and in eastern Gabon respectively. Camera trap data in Cameroon, obtained during my MSc thesis, were combined with pitfall trap data dedicated to study dung beetle assemblages along the same study area (MSc thesis of Laetitia Delbeke) and have been published in Biological Conservation (IF=7.5) in January 2020, in an article entitled 'Conservation value of tropical forests: Distance to human settlements matters more than management in central Africa' led by Simon Lhoest and I am the second author of this paper since I handled the collection and analyses of data related to mammals. In Gabon, camera trap and offtake surveys were implemented by eight MSc students in the frame of the Sustainable Wildlife Management (SWM) project. I co-supervised the work of the MSc students and I led this study as first author and the manuscript can be considered ready for submission.

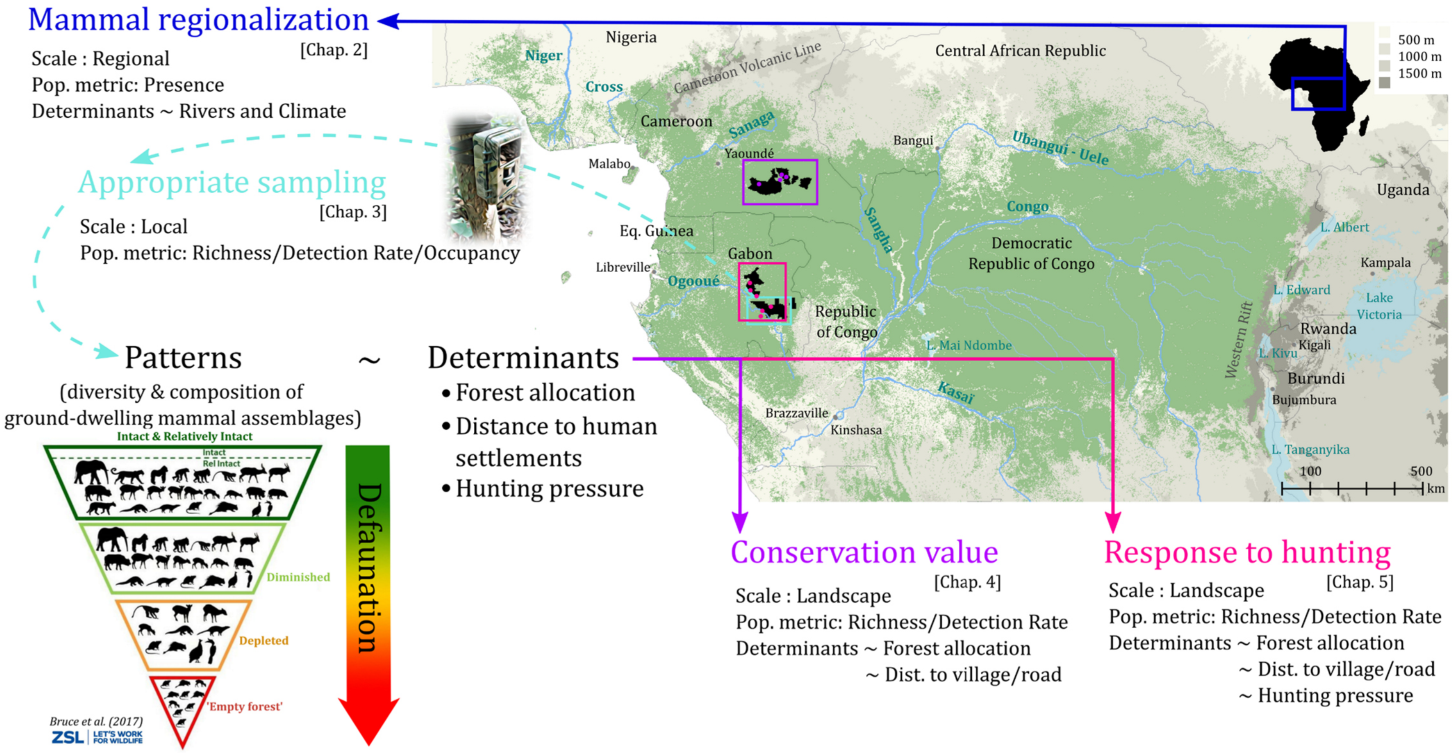

Figure 1.7 Research strategy depicting the four research axes, their study scale, the population metrics used, and the determinants tested.

2

Mammal regionalization

Preamble

In this chapter, we aimed to explore the diversity and uniqueness of large mammalian assemblages across central African tropical forests and identify their environmental and spatial determinants using more than 500 species lists coming from wildlife and bushmeat-related surveys. This regionalization is of primary importance to integrate biogeographic variation in future assessment of defaunation. By assessing the conservation status and the level of anthropogenic threats each identified zoodistricts faced, these results also inform regional conservation policy, allowing to target species and areas of interest for further sampling, and conservation and rewilding efforts.

- Paper 1: submitted -

Biogeography of central African forests: determinants, ongoing threats, and conservation priorities of mammal assemblages

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This paper has been resubmitted to *Diversity and Distributions* after a first review cycle in September 2022.

Abstract

Aim Central Africa shelters a diverse and iconic megafauna which is jeopardized by climate and land-uses changes and increased hunting-induced defaunation. Though being crucial for coordinating regional conservation actions, how species assemblages are spatially structured is still barely known. This study aims to fill this knowledge gap for mammals across central African forests.

Location Tropical moist forests from Nigeria to the Albertine Rift

Methods An extensive compilation of forest-dwelling mammal species lists was made from wildlife and bushmeat-related surveys across central Africa. To identify and delimit zoogeographic districts, separately for three orders well sampled, carnivores, primates and artiodactyls, a beta-diversity approach was implemented, enabling to cluster surveys with similar species composition despite various sampling methods and efforts. Random forest classification models were then used to identify the environmental determinants of the district's distribution and to produce a continuous zoogeographic map (and associated uncertainties) critical to assess the conservation status of each district and their ongoing threats.

Results While carnivores do not present a clear spatial structure within central African forests, our findings highlight the structuring role of rivers on both primate and artiodactyl assemblages' distribution. We retained eight and six spatially congruent districts for primates and artiodactyls, respectively. These districts were shaped by the Ubangi/Congo River system, and the Cross and Sanaga Rivers, with a secondary role of insularity and precipitation identified for primates. Highly threatened districts were highlighted, especially in Nigeria and in the Democratic Republic of Congo, the latter including vast areas that are understudied and poorly represented in the protected area network.

Main conclusions Beyond refining our understanding of the diversity and uniqueness of mammalian assemblages across central African forests, our map of zoogeographic districts has far-reaching implications for the conservation of highly threatened taxa, allowing to target species and areas of interest for further sampling, and conservation and rewilding efforts.

Keywords: Artiodactyls, biogeography, Carnivores, central Africa, Primates, terrestrial mammals, tropical forest, rivers

1 Introduction

Within the Afrotropics, the Guineo-Congolian forest that stretches along west and central Africa is recognized as one of the four ecologically distinct continental-scale herbivory regimes, or herbivome (*sensu* Hempson *et al.* 2015) dominated by small, non-social browsers, including many duiker species. Within the Guineo-Congolian Region, central Africa represents the second largest block of continuous tropical forest after the Amazon and harbors some of the most iconic mammals in the world (Kreft & Jetz 2010, Linder *et al.* 2012) such as forest elephants, gorillas, bonobos and okapis, among others. However, the entire region, which is a vast wilderness area (Mittermeier *et al.* 2003) and includes intact forest landscapes (Potapov *et al.* 2017), has never been recognized as a biodiversity hotspot (Myers *et al.* 2000, Ceballos & Ehrlich 2006), even when refined for Africa (Küper *et al.* 2004), and remains largely understudied (Verbeeck *et al.* 2011). For example, new mammal species are still being discovered such as *Cercopithecus lomamiensis* in the most recent national park (NP) of the Democratic Republic of Congo (DRC), the Lomami NP (Hart *et al.* 2012). To date, the map of ecoregions (Olson *et al.* 2001, Dinerstein *et al.* 2017) represents the most detailed classification available for the region. However, said system is greatly inspired by White's phytochoria (White 1983), and has never gone through a cross-taxa validation for large mammals using data-driven approaches based on replicable quantitative methods such as multivariate statistics and clustering analyses (Kreft & Jetz 2010).

While mammals are facing tremendous threats and environmental challenges across central Africa (Abernethy *et al.* 2016, Benítez-López *et al.* 2019, Bush *et al.* 2020, Grantham *et al.* 2020), we still lack a thorough understanding of how large mammal assemblages are distributed across the region, though being essential for planning coordinated conservation strategies and assessing where conservation gaps might persist. Historically, protected areas have been established in the region (i) to prevent excessive hunting and regulate recreational trophy hunting, (ii) to target emblematic species (*e.g.*, the Okapi Wildlife Reserve in the DRC), (iii) to protect remarkable landscapes (*e.g.*, the Mount Cameroon National Park (NP) or the Virunga NP in the DRC), or (iv) for geopolitical reasons such as protected areas aligned along borders (Doumenge *et al.* 2015). Where they exist, country-level conservation strategies were usually designed for protecting individual key areas and their surroundings. The few coordinated conservation actions at the regional scale have been promoted by international organizations, such as the CARPE program of the USAID or the "Larger than Elephant" (European Comission 2017) and the new "Naturafrica" (European Commission 2021) initiatives of the European Union (EU). The landscape approach they promote is based on networks of interconnected protected areas (transnationally or not) which aim to ensure ecological connectivity and maintenance of biodiversity at larger scales (*e.g.,* protected areas in a matrix of forests dedicated to sustainable forest management). However, beyond the presence of emblematic species, it is the richness and uniqueness of species assemblages that mainly determines the conservation value of an area, and, in most cases, this component has been neglected or has only been studied retrospectively after the creation of the protected areas.

In this study, we fill the dramatic knowledge gap on the biogeographic patterns and determinants of mammal assemblages across central African forests and we outline the implications for biodiversity conservation in the region. Specifically, we delineate zoogeographic districts at a scale suitable for the regional management of conservation actions and investments (Wyborn & Evans 2021), *i.e.*, the COMIFAC ("Commission des Forêts d'Afrique Centrale") working scale. To do so, we gathered species lists from wildlife and bushmeat-related surveys focusing on medium-sized up to large mammals. The combined dataset, available includes 6,840 occurrences across central Africa (**Figure 2.1**) for 31 species of carnivores (out of 35 species in the study area according to Wilson & Mittermeier 2009), 64 species of primates (out of 73 according to Mittermeier *et al.* 2013) and 49 species of artiodactyls (out of 57 according to Wilson & Mittermeier 2011) and a standardized analytical road map was used for delineating biogeographical regions based on (dis)similarity in species composition (Kreft & Jetz 2010). Beyond investigating how mammal assemblages are distributed, we also estimate their uniqueness across the region (assessing the indicator value of the species they hold), how well they are represented in the conservation network (assessing the protected area coverage), and we also identify the threats they face (assessing hunting-induced defaunation and loss of forest integrity). We specifically sought to address the following questions:

1) Is the variation in mammal assemblages congruent across taxonomic orders? While few studies examined the distribution of very specific groups (herpetofauna by Chifundera 2019; primates by Colyn *et al.* 1991; guenons by Colyn & Deleporte 2004; and birds by De Klerk *et al.* 2002), the distribution of large mammals across central African forests is still barely known.

2) What are the environmental and spatial determinants of mammal species assemblages? Previous studies have highlighted the role of river networks (Oliveira *et al.* 2017, Aliaga-Samanez *et al.* 2020), mountain ranges and insular isolation (Fa & Funk 2007) as important determinants of species distribution and species assemblages worldwide. However, the role of these determinants across central African forests, is yet to be proven.

3) What is the overall conservation status of the region and which assemblages are the most threatened and the least protected? We thus investigate how well each identified zoogeographic district is being protected by the existing protected area network and by quantifying the level of anthropogenic threat each district faces.

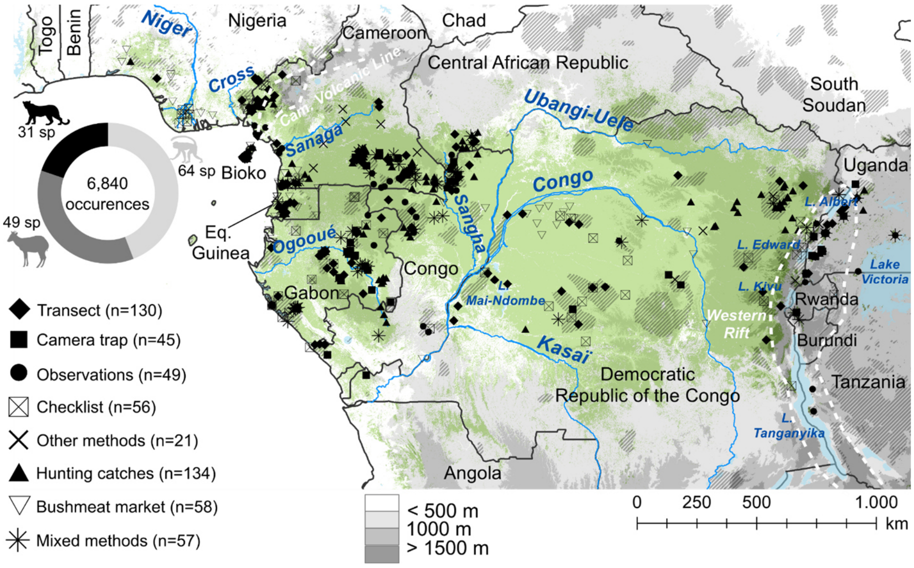

Figure 2.1 Location of the mammal species lists. Species lists were retrieved from wildlife surveys (transects, camera traps, observations, checklists, and other methods) and bushmeat-related surveys (hunting catches and bushmeat market records), and a mix of the two. The eight major rivers (in blue) and the two mountain chains (in white, dotted lines) are considered as potential biogeographical barriers. The distribution of the moist forest (in green) is derived from the Copernicus Global Land Cover classification (Buchhorn *et al.* 2020). Hatched areas correspond to protected areas (IUCN & UNEP-WCMC 2018). The background map corresponds to the altitude (grey scale) retrieved from the Shuttle Radar Topography Mission (Jarvis *et al.* 2008). The pie chart provided as inset shows the proportion and the number of species of each order in the dataset. Animal silhouettes were provided by courtesy of PhyloPic (www.phylopic.org) or adapted from Wilson & Mittermeier (2011).

2 Methods

2.1 Species lists and taxonomy standardization

We gathered mammal species lists from 550 surveys conducted in the lowland forests of central Africa and in the mountain forests of the Albertine rift (**Figure 2.1**). This dataset constitutes an original contribution[1] and has never been published before. Importantly, it aggregates much needed information for conservation from a highly diverse yet data-deficient region. Our study area matches the distribution of the moist forest biome in central Africa derived from the Copernicus Global Land Cover classification (Buchhorn *et al.* 2020) and encompasses the following countries: Nigeria, Cameroon, Equatorial Guinea (Rio Muni and Bioko Island), Gabon, Republic

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[1] Species occurrence and all survey data are available on the Dryad repository (https://datadryad.org/stash/share/E9shyCzW9ryDNf7hLhnat7Mv57ou7Bbw7v90uCtEW1o)

of Congo, Central African Republic, Democratic Republic of Congo, Uganda, Rwanda, Burundi, and Tanzania (**Figure 2.1**). We pulled together mammal species lists gathered from wildlife (*e.g.,* camera trap surveys, line transects) and bushmeat-related (*e.g.,* hunting bag data from rural villages, composition of stalls in bushmeat markets) surveys including the grey literature (*e.g.,* monitoring reports made in protected areas). We first employed a systematic search on Google Scholar by using keywords related to the taxonomic groups studied (mammals, and specific orders within mammals), the study area (central Africa, Congo basin and individual country names), the survey methods (line transect, camera trap, bushmeat or hunting study), and we also included surveys suggested by collaborators, fellow researchers, and conservation practitioners. We only included surveys providing evidence of species occurrence (*e.g.*, direct observations, hunting catches and DNA samples). Surveys conducted in the same area by different researchers and/or during different seasons and/or years were considered independent. A single location was given for surveys covering a wide area (*e.g.*, multiple line transects or camera trap grids) or a whole protected area (*e.g.*, checklist for an entire national park) and in these cases we chose the centroid. We recognized that the assembled species lists do not come from studies with similar objectives and similar methodologies, as shown in the detailed metadata provided with the dataset. Hunting studies, for example, only record species sought for the bushmeat trade, and do not necessarily reflect the whole mammalian community of a site. Since the surveys span a vast period, from 1932 to 2019, some assemblages reported here may no longer exist due to defaunation or forest clearing and some of the species might have gone locally extinct. Also, since we have included surveys from forest-savanna mosaics, a few savanna taxa are present in our combined dataset. Savanna taxa were not removed as forest-savanna mosaics are common in central Africa (*e.g.*, Lopé NP in Gabon, Odzala-Kokoua NP in the Republic of Congo), and might potentially display unique assemblages. Furthermore, the attribution of unique habitats to species remains subjective, especially for generalist species such as the leopard (*Panthera pardus*) or the chimpanzee (*Pan troglodytes*) that can occur in both forest and savanna.

When assembling data from vastly different collection methods and sources, data cleaning procedures are necessary and the approach we implemented is detailed below. Similar practices are needed when dealing with big data repositories such as the Global Biodiversity Information Facility (GBIF, www.gbif.org) which compiles highly valuable data for research (Zizka *et al.* 2020) and has revolutionized scientific biogeography (Edler *et al.* 2016). Rather than occurrence data of individual species, we here assembled species lists reflecting coexisting species, and we focused our analyses of species assemblages on carnivores, primates, and artiodactyls due to two reasons. First, these three orders hold the best sampling coverage in the combined dataset with 31, 64, and 49 species retrieved respectively, in 307, 514 and 386 surveys. Second, the identification at the species level for these three orders is better resolved and less prone to identification errors, contrary to rodents for instance, which pose important identification challenges. Original species identifications were deemed correct, and taxonomy was standardized and updated according to Mittermeier *et al.* (2013) and to Wilson and Mittermeier (2009, 2011). In a few cases, the new taxonomic status was followed by a change in the species' distribution range. We encountered this situation for one carnivore species, 12 primate species, and 19 artiodactyl species. For instance, the blue duiker, which was previously described as one species – *Cephalophus monticola* – is now divided into five different species in the study area, *Philantomba melanorhea, P. congica*, *P. simpsonii*, *P. anchietae* and *P. aequatorialis*. At this stage, we also reviewed the species' distribution ranges to discard unreliable data that might exist in our dataset compiling vastly different sources and including species identifications from non-zoological experts. For further analyses, we only kept occurrences within the known range of the species, and we specifically removed 6.5% of occurrences for carnivores, 4.6% for primates, and 2.5% for artiodactyls, respectively.

2.2 Zoogeographic districts and indicator species

All analyses were performed in R version R 3.6.3 (R Core Team, 2019). After the data checking and cleaning procedure, we applied a dissimilarity-based approach that is perfectly adapted to heterogeneous data of species composition. First, we quantified dissimilarity in species composition between each pair of surveys using the Simpson beta-diversity index which is known to be richness independent (Koleff *et al.* 2003). This index ranges between 0 (similar species composition between two surveys) and 1 (no shared species) and is particularly adapted for biogeographical analyses when dealing with presence-only data and unbalance sampling (Kreft & Jetz 2010, Linder *et al.* 2012). To account for artefacts due to rarity, we removed the species present in less than three surveys and the surveys recording less than three species, a standard practice in community analyses (Couteron *et al.* 2003). We used the *vegan* package (Oksanen *et al.* 2019) for computing the pairwise dissimilarity matrices for carnivores, primates and artiodactyls. Afterwards, we clustered all surveys according to their mammal species composition by applying Ward's hierarchical classification algorithm on the three dissimilarity matrices. As the means to divide the resulting classification into meaningful zoogeographic districts, we have stablished three criteria: 1) district's average silhouette width, 2) district's number of indicators species, 3) spatially coherent districts' distribution. We investigated all possible geographic divisions up to a maximum of 10 potential clusters per order. We calculated silhouette values by using the *cluster* package (Maechler *et al.* 2019). Silhouette scores range from -1 to 1 and indicate how strongly a given survey is associated to its cluster. Positive silhouette values indicate a good assignment and negative ones indicate a poor one, the survey being on average closer to surveys in another cluster than to surveys of its own cluster. To detect the significant indicator species of each cluster or combination of clusters, we calculated the indicator value (*indval*) with the *multipatt* function of the *indicspecies* package (De Cáceres & Legendre 2009). *indval* is based on two components, species specificity and fidelity (De Cáceres 2020). Since species detectability cannot be considered equal between different survey methods, we only considered the specificity component which is the probability that the survey belongs to the target cluster given the fact that the species has been found. Species specificity ranges from 0 (no association with the district) to 1 (full association with the district). Finally, from these clusters, we retained and labeled a set of zoogeographic districts that show a coherent spatial distribution and a particular species composition.

After identifying the different zoogeographical districts for each order, we checked whether data heterogeneity and species sampling incompleteness might have influenced the identification of our districts. First, we used an ordination (Non-Metric Multidimensional Scaling) for visualization of data heterogeneity and tested for significant differences between survey methods, survey headcount, year of data collection, and survey duration with a series of analysis of similarity (ANOSIM). We also used the *vegan* package (Oksanen *et al.* 2019) for these analyses. Second, we explored the issues of incompleteness and bias in species sampling (*e.g.*, non-game species in bushmeat surveys, arboreal species in ground camera trap surveys). To do so, we built a presence matrix for each order by intersecting over a 0.1° grid all IUCN species range maps, *i.e.*, an expert-based delineation of the species distribution also potentially biased and provided at a lower taxonomical resolution, and then applied the same methodological road map for delineating zoogeographic districts on these virtual species assemblages (Kreft & Jetz 2010, Linder *et al.* 2012).

2.3 Determinants and coverage of the districts

We tested the relative importance of climate (temperature and precipitation), forest structure (tree cover), rivers (riverbank side), insularity (Bioko vs continent) and elevation in structuring central African forests' mammal species assemblages. We retrieved values of annual mean, minimum and maximum temperature (Bio1, Bio5 and Bio6) and precipitation (Bio12, Bio13 and Bio14), and the precipitation variation coefficient (Bio15), from the 'WorldClim 2' Global Climate database (Fick & Hijmans 2017) at a 30 arc-second resolution. We assessed forest structure by relying on the percentage of tree cover (Hansen *et al.* 2013). We have also tested whether the river network acts as a driver of mammal species assemblages. To this end, we focused on the seven main rivers present in the region (**Figure 2.1**, the Kasaï River was not tested because of the lack of surveys on its left bank), and, for each river, we built a categorical variable to describe whether a survey was carried out on its right bank, left bank, or upstream of the river source. We have also tested the importance of elevation and insularity for explaining the regional patterns of mammal assemblages. Elevation data were extracted from the CGIAR-CSI SRTM 90 m database (Jarvis *et al.* 2008) and, for insularity, we created a categorical variable indicating whether surveys are located on Bioko Island or on the continent. To figure out the importance of environmental and spatial determinants and to predict the coverage of each district at the regional scale, we used a random forest classification model approach that is particularly suited when predictors are a mix of continuous and categorical variables (Strobl *et al.* 2009). Specifically, we trained 100 random forest classification models (with 1000 unbiased individual trees to grow in each model) for each order separately using the *party* package (Strobl *et al.* 2007). The model training was done on a calibration dataset only composed of surveys strongly associated to their district (with a silhouette score >0.2). Since the number of surveys for each district was unevenly distributed, which can cause model overfitting towards the best represented classes, we built our random forest models by allowing survey sampling with replacement (a single survey can be sampled more than once), a robust and suitable technique for handling class imbalance (Gosain & Sardana 2017). We have done this until all districts had the same number of surveys present in the best sampled district. By doing so, we achieved sampling evenness for all districts (n = 90 for primates, n = 147 for artiodactyls). We estimated model accuracy by assessing the out-of-bag error, which corresponds to the prediction error of the model obtained through a bootstrap aggregating technique. The importance of each predictor was assessed by testing how the accuracy of the results is affected when the predictor variable is randomly permuted (function *varimp* of the same package). We modeled the districts' spatial distribution and associated prediction uncertainty at 0.1° grid-resolution throughout the whole extent of the evergreen broadleaved forests (Buchhorn *et al.* 2020). We mapped the modeled districts by plotting the most frequently predicted district category for each pixel out of the 100 models built.

2.4 Conservation status and anthropogenic threats

To estimate the conservation status of each district and the level of anthropogenic threat they face, we gathered information on protected area coverage (**Figure 2.1**) and human-induced pressures. We retrieved the protected area network from the World Database on protected areas (IUCN & UNEP-WCMC 2018). We only considered nationally recognized protected areas with a designated or inscribed status (Grantham *et al.* 2020), and excluded aquatic reserves and marine parks. To estimate the level of anthropogenic pressures, we included in a composite map two threats, a defaunation index (DI), corresponding to the estimated hunting-induced reduction in mammal abundance (Benítez-López *et al.* 2019), and a Forest Landscape Integrity index (FLI) which integrates the observed and inferred human pressure associated to infrastructure, agriculture, recent deforestation and loss of forest connectivity (Grantham *et al.* 2020). The DI index we used here is a composite index equal to the minimum value between the original DI index for medium (1-20 kg) mammal species and the original DI index for large (>20 kg) mammal species (Benítez-López *et al.* 2019). To ease the comparison among districts, DI and FLI were both rescaled between 0 and 1. We then produced a composite map summarizing both threats on the study area categorizing each pixel as "highly", "moderately" and "weakly" impacted according to the thresholds proposed in the original studies.

3 Results

3.1 Congruence of biogeographic patterns across primates and artiodactyls

Carnivores did not exhibit a clear spatial structure across central African forests, and we ended up with a broad and unique Congolian district with no further spatially relevant divisions since the average silhouette value were constantly low starting from the first division (**Appendix A.1**). In contrast, species assemblages for primates and artiodactyls displayed refined and highly congruent distribution patterns. After the first split, separating surveys conducted on the eastern and western sides of the Ubangi-Congo River system, we retained nine clusters for primates and seven clusters for artiodactyls, which were supported by a high silhouette values and the many indicator species (**Appendix A.1**). Based on the spatial coherence and species composition of these clusters, we finally identified eight districts for primates (grouping two clusters into the “Atlantic” district) and six districts for artiodactyls (a “generalist” cluster being not recognized as a distinct district) across central African forests (**Figure 2.2**). From west to east, the following six districts were common to the two orders: “South Nigeria”, “Cameroonian Highlands”, “Inland” in Atlantic central Africa, “Congo-Kasaï”, “East Congo” and a last district corresponding to the “Rift". For primates, the surveys conducted on Bioko Island formed a distinct “Bioko” district from that of the “Cameroonian Highlands”, and an “Atlantic” district extending along the coast of Cameroon and Rio Muni and deeper inland in Gabon was identified. This “Atlantic” district was formed by the combination of two clusters (two branches in the dendrogram, **Figure 2.2**), and among them, the “Atlantic 2” cluster was composed of several surveys with low silhouette values (mean silhouette value of -0.04, **Appendix A.1**) indicating a transitional composition (empty circles on **Figure 2.2**). Furthermore, no species typified these clusters individually, but three significant indicators were identified when considering them combined in the “Atlantic” district. For artiodactyls, a “generalist” cluster was also identified but not recognized as a separate zoogeographic district because of its diffuse spatial distribution (**Figure 2.2**), of the very low silhouette values (**Appendix A.1**) and of a non-specific composition dominated by species vastly distributed species in the study area (**Appendix A.3**).

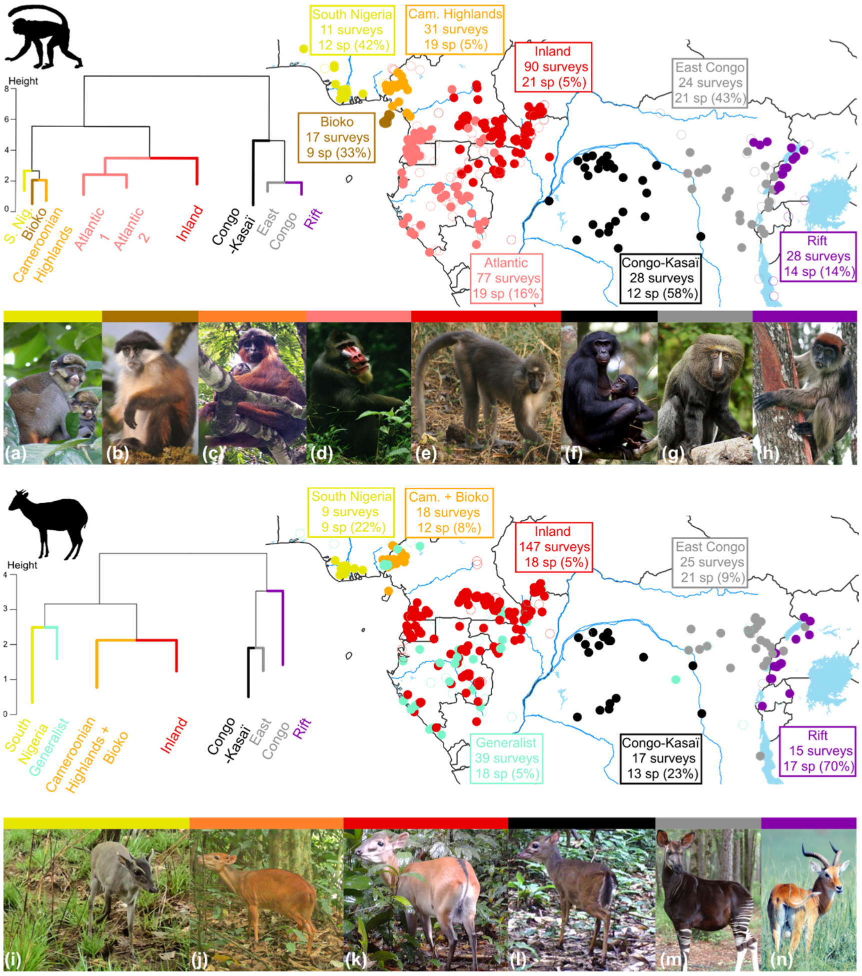


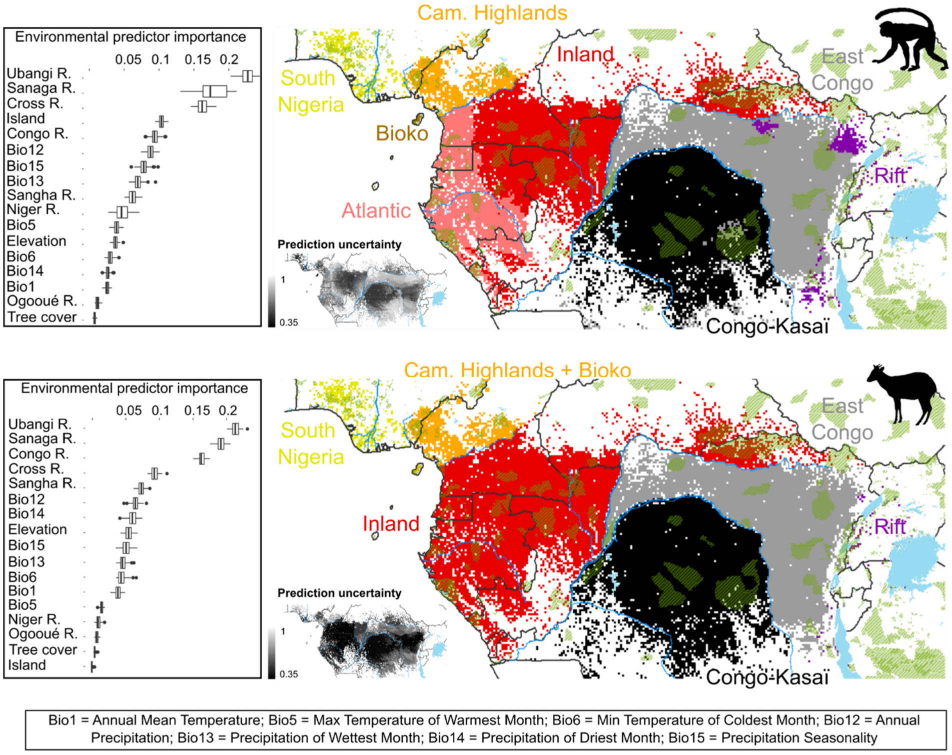
Figure 2.2 Zoogeographical districts for primates and artiodactyls across central African forests. The dendrograms (Ward's algorithm on Simpson dissimilarity) show the relatedness between districts that are also displayed on the map. Filled and empty circles respectively correspond to silhouette scores greater and lower than 0.2. The species pool, the proportion of indicator species (considering strict indicators, not in combination with other districts) and the number of surveys (with a silhouette score >0.2) is given for each district. Animal photographs display important indicator species of each district, following the same color scheme. Species name and photo courtesy are given for primates, *Cercopithecus sclateri* (a) by Lynne R. Baker, *Piliocolobus pennantii* (b) by Richard A. Bergl, *Piliocolobus preussi* (c) by A.N. Hofner, *Mandrillus sphinx* (d) & *Cercocebus agilis* (e) by Brent Huffman/UltimateUngulate, *Pan paniscus* (f) by Takeshi Furuichi, *Cercopithecus hamlyni* (g) by Paul Moine, *Piliocolobus tephrosceles* (h) by Thomas T. Struhsaker; and for artiodactyls, *Philantomba walteri* (i) by Délagnon Assou, *Cephalophus ogilbyi* (j) by WCS Nigeria, *Cephalophus leucogaster* (k) by Davy Fonteyn, *Philantomba simpsoni* (l) by John Hart/Frankfurt Zoological Society TL2 Project, *Okapia johnstoni* (m) by Bob Jenkins and *Kobus thomasi* (n) by Giuseppe Mazza.

The proportion of indicator species varied greatly among orders (**Figure 2.2**). Primates usually presented more endemic assemblages with 78% of the species (n = 50 out of 64) being significant indicator of at least one district. The proportion of indicator species also varied between districts with some districts being characterized by particularly unique mammal assemblages (**Figure 2.2, Appendix A.3**). For instance, more than half (58%) of the primate species occurring in the "Congo-Kasaï" district were strictly associated with this district, the Bonobo (*Pan paniscus*) being one of the most typical examples. With 42% and 33% of indicator species respectively, "South Nigeria" and "Bioko" also presented unique but species-poor primate assemblages. In contrast to primates, only a few artiodactyl species (n = 33 out of 49) were identified as significant indicators (**Appendix A.3**). Only one species strictly typified the "Cameroonian Highlands" (*Cephalophus ogilbyi*) and the "Inland" (*Cephalophus leucogaster*) districts, and the "generalist" cluster mentioned above (the generalist *Syncerus nanus*, with a very low species specificity = 0.53). By contrast, the "Rift" district showed a highly specific assemblage with 70% of artiodactyl species being significant indicators (**Appendix A.3**). However, some of these species are widespread across Africa such as the savanna buffalo (*Syncerus caffer*) and would not be indicators of the Rift in a larger analysis considering the full species range.

Then, we checked whether data heterogeneity and species sampling incompleteness might have influenced our districts' classification. First, we found only limited influence of surveys characteristics (method, headcount, year, and duration) on the (dis)similarity in species composition separately for primates and for artiodactyls, the value of all ANOSIM tests remaining very low ($R < 0.21$, **Appendix A.2**). In contrast, we found a strong and significant dissimilarity among districts (ANOSIM statistics close to 1, $R = 0.782^{**}$ for primates, and $R = 0.669^{**}$ for artiodactyls) that were well discriminated on the ordination (NMDS). Second, the zoogeographical patterns and the associated discontinuities obtained by the IUCN based analysis largely matched our districts' classification. The Ubangi-Congo River system emerged quickly in the hierarchical clustering, at k=3 for both primates and artiodactyls, and at k=2 for carnivores. For primates, the IUCN derived clusters were highly congruent with our regionalization and most primate districts were retrieved at k=7, with, however, two new districts in the DRC, in areas poorly sampled by ground surveys: the southern part of the Congo-Kasai interfluve and a vast eastern area covering the Maniema, and the North and South Kivu provinces (**Appendix B**). For artiodactyls, despite the East-West dichotomy, the lack of congruence between the two data sources (ground surveys *vs* IUCN range maps) likely reflects the lower resolution of the IUCN taxonomy.

3.2 Determinants and coverage of primate and artiodactyl assemblages

We identified the environmental and spatial determinants driving the districts' distribution with a random forest approach employed on the 306 primate surveys (73% of the dataset) and on the 270 artiodactyls surveys (82% of the dataset) well typifying the districts (with a silhouette value >0.2, empty circles on **Figure 2.2**). Our classification models were highly precise (out of bag error = 4.8% for primates, 1.7% for artiodactyls) and showed the leading role of rivers, specifically the Ubangi, Sanaga, Cross and Congo Rivers, in structuring primate and artiodactyl assemblages across central African forests (insets in **Figure 2.3**). For primates, insularity (separating Bioko's assemblage from those found on the continent) and precipitation-related variables (Bio12, 15 and 13) were also found important determinants. The latter discriminated the wetter and less seasonal forests of the "Atlantic" district from that of the drier and more seasonal "Inland" district (**Figure 2.3**), though we detected an important introgression between these two districts located nearby the north-eastern border of Gabon, and further north up to the Dja Faunal Reserve in Cameroon, and perhaps up to the surroundings of Yaoundé (**Figure 2.2**).



Bio1 = Annual Mean Temperature; Bio5 = Max Temperature of Warmest Month; Bio6 = Min Temperature of Coldest Month; Bio12 = Annual Precipitation; Bio13 = Precipitation of Wettest Month; Bio14 = Precipitation of Driest Month; Bio15 = Precipitation Seasonality

Figure 2.3 Environmental and spatial determinants and predicted distribution with associated uncertainties of the zoogeographical districts identified for primates and artiodactyls across central African forests. The importance of environmental and spatial predictors in the random forest classification models corresponds to the mean decrease in accuracy of the prediction when the predictor variable is randomly permuted in the training dataset. Each 0.1° pixel across the moist forest area derived from the Copernicus Global Land Cover classification (Buchhorn *et al.* 2020) is assigned to the most frequently predicted district by 100 random forest classification models (see Figure 2 for the district color scheme). The green hatched areas indicate the protected area network (IUCN & UNEP-WCMC 2018).

Using our random forest classification models, we further predicted the distribution of the zoogeographical districts and the associated uncertainties (**Figure 2.3**). The

"South Nigeria", "Rift" and to a lesser extent the "Cameroonian Highlands" appeared restricted in terms of spatial coverage (**Table 2.1**) and highly fragmented (**Figure 2.3**). The spatial predictions of the "Rift" district notably differ between primates and artiodactyls (**Table 2.1**, **Figure 2.3**) because of a few primate surveys in the lowlands and foothills that were included in this district (**Figure 2.2**). In contrast, the "Inland" district in Atlantic central Africa, and the "Congo-Kasai" and "East Congo" districts in the Congo basin covered more than 500,000 km^2 each (**Table 2.1**). The spatial extent of the "East Congo" district however remains to be evaluated with ground data since an immense area between the Ubangi and Congo Rivers do not contain any field survey, as reflected by the weak prediction of the model (**Figure 2.3**) and part of this area corresponds to the central Congo Basin peatland complex. Also, it is worth reminding that the mammal assemblage may not be as rich and diverse across all the districts' area because of local threats to biodiversity.

Table 2.1 Conservation status and anthropogenic threats faced by the zoogeographical districts. Total coverage and proportion of areas under protection status, mean defaunation index ($\overline{\text{DI}}$) (0 virtually represents a completely defaunated mammal community and 1 an intact community) (Benítez-López *et al.* 2019) and mean forest landscape integrity index ($\overline{\text{FLI}}$) ranging from no forest integrity (0) up to a complete forest integrity (1) (Grantham *et al.* 2020) is provided for each zoogeographical district.

Order District	Total area in km^2 (proportion in protected area, in %)		$\overline{\text{DI}}$	$\overline{\text{FLI}}$
Primates				
South Nigeria	40,740	(16.2)	0.16	0.44
Cameroonian Highlands	83,577	(17)	0.24	0.79
Bioko	1,474	(66.7)	0.53	0.62
Atlantic	231,991	(13.1)	0.47	0.81
Inland	539,904	(18.2)	0.59	0.88
Congo-Kasaï	614,250	(12.2)	0.61	0.76
East Congo	551,356	(11.7)	0.60	0.74
Rift	41,789	(19.7)	0.55	0.75
Artiodactyls				
South Nigeria	41,355	(17.8)	0.17	0.45
Cameroonian High. + Bioko	84,436	(17.1)	0.24	0.79
Inland	771,895	(16.7)	0.55	0.85
Congo-Kasaï	649,928	(12.4)	0.61	0.75
East Congo	550,580	(11.6)	0.60	0.75
Rift	6,886	(62.5)	0.37	0.53

3.3 Conservation status and level of threats

We further assessed the protected area coverage on the predicted distribution of the zoogeographical districts (**Figure 2.3**) and the levels of ongoing threats across the region (**Figure 2.4**), using existing maps of hunting-induced defaunation (Benítez-López *et al.* 2019) and disruption of forest integrity (Grantham *et al.* 2020). We found that the proportion of protected area ranged between 11% and 67% among districts

(**Table 2.1**). The “Congo-Kasaï” and “East Congo” districts in the DRC showed the lowest levels of protected area coverage, with only 12 and 11% of their area. It is worth noting that this protection level is relative to the current forest area and can be high and misleading for districts presenting small, protected patches of remnant forests, such as the “South Nigeria” and the “Rift”, and to a lesser extent the “Cameroonian Highlands”. The levels of ongoing threats varied across central African forests, and we detected scattered hotspots of anthropogenic threats and very few undisturbed areas (**Figure 2.4**). The unique “South Nigeria” mammal assemblage is by far the most strongly threatened district with high defaunation level (mean defaunation of the district, $\overline{DI}$ =0.16) and poor forest integrity ($\overline{FLI}$ = 0.44) even though 17% of its forests are protected (**Table 2.1**). While vastly protected (20-63%), the “Rift” district also undergoes high level of threats (**Figure 2.4**). Defaunation is also important in the “Cameroonian Highlands” and “Bioko” districts though forest integrity appeared relatively high. The largest districts, “Inland” (and “Atlantic” for primates), “Congo-Kasai” and “East Congo”, appeared less threatened, with vast areas in and nearby protected areas with low defaunation and high forest integrity.

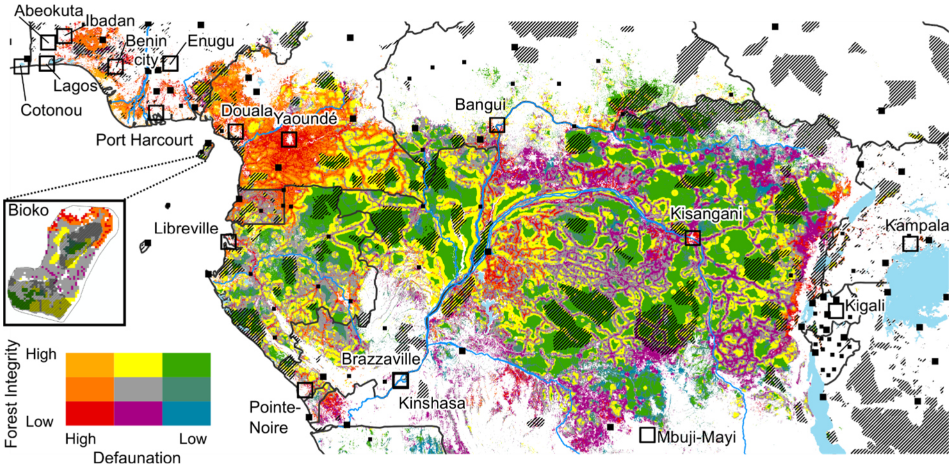


Figure 2.4 Consensus map of anthropogenic threats across central African forests, combining the levels of defaunation (Benítez-López *et al.* 2019) and of forest integrity (Grantham *et al.* 2020). Each pixel is colored according to the level of pressure it faces ranging from red “highly defaunated and a low forest integrity” to green “nearly intact mammal community and a high forest integrity”. The color code for intermediate pressure levels is presented in inset. A zoom on Bioko Island is also displayed as inset. Major urban centers (> 500,000 inhabitants), cities (50,000 – 500,000 inhabitants) and towns (less than 50,000 inhabitants) according to World Cities layer by ESRI (http://www.arcgis.com, Esri, DeLorme Publishing Company) are represented by black squares with a decreasing size according to the city population. The black hatched areas represent the protected area network (IUCN & UNEP-WCMC 2018).

4 Discussion

In this study we aimed to provide a detailed regionalization of the mammal assemblages across central African forests at a scale specifically adapted for coordinating conservations strategies. Covering a broad range of taxa, we refined previous zonations of primate communities in the Congo basin (Colyn *et al.* 1991, Gautier-Hion *et al.* 1999, Colyn & Deleporte 2004) and herbivore communities across the African continent (Hempson *et al.* 2015). First, we have found that carnivores form a broad and unique Congolian district. This lack of spatial structure reflects the vast distribution of most carnivore species in central Africa (*e.g.*, *Caracal aurata* , Bahaa-el-din *et al.* 2015) and their ecology, being highly mobile and having broad habitat and dietary niches (Wilson & Mittermeier 2009) like their Neotropical relatives (Cruz *et al.* 2022). In contrast, we found highly congruent spatial patterns for primate and artiodactyl assemblages across central African forests, and our dissimilarity-based approach applied on a newly assembled dataset from a data-deficient region (Verbeeck *et al.* 2011, Siddig 2019) allowed to identify six common districts including from west to east, “South Nigeria”, “Cameroonian Highlands” (for primates - “Cameroonian Highlands” and “Bioko”), “Inland” in Atlantic central Africa (for primates - “Inland” and “Atlantic”), “Congo-Kasaï”, “East Congo” and the “Rift". The highly fragmented “South Nigeria” district present unique but species-poor assemblages, notably for primates, probably due to long-lasting anthropogenic pressure in the region that had already led to a reduced diversity before the first studies were conducted (species list only available after 1980). Nigeria is by now the most populous country of sub-Saharan Africa (Vollset *et al.* 2020) and has been largely impacted by human activities (Venter *et al.* 2016), particularly by high volumes of bushmeat extraction from remnant forests (Fa *et al.* 2006). For the “Bioko” district, the thriving primate-oriented bushmeat trade (Cronin *et al.* 2017) has undoubtedly put an additional pressure on an already species-poor primate assemblage, since the island has gone through an extinction debt since its separation from the African continent 10,000-14,000 years ago (Jones 1994). Though highly fragmented, the “Rift” district showed a highly specific assemblage, notably for artiodactyls, revealing the richness and uniqueness found at the boundary of the forest and savanna biomes. This area is also a particular biogeographical unit for birds (De Klerk *et al.* 2002), amphibians and reptiles (Chifundera 2019), and a regional mosaic for plants (White 1983). It is, however, for the “Rift” district that artiodactyls and primates show the less congruent spatial patterns probably because most primates are confined to the forest habitat while many artiodactyl species occurring in this district (including indicator species) are savanna species. Within the lowland tropical forests of DRC, we identified a whole range of primate and artiodactyl species, besides the flagship ones like the bonobo and the okapi, that make the “Congo-Kasaï” and “East Congo” districts particularly unique. In contrast, the “Cameroonian Highlands” and "Inland" districts, and “Atlantic” for primates, exhibit rich species assemblages, but mostly composed of widely distributed species with low indicator value (**Appendix A.3**) such as the putty-nosed monkey (*Cercopithecus nictitans*) or the red river hog (*Potamochoerus porcus*).

The Ubangi-Congo River system was found to be an important discontinuity, driving the first split in the clustering for both primate and artiodactyl assemblages, and this result was also supported by the IUCN based analysis for the three orders, including carnivores (**Appendix B**). It is also an important discontinuity for trees (White 1983) and other vascular plants (Droissart *et al.* 2018, Marshall *et al.* 2021) dividing two subregions in central Africa, *i.e.*, the Lower Guinea and Congolia subcenters of endemism though the separation between the two is much larger and corresponds to the Sangha River Interval, a 400 km wide forest area (14 - 18°E), recognized for its low plant endemism (White 1983). Rivers, especially large ones (>1 km) that are not easily crossed, act as natural dispersal barriers to numerous taxa across the globe (Chapman *et al.* 1999, Kingdon *et al.* 2013, Oliveira *et al.* 2017, Aliaga-Samanez *et al.* 2020) and the riverine barrier mechanism has been proposed as a possible scenario for explaining the diversification of tropical African biodiversity (Couvreur *et al.* 2021). In central Africa, the current river network was earlier linked to the distribution of forest primates (Colyn *et al.* 1991, Colyn & Deleporte 2004), but our study formally tested the role of rivers on the whole of primate and artiodactyl assemblages. Major rivers also explained current patterns of genetic diversity among a few rodent (Nicolas *et al.* 2011), primate (Telfer *et al.* 2003, Eriksson *et al.* 2004, Gonder & Disotell 2006, Anthony *et al.* 2007) and artiodactyl (Moodley & Bruford 2007) species. The Ogooué and Sangha Rivers, although important drivers of genetic variation amongst gorilla and mandrill populations (Telfer *et al.* 2003, Anthony *et al.* 2007), were not found as major barriers differentiating primate communities at this regional scale. Also, we did not identify the Cameroon Volcanic Line to be a major discontinuity for both primates and artiodactyls, though playing an important role for amphibians (Portik *et al.* 2017). Insularity and precipitation-related variables were found important predictors of primate districts' distribution. Some primate species found on Bioko Island are indeed endemic like *Piliocolobus pennantii* and differ from their sister species found on the continent (Mittermeier *et al.* 2013) while the role of precipitations is certainly associated with changes in forest composition and functioning. Indeed, the shift between the "Atlantic" and the "Inland" districts for primates, which closely matches the limit between the Congolian coastal forests and the Northwest Congolian lowland forests ecoregions (*sensu* Dinerstein *et al.* 2017, **Appendix C**), corresponds to a shift from the wetter and less seasonal evergreen forests to the drier and more seasonal semi-deciduous forests (Fayolle *et al.* 2014, Réjou-Méchain *et al.* 2021). This shift most likely translates into differences in quality, quantity and seasonality of fruits, seeds and leaves, the main components of a primate's diet (Chapman 1995, Gautier-Hion *et al.* 1999). For example, *Colobus satanas* is an "Atlantic" species whose diet is primarily based on seeds (up to 60%) and evergreen forests dominating in its distribution area are extremely rich in legumes producing many pods and seeds. In contrast, *Colobus guereza* is an "Inland" species which exhibits a flexible diet between folivory and frugivory, and semi-deciduous forests stretching deeper inland are known for the greater and longer abundance of fleshy fruits (Gautier-Hion *et al.* 1999). This association with the forest type seems to be restricted to primates as we did not encounter a similar pattern for artiodactyls, perhaps due to their less selective diet than that of small arboreal primates. In the same line, the zoogeographical patterns obtained from the IUCN based analysis for primates, which were highly congruent with our districts obtained from ground surveys, also provided the most refined regionalization (**Appendix B**), supporting the relevance of these highly forest dependent taxa for understanding the zoogeography of central African forests (Colyn *et al.* 1991, Colyn & Deleporte 2004).

The new regionalization of central Africa we provided is also highly congruent with the WWF ecoregions (Dinerstein *et al.* 2017) that have been widely used for conservation planning (**Appendix C**). Here, we also detailed the conservation implications of the congruent biogeographic patterns retrieved between primates and artiodactyls from ground surveys, notably integrating the protected area coverage, and the levels of anthropogenic threats. The current distribution of protected areas covers 14.2% of central African forests and covers all the districts we delimited. With only 12 and 11% of protected area coverage, the "Congo-Kasaï" and "East Congo" districts in the DRC were below the threshold of 17% of land and inland waters promoted by the 2020 Aichi Target 11 (UN CBD 2010), but the protected area coverage needs to be confronted to the current forest area and to the levels of anthropogenic threats. For instance, the protected area coverage of the "Rift" district can appear satisfactory (~20% for primates and >60% for artiodactyls) though the district is highly fragmented and threatened. By joining maps which identify areas threatened by hunting-induced defaunation (Benítez-López *et al.* 2019) and by disruption of forest integrity (Grantham *et al.* 2020), we detected scattered hotspots of anthropogenic threats and very few undisturbed areas across central African forests. Indeed, almost no areas in the world can be classified as faunally pristine (Allan *et al.* 2019, Plumptre *et al.* 2021), even in the tropics and within protected areas (Laurance *et al.* 2012). Across central African forests, "South Nigeria" is by far the most strongly threatened district, with severely depleted forests in wildlife and only little forest integrity, probably due to the rise and expansion of many cities and urban centers along the coast. The high level of defaunation retrieved in the "Cameroonian Highlands" and "Bioko" districts is due to the important human density in the Cross-Sanaga region and in Bioko, particularly around the main city of Malabo, north of the island (Fa *et al.* 2014). Regarding the "Inland" district ("Inland" and "Atlantic" for primates), the most extensive district according to our model's predictions, large forest tracts remain relatively undisturbed in Gabon and in Republic of Congo, in protected areas, and in their surroundings mostly granted to logging concessions. It is not true for south-west Cameroon and at the southern tip of the Mayumbe forest along the coast of Congo and of the DRC, both areas being highly impacted by anthropogenic threats. Dramatic pressures also occur in eastern central Africa and emerging deforestation hotspots were recently detected across most of the "Congo-Kasaï" district and at the edge of the "East Congo" district (Harris *et al.* 2017, Vancutsem *et al.* 2021). While vastly protected, either in the DRC (*e.g.*, Virunga NP, Kahuzi-Biega NP) or in Uganda (*e.g.*, Kibale NP or Bwindi Impenetrable NP), a high level of threats also occurs along the Albertine Rift and its foothills making the "Rift" district particularly at risk.

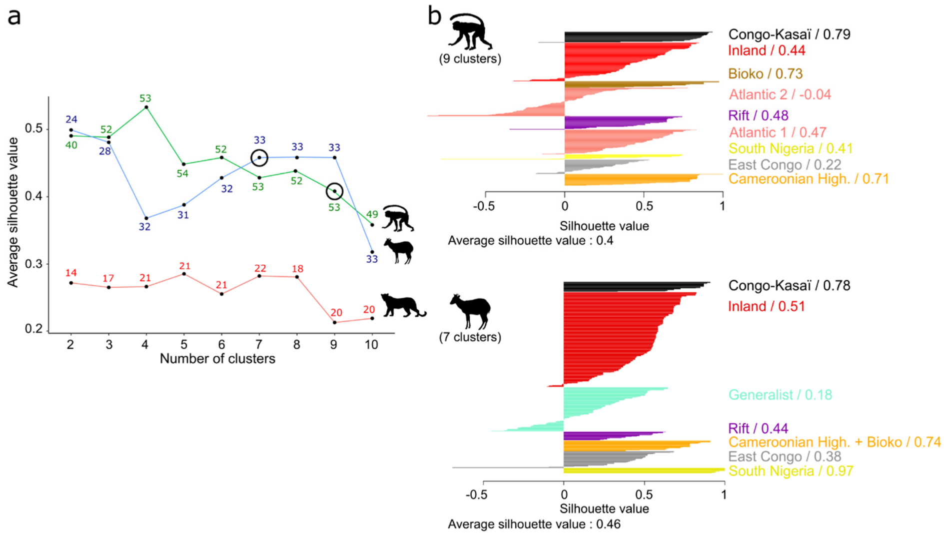
Since anthropogenic disturbances and environmental changes rapidly occur throughout central Africa (Abernethy *et al.* 2016) already inducing cascading effects on the megafauna (Bush *et al.* 2020), there is an urgent need to implement actions to conserve all identified districts. Our results call for two types of conservation policies that can be formulated in complementary ways. On one side, priority must be given in the most disputed, deforested and anthropized areas which harbor unique and highly threatened mammal assemblages such as the ones retrieved in the "South Nigeria", "Cameroonian Highlands", "Bioko", and "Rift" districts. In this case, the conservation of small areas through sanctuaries and community management areas must be privileged, while maintaining and connecting the isolated existing protected areas. In these highly threatened districts, the reported species pool (**Appendix A.3**) constitutes a valuable tool for assessing potential missing species (by comparing expected composition with the observed one) and will provide guidance for rewilding programs. On the other side, districts that are characterized by vast remote forest areas with little deforestation and low population density are already covered by several protected areas (*e.g.*, Dzangha-Sangha NP in the "Inland" district, the Salonga NP and Lomami NP in the "Congo-Kasaï" district, the Hunting Domain of Rubi-Tele, Okapi Wildlife Reserve and Maiko NP in the "East Congo" district) must remain central to conservation policies at regional and national level. However, large, and relatively intact areas persist in the DRC and could be used to expand the protected area network if their conservation value is confirmed by exploratory field investigations. These new protected areas would probably be the last ones although political instability may hinder such initiatives. Though vastly understudied, the country harbors great future discovery potential for mammalian taxa (Moura & Jetz 2021) as confirmed by recent (re)discoveries of species (Hart *et al.* 2012, Maisels & Devreese 2020). Specifically undersampled, a large part of the "East Congo" district including the central Congo Basin peatland complex where *terra firme* forests alternate with swamp forests, either dominated by palm or hardwood species, and savannas (Dargie *et al.* 2017), remains largely enigmatic for mammal assemblages and might be further divided if better documented. Finally, to ensure large-scale ecological connectivity, interconnection between protected areas must be maintained and promoted in regional- and country-level conservation strategies. Public-private partnerships could be part of these strategies integrating conservation actions in well-managed logging concessions in the periphery of protected areas (*e.g.*, TRIDOM-TNS conservation landscape in the "Inland" district).

5 Conclusion

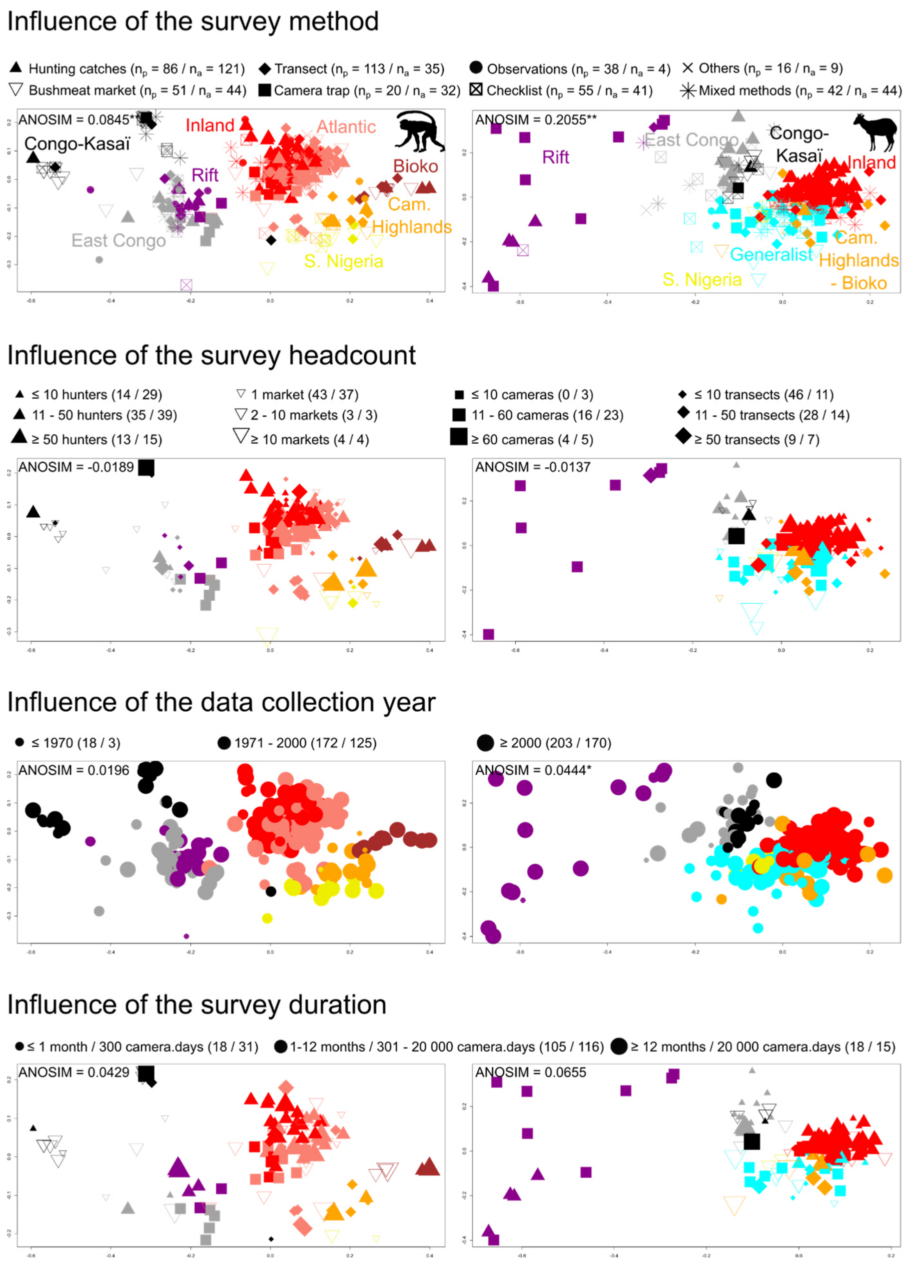
In this study, we provided a detailed regionalization scheme for central African forests' mammal assemblages using an extensive and original dataset of species lists. Both primates and artiodactyls present spatially structured assemblages, while carnivores only form a unique and broad Congolian district with no clear further divisions. We also evidenced the structuring role of rivers on both primate and artiodactyl assemblages' geographic distribution and the importance of insularity and precipitation on primate species composition specifically. Our classification into districts provides an important benchmark for assessing the conservation status of the large mammalian fauna of the region, highlighting priority districts that are threatened and poorly represented in the protected area network. The reported species pool and indicator species from each district can also be used to identify some of the missing species in newly sampled areas as well as to select target species for rewilding efforts. It should also be noted that our compilation of existing literature also highlighted those broad areas that remain understudied in central Africa, including, but not limited to, large parts of the DRC and the central Congo Basin peatland complex.

6 Appendices

Appendix A Clustering on surveys



Appendix A.1 Average silhouette values according to the number of clusters chosen to partition the dataset for each order (a). The circles indicate the number of clusters retained, 9 for primates and 7 for artiodactyls. The final number of districts retained was also supported by the spatial coherence of the regionalization patterns and the total number of indicator species (numbers displayed along with the graph lines). Silhouette scores for each survey sorted by district and average silhouette value for each district (b). For primates, Atlantic 1 & Atlantic 2, in pink, have been merged into a unique Atlantic district since their indicator species only typified them when considered together. Silhouette scores range from -1 to 1 and indicate how strongly a given survey is associated to its district (see Methods).



Appendix A.2 Non-metric multidimensional scaling for primates (left) and artiodactyls (right). Each point represents a survey. Point color follows the district color scheme presented in Figure 2.2. Point shape and size represents the survey method, the survey headcount, the year of data collection and the survey duration. The number of surveys considered for each category is shown in brackets, separately for primates and for artiodactyls. The result of the ANOSIM (analysis of similarity) test is displayed in each panel.

Appendix A.3 District species pool. Indicator species of one district (background coloured in dark grey) or a combination of districts (background coloured in light grey) are displayed for primates and artiodactyls. Specificity values are only displayed for species typifying a unique district (*i.e.*, strict indicators). * indicates species present in the district but not retained as indicator of the district.

	South Nigeria	Cam. Highlands	Bioko	Atlantic	Inland	Congo-Kasaï	East Congo	Rift
Primates								
Cercopithecidae								
Allenopithecus nigroviridis					*	0.98		
Allochrocebus lhoesti							0.73	*
Allochrocebus preussi		*	0.83					
Allochrocebus solatus				*				
Cercocebus agilis				*	0.79		*	*
Cercocebus chrysogaster						1		
Cercocebus torquatus	░	░		░				
Cercopithecus ascanius						░	░	░
Cercopithecus cephus				░	░			
Cercopithecus denti							1	
Cercopithecus doggetti								
Cercopithecus dryas						1		
Cercopithecus erythrogaster	1							
Cercopithecus erythrotis		░	░					
Cercopithecus hamlyni							1	
Cercopithecus kandti								
Cercopithecus lomamiensis								
Cercopithecus mitis							░	░
Cercopithecus mona	░	░						
Cercopithecus neglectus				░	░	░	░	*
Cercopithecus nictitans	░	░	░	░	░			
Cercopithecus pogonias		░	░	░	░			
Cercopithecus sclateri	1							
Cercopithecus wolfi						0.96	*	
Chlorocebus tantalus								
Colobus angolensis						░	░	*
Colobus guereza				*	░		*	░
Colobus satanas		*	░	░	*			
Erythrocebus patas								
Euoticus elegantulus				*	*			
Euoticus pallidus	░	░						
Galago matschiei							1	
Galago senegalensis					*		*	
Galagoides demidovii	0.53	*	*	*	*	*	*	

Galagoides thomasi		*				*	0.62	*
Lophocebus albigena		*						
Lophocebus aterrimus						1		
Lophocebus johnstoni							0.87	*
Lophocebus ugandae								1
Mandrillus leucophaeus								
Mandrillus sphinx				0.97	*			
Miopithecus ogouensis		*		0.75	*			
Otolemur crassicaudatus							*	
Papio anubis	*				*			
Papio cynocephalus								
Piliocolobus foai								
Piliocolobus oustaleti					*			*
Piliocolobus pennantii			1					
Piliocolobus preussi		1						
Piliocolobus semlikienis							1	
Piliocolobus tephrosceles								1
Piliocolobus tholloni						1		
Procolobus verus								
Sciurocheirus alleni			1					
Sciurocheirus cameronensis								
Sciurocheirus gabonensis				0.84	*			
Hominidae								
Gorilla beringei							1	
Gorilla gorilla		*						
Pan paniscus						1		
Pan troglodytes	*				*			
Lorisidae								
Arctocebus aureus				*	*			
Arctocebus calabarensis	0.69	*						
Perodicticus edwardsi	0.64	*		*	*			
Perodicticus ibeanus							1	

	South Nigeria	Cam. Highlands + Bioko	Inland	Congo-Kasaï	East Congo	Rift	Generalist
Artiodactyla							
Bovidae							
Aepyceros melampus							
Cephalophus arrhenii					1		
Cephalophus callipygus							
Cephalophus castaneus	*						*
Cephalophus crusalbum			*				*
Cephalophus curticeps						1	
Cephalophus hypoxanthus							

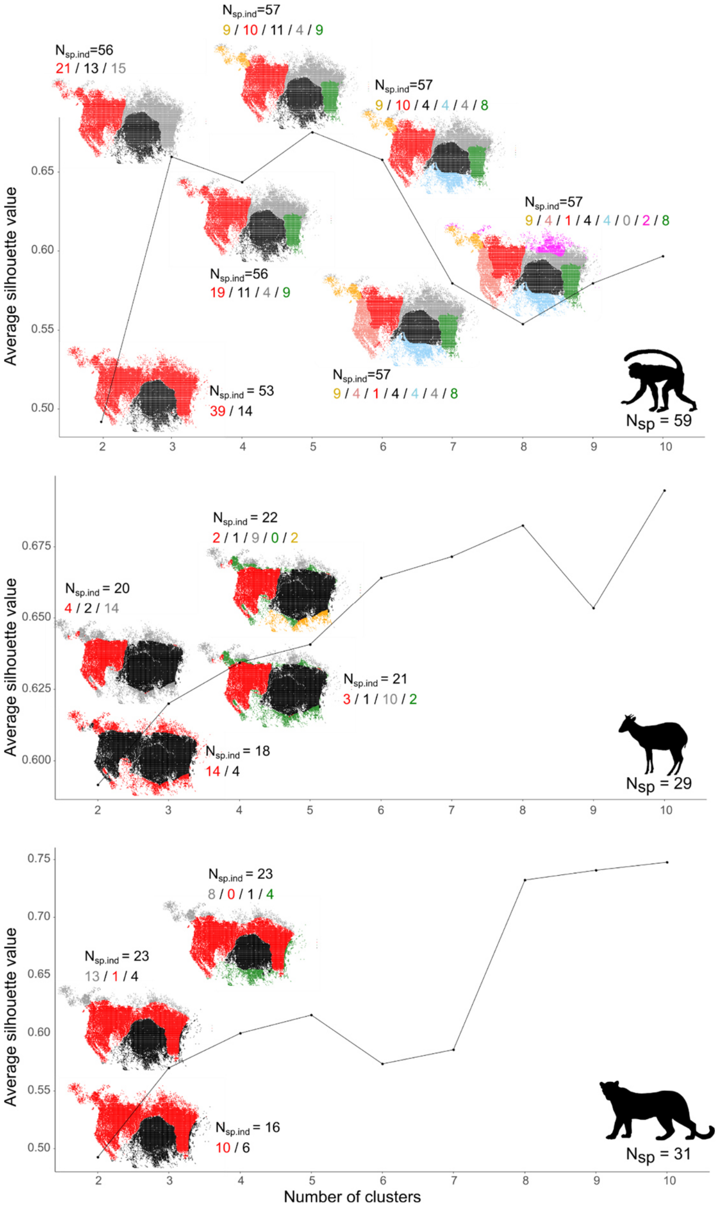
Cephalophus johnstoni					*	0.69	
Cephalophus lestradi							
Cephalophus leucogaster			0.90				*
Cephalophus niger							
Cephalophus nigrifrons		*					*
Cephalophus ogilbyi	*	0.9					
Cephalophus rubidus							
Cephalophus rufilatus			*				
Cephalophus silvicultor							
Cephalophus weynsi				0.73	*		
Damaliscus ugandae					*	*	
Hippotragus equinus							
Kobus defassa					*	0.77	*
Kobus loderi							
Kobus thomasi						1	
Neotragus batesi			*				*
Ourebia montana						1	
Philantomba aequatorialis							
Philantomba congica							
Philantomba melanorhea		*					
Philantomba simpsoni				1			
Philantomba walteri	1						
Redunca bohor						1	
Sylvicapra grimmia				*	*	0.73	*
Syncerus caffer						1	
Syncerus nanus		*	*	*	*		0.53
Taurotragus oryx							
Tragelaphus bor					*	0.95	
Tragelaphus eurycerus			*	*	*		*
Tragelaphus gratus		*					
Tragelaphus ornatus							
Tragelaphus phaleratus	0.5	*	*	*		*	*
Tragelaphus selousi			*	0.96			
Tragelaphus spekii					*	0.81	
Giraffidae							
Giraffa camelopardalis							
Okapia johnstoni					1		
Hippopotamidae							
Hippopotamus amphibius	*	*	*		*	0.54	*
Suidae							
Hylochoerus meinertzhageni			*				*
Phacochoerus africanus							
Potamochoerus larvatus						1	
Potamochoerus porcus							
Tragulidae							
Hyemoschus aquaticus							

Appendix B Clustering on IUCN species range maps

We explored the issues of incompleteness and bias in species sampling from field surveys (*e.g.*, non-game species in bushmeat surveys, arboreal species in ground camera trap surveys). We built a presence matrix for the three orders studied (carnivores, primates and artiodactyls) by intersecting all IUCN species range maps over a 0.1° grid. The resulting presence matrix (17,126 pixels) was used to quantify the dissimilarity in species composition between each pair of pixels using the Simpson beta-diversity index (Koleff *et al.* 2003). We kept the species present in at least one hundred pixels (31 out of 40 carnivore species, 59 out of 71 primate species, and 29 out of 41 artiodactyl species) and the pixels with at least three species (less than 0.1% of the pixels) to account for artefacts due to rarity as done for the survey point data. We then clustered all the pixels up to 10 groups by applying Ward's hierarchical classification algorithm (Kreft & Jetz 2010). For each cluster division, we computed the district's average silhouette width and the district's number of indicators species according to De Cáceres & Legendre (2009). As the district's average silhouette width was high for all division (between 0.5 and 0.75), we stopped dividing into new clusters when no new indicator species appeared.

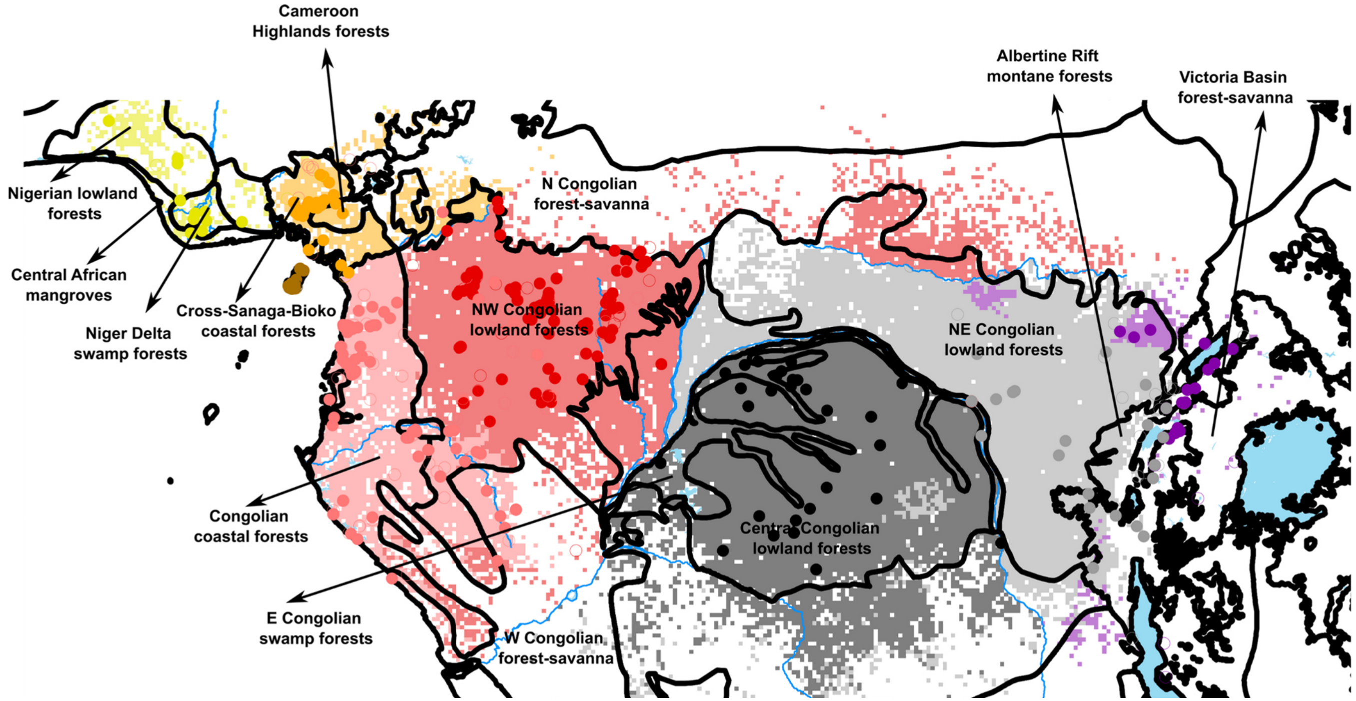
The IUCN based analysis provides both confirmatory and complementary results, but most importantly confirms that the major discontinuity in the region corresponds to the Ubangi-Congo River system which emerged quickly in the hierarchical clustering at k=3 for primates and artiodactyls, and k=2 for carnivores. Interestingly, this discontinuity was supported for the three different orders including carnivores contrasting with our results (see Figure 2 in the main text). Primates still depicted the finer patterns in species composition supporting the relevance of these highly forest dependent taxa in understanding the zoogeography of the region. Most of our primate districts were retrieved with the IUCN based approach like the "Inland" and "Atlantic" districts (k=6) while others have been partitioned like the "Congo-Kasaï" and the "East Congo" districts or not properly identified like the "Cameroonian Highlands", "Bioko" and the "Rift" districts. We obtained less congruence for the artiodactyls since no spatially consistent pattern was retrieved after the initial East-West dichotomy at k=3.

Two reasons can explain the discrepancies observed between the results of the two approaches (ground surveys vs IUCN based analysis). Firstly, the taxonomy adopted in this study (Mittermeier *et al.* 2013 for primates; Wilson & Mittermeier 2009, 2011 for carnivores and hoofed mammals) is at a higher resolution than the one used by the IUCN, with some species being split in multiple new taxa (*i.e.*, "the lumper-splitter paradigm"). The illustrative case of the genus *Philantomba* is described in the main text. This difference in taxonomy is also highlighted by the differing number of species considered for each order (31 species for carnivores in both approaches, 64 versus 59 species for primates and 49 versus 29 species for artiodactyls). Secondly, new clusters have been detected with the IUCN based analysis in areas undersampled by ground surveys like the southern and the southeastern parts of the DRC's forest. This points out the difficulties of accurate prediction in these particularly understudied areas (see model uncertainties in Figure 3 in the main text).



Appendix B.1 Average silhouette values according to the number of clusters chosen to partition the dataset for each order. The distribution map of the clusters is presented until a cluster with no indicator species emerges in the division. The total number of species (N_{sp}) considered for each order is displayed on each panel. For each cluster division, the total number of indicator species ($N_{sp.ind}$) and the number of indicator species for each cluster is indicated with the color scheme of the map shown as inset.

Appendix C Congruence with the ecoregion classification



Appendix C.5 Map of the eight zoogeographic districts identified in this study for primates, South Nigeria (yellow), Cameroonian Highlands (orange), Bioko (brown), Atlantic (salmon), Inland (red), Congo-Kasaï (black), East Congo (grey), and Rift (magenta), overlaid by the original surveys used for the district classification (filled and empty circles respectively correspond to silhouette scores greater and lower than 0.2), and by the WWF ecoregions (Dinerstein *et al.* 2017).

Appendix C.2 Confusion matrix between the WWF ecoregions (Dinerstein *et al.* 2017) and the zoogeographic districts identified in this study for primates. We found good correspondence between the ecoregions and our districts, as shown by the distribution of surveys along the diagonal. Ecoregions with more than 50% of the surveys corresponding to one of our districts are shown in bold and highlighted according to our color scheme. Ecoregions with less than three surveys (*e.g.*, Western Congolian swamp forests) were not considered here.

	South Nigeria	Cam. Highlands	Bioko	Atlantic	Inland	Congo-Kasaï	East Congo	Rift
Nigerian lowland forests	**4**							
Niger Delta swamp forests	**6**							
Central African mangroves	1	1		3				
Cross-Sanaga-Bioko coastal forests	2	**28**	18	5		1		
Cameroon Highlands forests		**2**		1				
Congolian coastal forests		1		**74**				
Western Congolian forest-savanna				**12**	1			
Northern Congolian forest-savanna				1	**5**		2	
Northwest Congolian lowland forests				48	**99**			
Eastern Congolian swamp forests				1		**4**	3	
Central Congolian lowland forests						**23**		
Northeast Congolian lowland forests							**14**	3
Albertine Rift montane forests							18	**24**
Victoria Basin forest-savanna							2	**4**

3

Appropriate sampling

Preamble

In **Chapter 2**, I showed how species composition data derived from wildlife surveys can inform regional conservation policy for medium and large mammals in central African forests. Camera trap surveys represent a rich and reliable source of such data that allows for a detailed documentation of the species assemblage coexisting on a given site. In this chapter, we specifically investigated how the placement strategy of camera trap devices in the forest understorey might influence the detected species assemblages from species richness and detectability up to the species composition of the overall assemblage.

- Paper 2: published -

Wildlife trail or systematic? Camera trap placement has little effect on estimates of mammal diversity in a tropical forest in Gabon

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This paper is published in *Remote Sensing in Ecology and Conservation*, 7(2), 321-336

Abstract

Camera traps (CTs) have been increasingly used for wildlife monitoring worldwide. In the tropics, most CT inventories target wildlife-friendly sites, and CTs are commonly placed towards wildlife trails. However, it has been argued that this placement strategy potentially provides biased results in comparison to more systematic or randomized approaches. Here, we investigated the impact of CT placement on the remotely sensed mammal diversity in a tropical forest in Gabon by comparing pairs of systematically placed and wildlife-trail-oriented CTs. Our survey protocol consisted of 15–17 sampling points arranged on a 2 km^2 grid and left for one month in the field. This protocol was replicated sequentially in four areas. Each sampling point comprised a CT pair: the ‘systematic CT’, installed at the theoretical point and systematically oriented towards the most uncluttered view; and the ‘trail CT’, placed within a 20-m radius and facing a wildlife trail. For the vast majority of species, the detection probabilities were comparable between placements. Species average capture rates were slightly higher for trail-based CTs, though this trend was not significant for any species. Therefore, the species richness and composition of the overall community, such as the spatial distribution patterns (from evenly spread to site-restricted) of individual species, were similarly depicted by both placements. Opting for a systematic orientation ensures that pathways used preferentially by some species—and avoided by others—will be sampled proportionally to their density in the forest undergrowth. However, trail-based placement is routinely used, already producing standardized data within large-scale monitoring programs. Here, both placements provided a comparable picture of the mammal community, though it might not be necessarily true in depauperate areas. Both types of CT data can nevertheless be combined in multi-site analyses, since methods now allow accounting for differences in study design and detection bias in original CT data.

Keywords: Camera placement, Wildlife monitoring, Occupancy modelling, Detection probability, Diversity, Composition

1 Introduction

Over the last decades, dramatic declines in wildlife populations have been reported worldwide (Collen *et al.* 2009, Craigie *et al.* 2010, Dirzo *et al.* 2014, Ceballos *et al.* 2017). These declines, and the overall degradation of natural ecosystems, are a direct consequence of growing demographic pressure, unsustainable logging and hunting, urbanisation and agricultural conversion (Sala *et al.* 2000, Hoffmann *et al.* 2010, Malhi *et al.* 2014, Gillet, Vermeulen, Feintrenie, *et al.* 2016, Edwards *et al.* 2019).

In tropical Africa, massive losses of iconic megafauna, which includes flagship species such as elephants (*Loxodonta africana*) (Maisels, Strindberg, *et al.* 2013) and the great apes (*Gorilla spp.* and *Pan spp.*) (Strindberg *et al.* 2018) have been experienced. Species formerly considered less emblematic, such as pangolins (*Smutsia spp*. and *Phataginus spp.*), are also presently highly threatened (Heinrich *et al.* 2017, Mambeya *et al.* 2018). The spread of the illegal wildlife trade and modern hunting techniques up to the most isolated rural communities (Abernethy *et al.* 2013) has been promoted by the expansion of the road network for extractive activities, such as mining or logging (Kleinschroth *et al.* 2019). Production forests managed responsibly may, however, play an important buffer role, specifically in the periphery of protected areas, as long as integrated wildlife management is safeguarded and coupled with a strict control of forest access (Edwards *et al.* 2014, Lhoest *et al.* 2020). Continuous monitoring is essential in order to prioritize conservation actions both in well-protected areas and production forests, and user-friendly techniques and standardized methodologies are required to properly assess and monitor wildlife communities.

Camera traps (CTs) are used worldwide by scientists and private operators to study and monitor wildlife populations across a wide range of habitats and latitudes. Constant progress in technology, falling prices over time (Agha *et al.* 2018) and advances in data management software (Forrester *et al.* 2016, Scotson *et al.* 2017) have enabled the spread of this technique. In remote environments, such as tropical forests, the cost and time-efficiency of CTs, as well as their complementarity with other wildlife assessment methods, have been amply proven (Rovero & Marshall 2009, Gogarten *et al.* 2020). CT inventories provide crucial information for wildlife managers on population state variables in a rapid and non-invasive manner. They allow the estimation of animal density for marked (Royle *et al.* 2009) and unmarked species (Rowcliffe *et al.* 2008, Howe *et al.* 2017, Nakashima *et al.* 2020), studying occurrence patterns through occupancy modelling (MacKenzie *et al.* 2017) and/or providing species capture rates, usually described with the relative abundance index (RAI) when standardized by the sampling effort.

To be comparable across space and time, CT studies should follow standardized, or at least comparable, approaches. In many surveys, the choice of CT location relies on subjective criteria based on accessibility or expectations of wildlife occurrence (Burton *et al.* 2015). More robust approaches relying on randomized or systematic sampling designs (*e.g.*, regularly spaced grids with a predefined CT density) are also followed, sometimes applied across multiple sites, such as the TEAM monitoring network (Jansen *et al.* 2014). In most cases, the selection of the exact CT location is still based on the presence of wildlife trails or signs to select the “optimal” location to capture the largest number of species, corresponding *de facto* to a non-random orientation (TEAM Network 2011, Cusack, Dickman, *et al.* 2015, Kolowski & Forrester 2017). In contrast, a random orientation of CTs is needed for the density estimation of unmarked species using the random encounter model (REM) proposed by Rowcliffe *et al.* (2008) or the distance sampling approach described in Howe *et al.* (2017). This random orientation ensures that habitat features either bypassed or used preferentially by animals are representatively sampled in the forest undergrowth (Rowcliffe *et al.* 2013). Both REM and distance sampling methods have been successfully used for tropical species (Cusack, Swanson, *et al.* 2015, Gray 2018, Cappelle *et al.* 2019, Bessone *et al.* 2020).

Camera-related parameters such as trigger characteristics (Rovero *et al.* 2013) or inclination (Moore, Valentine, *et al.* 2020) are known to induce large fluctuations in detection, although there have been few studies on the impact of CT placement on detectability (Burton *et al.* 2015). Previous experiments have used an uncoupled design, which did not allow the dissociation of the effect of the placement from the effect of local habitat heterogeneity (Kays *et al.* 2009). In African savannahs, Cusack *et al.* (2015) used a spatially close paired design and found that inferences at the community scale were not biased, given a sufficient sampling effort. However, they recognized the need to replicate the approach in denser habitats, such as tropical forests. In the Neotropics, Blake and Mosquera (2014) and Di Bitetti *et al.* (2014) found contrasting impacts of pre-existing trails and roads (*i.e.*, not natural wildlife trails) on the detected species diversity and community composition based on a relatively small sampling effort. More recently, Kolowski and Forrester (2017) showed that small-scale features in north American temperate forests, specifically fallen logs and wildlife trails, may significantly affect species detection. The question of whether CT surveys with different placement strategies provide comparable data at the species and community scales remains to be addressed in tropical forests.

Here, in a tropical forest in Gabon, where wildlife is diverse and abundant, we implemented a paired design composed of a systematically oriented camera and a trail-based camera, and developed a four-step approach for the analysis of paired CT data. Specifically, we tested whether the placement of the CT influences the overall species richness (step 1), and for individual species, the detectability and capture rate (RAI) (step 2). We expected a greater level of species richness and higher RAI for the trail placement by assuming the non-random movements of animals (species preferentially moving along wildlife trails) (Wearn *et al.* 2013, Mann *et al.* 2015). We also tested whether the CT placement influences the spatial distribution patterns (from evenly spread to site-restricted) at the species and community scales (step 3), as well as the species composition of the detected mammal community (step 4). Overhunting has been demonstrated to result in depleted assemblages dominated by generalist taxa, with a size-selective defaunation gradient radiating from human settlements (Abernethy *et al.* 2013, Lhoest *et al.* 2020). Therefore, we also tested whether species body mass and conservation status, along with forest accessibility, drive these patterns.

2 Methods

2.1 Study area

The study was conducted in eastern Gabon in the production forests granted to the Precious Woods Gabon - Compagnie Equatoriale des Bois, PWG-CEB, a logging company operating on approximately 600 000 ha with a 25-year cutting cycle. The company has established reduced-impact logging practises, harvesting on average 1.4 trees/ha (~10.4 m^3/ha [Precious Woods - CEB, 2018]), and the Forest Stewardship Council and Pan-African Forest Certification labels, obtained in 2008 and 2017, respectively, require strict control of the impacts of logging on biodiversity. The concession encompasses old-growth evergreen forests in the northwest, near the Ivindo National Park (NP, **Figure 3.1 a**), as well as younger evergreen forests (dominated by *Aucoumea klaineana*) intertwined with included savannah patches in the southeastern part of the concession (**Figure 3.1 b**, brown patches). The total annual rainfall reaches 1710 mm, with a short dry season between June and August (Fick & Hijmans 2017).

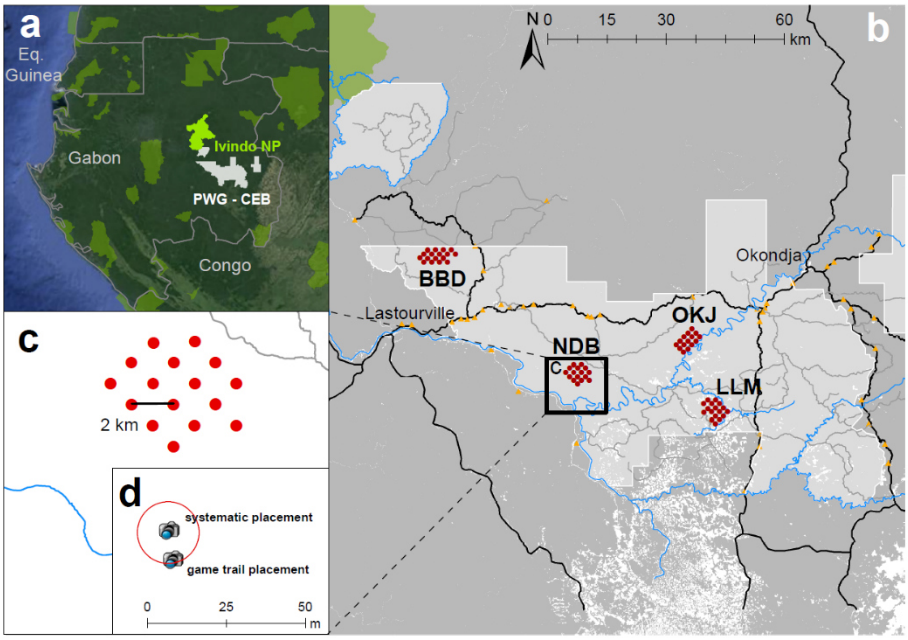


Figure 3.1 (a) Location of the PWG - CEB logging concession (in light grey) in Gabon and distribution of the protected area network (in green, the Ivindo NP is highlighted) on a Google Earth background map. (b) The location of the four CT grids, each composed of 15–17 sampling points (red dots), is shown on a background map of tree cover > 60% (Hansen *et al.* 2013). Major rivers (in blue), roads (national roads in black and main logging roads in grey), and villages (orange triangles) are also mapped. A zoom on the sampling design at the grid scale (density of installation = 1 camera site/2 km^2) (c) and camera scale (pointing out the paired design) (d) is also provided.

2.2 CT inventory

The CT inventory followed a grid design replicated sequentially in four areas (**Figure 3.1b**) named according to the forest management unit to which they belong (BBD for Bambidie, OKJ for Okondja, and LLM for Lélama) and to the proximity of an old base camp (NDB for Ndambi). These inventories were implemented between September and December 2018, which corresponds to the long rainy season. Each grid was composed of 15–17 sampling points placed at a density of one per 2 km^2 (**Figure 3.1 b,c**) and left for one month in the field. To test the influence of the CT placement on the detected diversity, we set up a CT pair at each sampling point (**Figure 3.1 d**). The first camera (hereafter referred to as the 'systematic camera') was placed close to the theoretical position and systematically oriented towards the most naturally cleared area, which may or may not encompass a wildlife trail. The second camera (hereafter referred to as the 'trail camera') was installed within a 20 m radius of the systematic camera to ensure a similar microhabitat, but was placed towards a wildlife trail or a crossing of several trails, following the TEAM recommendations (TEAM Network 2011). The CTs (Bushnell Trophy Cam HD; Bushnell, Overland Park, KS, USA) were installed on trees at knee level (30–50 cm) and set up to record 5 s videos with a minimum trigger delay of 1 s between detection events. Surrounding grasses and lianas were cut within a 3 m radius of the camera to reduce false triggers while leaving the undergrowth mostly unchanged.

2.3 Species identification

Videos were processed into Camera Base version 1.7., an open access database (Tobler 2015). Records of the same species were considered independent beyond a time interval of 30 min (Meek *et al.* 2014). Only mammals were considered for identification; mostly ground-dwelling species and a few semi-arboreal species were also included (**Table 3.1**). Species nomenclature followed the IUCN Red List of Threatened Species. Four species complexes were considered due to the difficulties in species identification on video: (1) the large-spotted genet complex comprises *Genetta servalina* and *Genetta maculata* (Hedwig *et al.* 2018); (2) the "mongoose" species complex encompasses the long-nosed mongoose (*Herpestes naso*) and marsh mongoose (*Atilax paludinosus*) because they share similar habitats and show only slight anatomical differences (Wilson & Mittermeier 2009); (3) the forest squirrel complex includes seven species from five different genera of the Sciuridae family, all showing small stature and similar coat patterns in the study area; (4) the last species complex corresponds to the "small pangolins", because despite anatomical and color differences, the long-tailed pangolin (*Phataginus tetradactyla*) and white-bellied pangolin (*Phataginus tricuspis*) were difficult to distinguish on night-time videos. Finally, for all detected species, the mean adult body mass was collected from Mittermeier *et al.* (2013) for primates, Wilson *et al.* (2016) for rodents, and Wilson and Mittermeier (2009, 2011) for carnivores and hoofed mammals, and the conservation status was obtained from the IUCN Red List of Threatened Species.

2.4 Environmental and anthropogenic variables

Accessibility variables were derived for each CT by computing the distance to the nearest permanent logging road, national road, and village using ArcGIS software. In our study area, the entrances of logging roads are kept under surveillance, and access is restricted to company vehicles. We therefore considered this specific variable as a proxy for landscape fragmentation rather than human disturbance. National roads, which cross almost the entire logging concession, and villages can be considered as proxies of landscape fragmentation and human pressure by acting as preferable access points for hunters.

2.5 Data analyses

To test the impact of the CT placement strategy on the remotely sensed mammal diversity, we developed a four-step approach targeting species richness (step 1), species detectability and capture rate (step 2), species and community–site association (step 3), and species composition (step 4). The environmental correlates were investigated in the last step (ordination, step 4).

First, we used sample-based rarefaction curves to test the effect of placement on species richness. The accumulation of species richness with cumulative sampling effort was performed at the grid scale using the *rarefy* function of the *vegan* package (Oksanen *et al.* 2019). The Sørensen index of similarity was also computed using the *vegdist* function of *vegan* to evaluate species similarity between placements in each grid. Richness differences between CT pairs were also compared using a Wilcoxon signed-rank test.

Second, for each detected species (including the four species complexes), we generated the detection history (*i.e.*, the sequence of detections and non-detections, MacKenzie *et al.* 2017) with the *camtrapR* package, considering 7-day sampling occasions (Niedballa *et al.* 2016). Then, we modeled the detection probability within a multi-method occupancy model (Nichols, Bailey, *et al.* 2008) using the *occMod* function of the *RPresence* package (MacKenzie & Hines 2018). This modelling framework is particularly suited for paired design (Kolowski & Forrester 2017). In addition to large-scale occupancy (ψ), which represents the probability that a focal species is present in the broad sampling area surrounding the CT pair (in our case, a circle of 0.707 km radius), the multi-method occupancy framework modeled an additional local occupancy parameter (θ) corresponding to the direct surroundings of the CT pair (Nichols, Bailey, *et al.* 2008, Kolowski & Forrester 2017). To specifically investigate the impact of CT placement on the detection probability, we selected the most likely multi-method occupancy model for each species using Akaike's Information Criterion corrected for small sample size (AIC_c; Hurvich & Tsai 1995); however, we restricted this analysis to the 13 species presenting at least 10 independent detection events for each placement (Ahumada *et al.* 2013). Specifically, we compared the general model with ψ, θ, and p held constant to the model, considering the detection probability as placement-dependent. We additionally tested if the detection probability was different between grids and between placements and grids. Then, for each individual species and for each placement, we computed the RAI, which corresponds to the mean number of independent events per trap day and camera (Rovero & Marshall 2009). We tested the influence of placement on the average RAI using Wilcoxon signed-rank test, and *P*-values were adjusted with the Benjamini–Hochberg correction, and we examined the systematic deviation (bias) using Bland–Altman concordance analysis. To integrate the heterogeneity of species RAI across CTs, we used a bootstrap approach. In each run (n = 1000), we sampled with replacement 43 CT pairs. We computed the species average RAI in each placement, and tested the correlation between placements using the Pearson coefficient. Finally, we computed the mean and quantiles of all 1000 correlations.

Third, we analyzed site association (hereafter SSA) for species with at least three detections in each placement (n = 19) following a habitat specialisation approach initially developed by Julliard *et al.* (2006). SSA corresponded to the coefficient of variation (standard deviation/mean) of species RAI across all CTs. Species spread evenly across the study area present a low SSA, whereas site-restricted species, detected only by a few CTs, showed high SSA. We tested the influence of species body mass and IUCN status on SSA using Tukey's HSD test within placements and Wilcoxon's signed-rank test between placements. A community–site association (CSA) index was then computed for each CT, which corresponded to the average site association of species found in the detected community. The CSA index revealed, therefore, the prevalence of site-restricted or evenly spread species. For both SSA and CSA, we tested the correlation between placements (Pearson's coefficient) and examined the systematic deviation (Bland–Altman analysis).

Finally, considering all CT data, we applied a non-metric multidimensional scaling using the *metaMDS* function in *vegan* (Oksanen *et al.* 2019) to examine the difference between placements in species composition. The dissimilarity matrix (Bray–Curtis index) was computed using the species RAI. Ecological dissimilarities among CTs within and between placements were analyzed with respect to geographic distances between CTs. Environmental correlates, species richness and CSA were plotted as supplementary variables on the ordination.

All analyses were performed in R version R 3.6.1 (R Core Team, 2017) using the package *ggplot2* for plots (Wickham 2016).

3 Results

3.1 Inventory data

Preliminary analyses of the data showed that 111 (85%) of the 130 cameras deployed worked perfectly, that is operating more than 20 consecutive days and without the accumulation of moisture on the lens. Among those, 98 CTs (88%) were located in moist forests and 13 in included savannahs (**Figure 3.1 b**). A total of 3159 camera days were accumulated over the four consecutive inventories, allowing the detection of 25 terrestrial mammal species and four species complexes (**Table 3.1**), with a mean of 6 [1–14] species detected per CT. The detected species included taxa with strong conservation concerns, such as the critically endangered western lowland gorilla (*Gorilla gorilla gorilla*) or the giant pangolin (*Smutsia gigantea*). Some species, such as the central bushbuck (*Tragelaphus scriptus*) and African forest buffalo (*Syncerus caffer nanus*), were only detected in savannahs.

To test the impact of CT placement on species diversity and community composition, we only kept data from CT pairs that worked successfully and simultaneously. The CTs located in the included savannahs were also removed due to contrasting composition and too few replicates. The total sampling effort for all subsequent analyses was therefore 43 CT pairs in moist forest, totalling between 206 and 438 camera days for each placement (**Figure 3.2**).

Table 3.1 List of detected species with the identifier (ID) used in the figures, IUCN status (listed as 'Least Concern' [LC], 'Near Threatened' [NT], 'Vulnerable' [VU], 'Endangered' [EN], or 'Critically Endangered' [CR]), and mean adult body mass following Mittermeier *et al.* (2013) for primates, Wilson *et al.* (2016) for rodents, and Wilson & Mittermeier (2009, 2011) for carnivores and hoofed mammals. The species average relative abundance index (RAI) and species site association (SSA) are given for each species and for each placement ('Syst' for systematic placement and 'Trail' for wildlife trail placement).

Order **Species**	**ID**	**IUCN**	**Body mass (kg)**	**Population parameters in forest CTs**			
				RAI		**SSA**	
				Syst	***Trail***	***Syst***	***Trail***
Artiodactyla							
Cephalophus callipygus	1	LC	22.05	0.195	0.234	1.19	0.875
Cephalophus dorsalis	2	NT	21.3	0.072	0.103	1.657	1.804
Cephalophus leucogaster	3	NT	15.75	0.014	0.012	1.846	2.336
Cephalophus nigrifrons	4	LC	14.5	0.001	0.001	/	/
Cephalophus ogilbyi	5	LC	20	0.01	0.02	1.929	2.397
Cephalophus silvicultor	6	NT	62.5	0.039	0.057	2.037	1.252
Neotragus batesi	7	LC	2.5	0.001	/	/	/
Philantomba monticola	8	LC	5	0.086	0.14	1.191	1.124
Syncerus caffer ×	9	NT	292.5	/	/	/	/
Tragelaphus scriptus ×	10	LC	52	/	/	/	/
Potamochoerus porcus	11	LC	80	0.032	0.035	1.917	1.623
Hyemoschus aquaticus	12	LC	11.5	0.024	0.018	2.858	2.976
Carnivora							
Panthera pardus	13	VU	46	/	0.002	/	/
Caracal aurata	14	VU	11	0.003	0.006	3.892	3.48
Bdeogale nigripes	15	LC	3.4	0.005	0.004	4.625	3.306
Mongoose	16	LC	3.2	0.007	0.007	2.964	2.488
Nandinia binotata *	17	LC	2.15	/	0.001	/	/
Civettictis civetta	18	LC	13.5	0.002	0.001	/	/
Large-spotted genet *	19	LC	2.25	0.002	0.007	3.698	3.245
Pholidota							
Smutsia gigantea	20	EN	30	0.004	0.005	3.424	3.024
Small pangolins *	21	EN	2.55	0.002	0.002	/	/
Primates							
Gorilla gorilla *	22	CR	124	0.008	0.008	1.851	2.925
*Pan troglodytes**	23	EN	45	0.025	0.026	1.788	1.547
Proboscidea							
Loxodonta africana	24	VU	4350	0.004	0.01	2.805	3.151

Rodentia							
Atherurus africanus	25	LC	2.9	0.059	0.08	1.389	1.863
Cricetomys emini	26	LC	0.9	0.02	0.021	2.188	2.09
Forest squirrels *	27	LC	0.65	0.019	0.019	2.328	2.113
Thryonomys swinderianus	28	LC	4.2	/	0.001	/	/
Tubulidentata							
Orycteropus afer	29	LC	52.5	/	0.001	/	/

× indicates savannah species
* indicates semi-arboreal species
§ Additional species observed in the study area through CTs (May 2019) or field observations: *Tragelaphus spekii*, *Mellivora capensis*, *Poiana richardsonii*, *Cercocebus agilis*, *Mandrillus sphinx*

3.2 Impact of placement on species richness

Species richness was barely influenced by the CT placement, as shown by the large overlap between rarefaction curves, except for NDB (**Figure 3.2**). The discrepancy in this specific area corresponded to scarcely detected species (with only three detections at most). Between 16 and 23 species were detected in each area and placement, with a strong similarity in the detected species (Sørensen index: 0.63–0.87). Similar richness was also reached between pairs according to the Wilcoxon signed-rank test ($P = 0.291$). Considering all data, four species were only detected by trail CTs; these were mostly elusive species, such as the leopard (*Panthera pardus*), with very few detection events (**Table 3.1**, species #13).

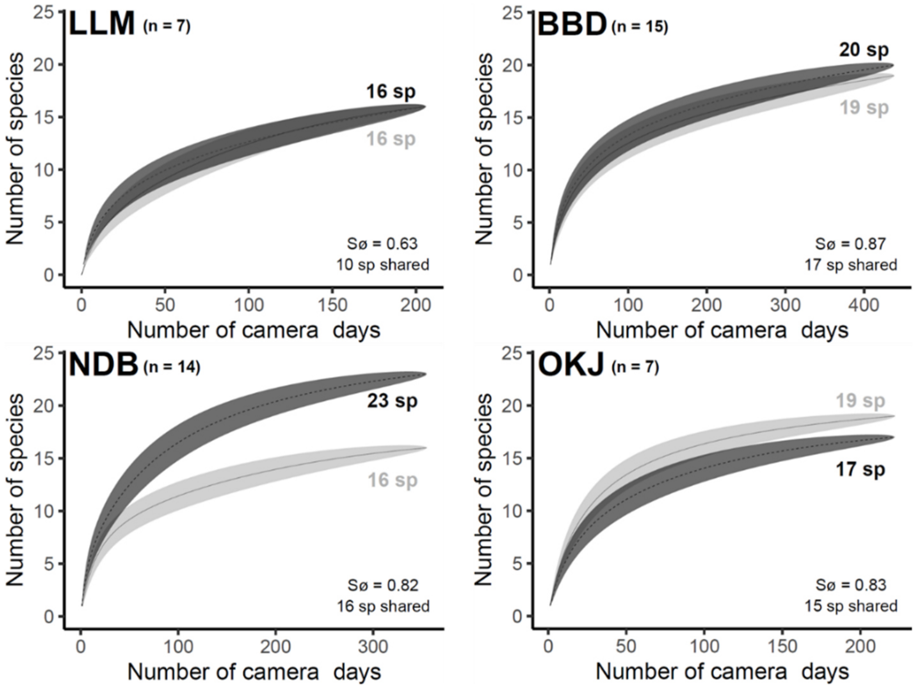


Figure 3.2 Rarefaction curves showing the accumulation of the number of mammal species detected in the four different areas as a function of the number of camera days. Grey and black lines correspond to systematic and trail CTs, respectively. Shaded polygons correspond to the standard deviation around the mean rarefied richness. The number of pairs in each area is given in parentheses. The Sørensen similarity index (Sø) and number of shared species between placements are given at the bottom of each panel.

3.3 Impact of placement on species detection and capture rates

The CT placement did not impact the detection probabilities (p) for most species (**Table 3.2 a**). Only *Cephalophus silvicultor* had a significantly greater detectability with trail CTs within each grid or over the whole study area (**Table 3.2 b**). Variation in p between grids was supported for seven species, and considered significant ($\Delta AIC_c > 2$, Burnham & Anderson 2004) for five of them compared to the reference occupancy model ($\psi()\theta()p()$) (**Table 3.2 a**).

Using species average RAI rather than detection probabilities, the correlation between placements was even stronger ($r_{btp} = 0.97$), and most species presented slightly higher average RAIs (below the 1:1 line) for the trail CTs than for the systematic ones (**Figure 3.3**). This was even more valid for the most captured species, such as the Peters's duiker (*Cephalophus callipygus,* #1) and blue duiker (*Philantomba monticola*, #8). This trend was corroborated by the positive relation (estimated slope = 0.26, $P < 0.001$) revealed by Bland–Altman analysis. However, the Wilcoxon signed-rank tests showed significant deviation for only two species, *Cephalophus silvicultor* and *Philantomba monticola*, which were no longer considered significant after P-value adjustment (all P values > 0.505). The variation between grids was weak and concerned infrequent species, mostly detected only once or twice by one or the other placement (**Appendix A**).

Table 3.2 (a) Multi-method occupancy model likelihood selection based on AIC$_c$ for the 13 species with more than 10 detection events in both placements. Four occupancy models were compared: model (1), $\psi()\theta()p()$, model (2) considering p different between placements $\psi()\theta()p(\text{placement})$, model (3) considering p different between grids $\psi()\theta()p(\text{grid})$, and model (4) considering p different between placements and grids $\psi()\theta()p(\text{placement + grid})$. ΔAIC$_c$ corresponds to the AIC$_c$ difference between the given occupancy model and the reference occupancy model $\psi()\theta()p()$ and bold values represent a significant difference ($\Delta\text{AIC}_c > 2$). (b) Estimated p and associated 95% confidence interval of *Cephalophus silvicultor* for each grid and placement when considering the occupancy model $\psi()\theta()p(\text{placement + grid})$, and for each placement when considering the occupancy model $\psi()\theta()p(\text{placement})$.

	Model	AIC$_c$	ΔAIC$_c$
Cephalophus callipygus	(1) $\psi()\theta()\mathrm{p}()$	428.89	0
	(2) $\psi()\theta()\mathrm{p}(\text{placement})$	429.37	–0.48
	(3) $\psi()\theta()p(\text{grid})$	434.9	**–6.01**
	(4) $\psi()\theta()p(\text{placement + grid})$	435.79	**–6.9**
Cephalophus dorsalis	(1) $\psi()\theta()p()$	370.56	0
	(2) $\psi()\theta()p(\text{placement})$	372.13	–1.57
	(3) $\psi()\theta()p(\text{grid})$	377.43	**–6.87**
	(4) $\psi()\theta()p(\text{placement + grid})$	379.43	**–8.87**
Cephalophus leucogaster[1]	(1) $\psi()\theta()p(\text{grid})$	188.95	**7.12**
	(2) $\psi()\theta()p(\text{placement + grid})$	191.67	**2.28**
	(3) $\psi()\theta()p()$	196.07	0
	(4) $\psi()\theta()p(\text{placement})$	198.35	**–2.28**
Cephalophus ogilbyi	(1) $\psi()\theta()p()$	169.48	0
	(2) $\psi()\theta()p(\text{placement})$	169.60	–0.12
	(3) $\psi()\theta()p(\text{grid})$	176.24	**–6.76**
	(4) $\psi()\theta()p(\text{placement + grid})$	176.84	**–7.36**
Cephalophus silvicultor[2]	(1) $\psi()\theta()p(\text{placement + grid})$	329.86	**4.14**
	(2) $\psi()\theta()p(\text{placement})$	331.43	**2.57**
	(3) $\psi()\theta()p(\text{grid})$	332.28	1.72
	(4) $\psi()\theta()p()$	334	0
Philantomba monticola	(1) $\psi()\theta()p(\text{placement + grid})$	432.16	1.84
	(2) $\psi()\theta()p(\text{placement})$	432.54	1.46
	(3) $\psi()\theta()p(\text{grid})$	433.26	0.74
	(4) $\psi()\theta()p()$	434	0
Potamochoerus porcus[1]	(1) $\psi()\theta()p(\text{grid})$	248.53	**4.82**
	(2) $\psi()\theta()p(\text{placement + grid})$	250.73	**2.62**
	(3) $\psi()\theta()p()$	253.35	0
	(4) $\psi()\theta()p(\text{placement})$	255.05	–1.7
Hyemoschus aquaticus[1]	(1) $\psi()\theta()p(\text{placement + grid})$	92.01	**7.16**
	(2) $\psi()\theta()p(\text{grid})$	92.16	**7.01**
	(3) $\psi()\theta()p(\text{placement})$	98.67	0.5

	(4) $\psi()\theta()p()$	99.17	0
Gorilla gorilla	(1) $\psi()\theta()p()$	144.09	0
	(2) $\psi()\theta()p(\text{placement})$	146.46	**–2.37**
	(3) $\psi()\theta()p(\text{grid})$	150.05	**–5.96**
	(4) $\psi()\theta()p(\text{placement + grid})$	152.85	**–8.76**
Pan troglodytes[1]	(1) $\psi()\theta()p(\text{grid})$	230.3	**14.53**
	(2) $\psi()\theta()p(\text{placement + grid})$	233.16	**11.67**
	(3) $\psi()\theta()p()$	244.83	0
	(4) $\psi()\theta()p(\text{placement})$	247.26	**–2.43**
Atherurus africanus[1]	(1) $\psi()\theta()p(\text{grid})$	352.11	**7.88**
	(2) $\psi()\theta()p(\text{placement + grid})$	354.61	**5.38**
	(3) $\psi()\theta()p()$	359.99	0
	(4) $\psi()\theta()p(\text{placement})$	362.08	**–2.09**
Cricetomys emini	(1) $\psi()\theta()p(\text{grid})$	190.91	0.97
	(2) $\psi()\theta()p()$	191.88	0
	(3) $\psi()\theta()p(\text{placement + grid})$	193.71	–1.83
	(4) $\psi()\theta()p(\text{placement})$	194.26	**–2.38**
Forest squirrels complex	(1) $\psi()\theta()p(\text{grid})$	201.19	1.81
	(2) $\psi()\theta()p()$	203	0
	(3) $\psi()\theta()p(\text{placement + grid})$	204.02	–1.02
	(4) $\psi()\theta()p(\text{placement})$	205.4	**–2.4**

(1) $\psi()\theta()p(\text{placement + grid})$

	p_{trail}	$p_{\text{systematic}}$
BBD	0.46 [0.26–0.68]	0.27 [0.14–0.47]
LLM	0.53 [0.26–0.78]	0.33 [0.14–0.6]
NDB	0.85 [0.64–0.95]	0.71 [0.47–0.87]
OKJ	0.64 [0.37–0.84]	0.44 [0.22–0.69]

(2) $\psi()\theta()p(\text{placement})$

p_{trail}	$p_{\text{systematic}}$
0.64 [0.46–0.79]	0.45 [0.31–0.6]

[1] indicates species for which detection probabilities varied significantly between grids.

[2] indicates the one particular species for which detection probabilities varied significantly with placement.

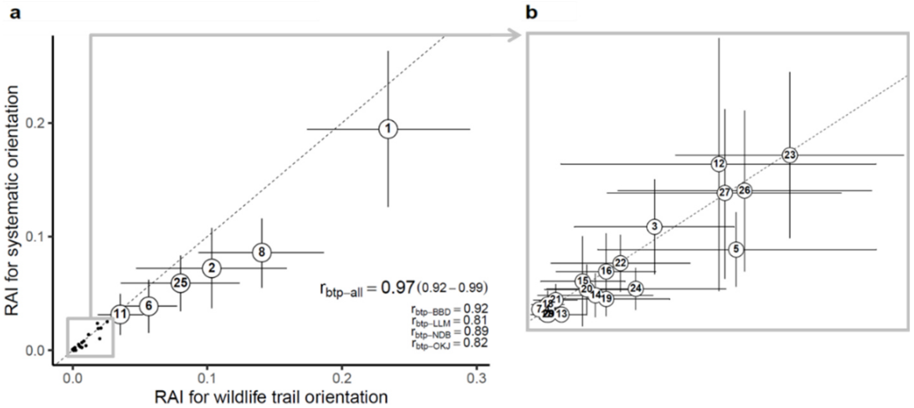


Figure 3.3 (a) Species average relative abundance index (RAI) in each placement strategy (systematic versus wildlife trail) considering all CT data and (b) zoom on the less detected species. One point represents one species, see Table 3.1 for species ID. Confidence intervals result from a bootstrap approach. In each run (n = 10000), we sampled with replacements 43 CTs and computed the species average RAI in each placement. Then, we computed the mean and quantiles of all 10000 means. The bootstrap Pearson correlation coefficient (r_{btp}) between species average RAI from both placements considering all CT data across the study area is given along with the 2.5% and 97.5% quantiles. The bootstrap Pearson correlation coefficient for each grid is also displayed.

3.4 Impact of placement on site association of species and communities

For most species, the SSA index was significantly correlated between placements, revealing similar distribution patterns ($r = 0.83$, $P < 0.001$**, Figure 3.4 a**). The SSA varied from 0.87 to 4.62 between species evenly spread across the whole study area (*e.g.*, the Peters's duiker, #1) and site-restricted ones (*e.g.*, the black-legged mongoose, *Bdeogale nigripes*, #15). Infrequent species such as the golden cat, *Caracal aurata* [#14], were identified for both placements as site-restricted, with a high SSA value. The SSA was not found to be correlated with either species body mass (all P values > 0.816) or IUCN status (all P values > 0.242) within placements, and differences between placements were not significant (all P values > 0.333). Community–site association assessed at the CT scale was well correlated between placements ($r = 0.61$, $P < 0.001$, **Figure 3.4 b**), and the differences were mostly due to slight variation in species RAI within CT pairs and/or in SSA values between placements.

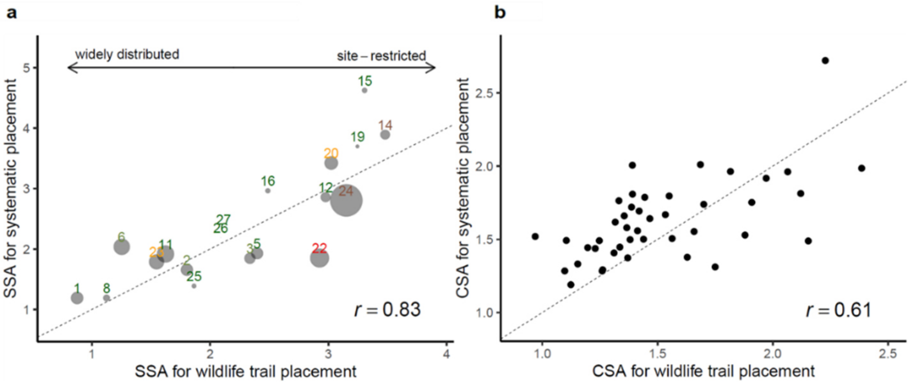


Figure 3.4 (a) Species site association (SSA) for each placement. One point represents one species, see Table 3.1 for species ID, and point size is proportional to the mean adult body mass. Species IDs are colored according to the IUCN status (dark green for 'Least Concern' [LC], light green for 'Near Threatened' [NT], brown for 'Vulnerable' [VU], yellow for 'Endangered' [EN] and red for 'Critically Endangered' [CR]). (b) Community–site association (CSA) of each CT for each placement strategy. One point represents one sampling point (CT pair). The Pearson correlation coefficient (r) between both placements is given for both indices.

3.5 Impact of placement on community composition

Supporting earlier results, the CT placement had little impact on the overall species composition, as shown by a strong overlap in the ordination (**Figure 3.5**). CTs presented a stronger similarity with their paired CT than with any other CTs (**Appendix B**). Spatial variables related to human settlements and accessibility explained the first ordination axis (**Figure 3.5 a**) and the underlying gradient in species composition, corresponding to more vulnerable species detected far from human settlements and roads. Indeed, the first ordination axis opposed communities with threatened or large-bodied species on the right, like the golden cat [#14], the gorilla [#22], and the forest elephant [#24], to communities with lower body mass species and rodents such as the African brush-tailed porcupine (*Atherurus africanus*) [#25], Emin's pouched rat (*Cricetomys emini*) [#26], and forest squirrels [#27] (**Figure 3.5 b**).

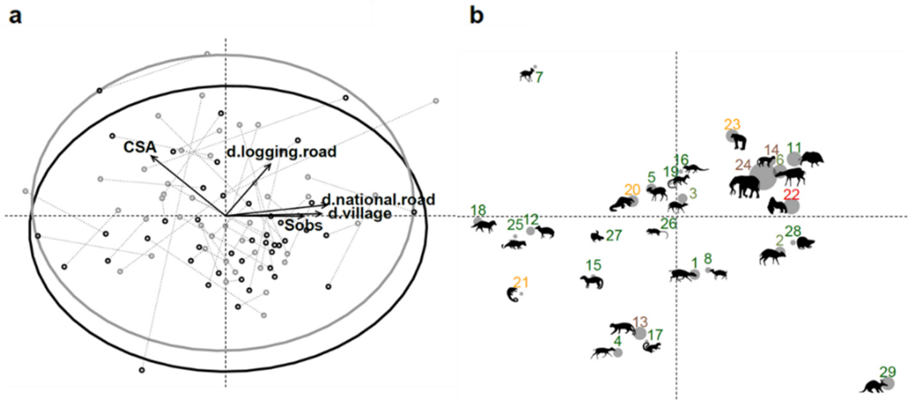


Figure 3.5 Non-metric multidimensional scaling analysis computed on the camera trap (CT) dissimilarity matrix, corresponding to the Bray–Curtis index computed using the species average relative abundance index (RAI). The locations of CTs (a) and species (b) are shown on the ordination axes. (a) Grey and black circles correspond to systematic and trail CTs, respectively. Paired CTs are joined with a dashed line. Arrows show the projection of supplementary variables: distance to the nearest permanent logging road (d.logging.road), distance to the nearest national road (d.national.road), distance to the nearest village (d.village), CSA, and species richness (Sobs). (b) Species averages on the ordination axes are shown with points proportional to the mean adult body mass (see Table 3.1 for species ID), and colored according to the IUCN status (dark green for 'Least Concern' [LC], light green for 'Near Threatened' [NT], brown for 'Vulnerable' [VU], yellow for 'Endangered' [EN] and red for 'Critically Endangered' [CR]).

4 Discussion

CT technology has enabled a tremendous leap forward for monitoring medium- to large-bodied terrestrial mammals in remote areas as complex and diversified as tropical moist forests. Although species characteristics (Harmsen *et al.* 2010, Rowcliffe *et al.* 2011), abiotic factors (Noss *et al.* 2003) and camera-related parameters (Rovero *et al.* 2013, McIntyre *et al.* 2020, Moore, Valentine, *et al.* 2020) have been shown to influence the detection process, the impact of the placement strategy on the detected diversity has been little studied in tropical forests. Here, we demonstrated that the CT placement had little impact on species richness and composition and provided a similar picture of the particularly rich ground-dwelling mammal community in a tropical forest in Gabon. At the species level, detectability was similar for most species, but capture rates were found to be slightly, but not significantly, impacted by the CT placement, with higher species RAI when CTs were placed towards wildlife trails.

The total number of detected species was very close between placements, with a high proportion of shared species. The small remaining differences concerned elusive species occurring naturally at low densities (*e.g.*, leopard), which is congruent with the results obtained by Cusack *et al.* (2015) in savannahs. In most surveyed areas, CTs placed on wildlife trails did not accumulate new species faster than those placed systematically, which is contrary to observations in savannahs (Cusack, Dickman, *et al.* 2015) and temperate forests (Kolowski & Forrester 2017). Even though a proper comparison between production and protected forests was not implemented in this study, the studied forest holds a rich and well-preserved fauna with species richness levels similar to the updated species lists of the surrounding protected areas in Gabon, namely the Ivindo, Minkébé, and Mwagna NPs (Vande weghe *et al.* 2016). This result confirms the previously highlighted potential conservation role of production forests (Putz *et al.* 2012).

Beyond species richness, wildlife managers are often looking for estimations of wildlife abundance, a key parameter in monitoring programs. The non-random deployment of CTs in the field, which is particularly common across the tropics, may, however, provide a flawed picture of the community due to differential travelling habits between species (Mann *et al.* 2015). Large carnivores may prefer trails as travel routes and are therefore more often captured with trail-based CTs, even though this is not always the case for their prey (Harmsen *et al.* 2010, Mann *et al.* 2015). Similar-sized species that share comparable ecological niches (*e.g.*, wild Bornean felid species) may also display different space use patterns, resulting in contrasting detection frequencies between placement strategies (Wearn *et al.* 2013). In our study, detection probabilities based on presence data were not substantially influenced by placement, but trail-based cameras provided a slightly higher RAI for most species, though the difference was not significant. All trophic guilds followed this trend here, while in savannahs, Cusack *et al.* (2015) considered this deviation as only significant for carnivores. A significant shift in the rank species occupy in the detected community was also observed by Cusack *et al.* (2015) when comparing random and trail-based CTs. Here, the RAI shift only started from the eighth species, with the dominant species being similarly ranked. The RAI is an extensive, but controversial, method of valuing CT data (Burton *et al.* 2015). Apart from the true population density, a range of variables, such as animal-specific factors (body mass, behavior, space use, etc.) and the characteristics of the detection area (*e.g.*, vegetation density and the presence of trails) may induce fluctuations in capture rates (Broadley *et al.* 2019, Hofmeester *et al.* 2019). Together, these variables induced imperfect species detection, which is probably not uniform across populations (O'Brien 2011). The RAI is therefore more comparable to a predictor of microhabitat use, reflecting both density and movement, rather than a suitable surrogate of local abundance (Broadley *et al.* 2019, Hofmeester *et al.* 2019). Finally, based on an important sampling effort (43 paired CTs), we also concluded that the overall detected mammal community was similar between placements in terms of species composition, which is congruent with the previous study of Blake and Mosquera (2014) in Ecuador.

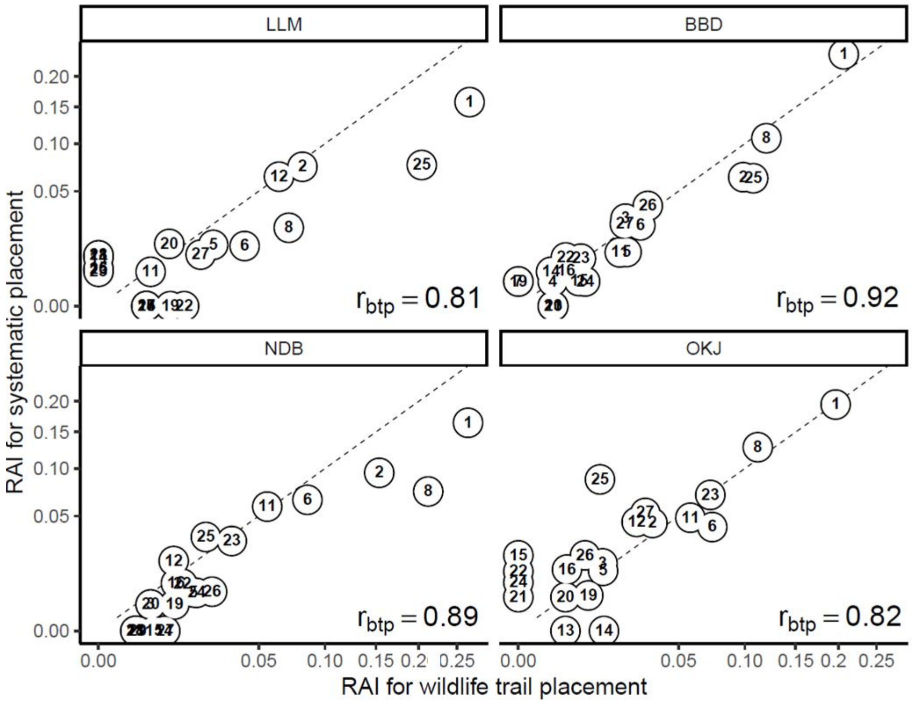
The apparent weak effect of CT placement strategy on the detected species and communities reported here may arise from the distinct but non-exclusive explanations listed below. The first explanation is linked to the forest understory structure surrounding the CT, which may induce locally different travelling patterns between and within species by channelling animal movements through trails in a particularly dense environment (Harmsen *et al.* 2010). Vegetation, by restraining the transmission of infrared radiation towards the sensor, may also induce local variation in detectability (Hofmeester *et al.* 2017). Although we did not properly characterize the visibility within the CT detection area, the very short distance between paired CTs ensured a similar undergrowth, and vegetation density at the CT scale was therefore assumed to be comparable within pairs. The second explanation is linked to the abundant wildlife populations present in the study area and the associated dense network of wildlife trails. In places where hunting pressure has already led to depauperate wildlife assemblages (Ziegler *et al.* 2016, Benítez-López *et al.* 2019), trails could be more scarcely and unevenly distributed, leading possibly to contrasting results. The third explanation is linked to the spatial use of species. Different species can display different microhabitat preferences, and species detection might be influenced by the affinity of individual species for different types of trails (*e.g.*, Weckel *et al.* 2006, Harmsen *et al.* 2010, Wearn *et al.* 2013). Trail size has been demonstrated to be positively correlated with capture rates for cats in Belize, while some of their potential prey showed the opposite trend (Harmsen *et al.* 2010). In temperate forests, Kolowski and Forrester (2017) also showed the substantial impact of trails, specifically larger and well-defined ones, on the detection of white-tailed deer. In savannahs, Cusack *et al.* (2015) only considered trails as continuous bare routes larger than 1 m, with recent signs of use. In this study, wildlife trails were narrower (<1 m), and like in Blake and Mosquera (2014), easily blended into the undergrowth background.

Beyond these factors, other confounding variables associated with the consensus required by multi-species monitoring, such as the trap density (grid size) or the sampling effort, might have impacted detectability (Hofmeester *et al.* 2019). The selected CT spacing may be optimal for certain target species but not for others (Foster & Harmsen 2012). Here, we followed the grid size recommended by the TEAM Network, which represents a compromise for ground-dwelling vertebrates in the tropics. However, highly mobile species with large home ranges (*e.g.*, forest elephants) and occurring sometimes at low densities (*e.g.*, leopards) might be missed or underestimated with such a design. Home range size, which remains scarcely known for tropical species, has already been shown to induce variation in detection between species through simulations (Sollmann *et al.* 2013). A few more relevant animal characteristics that might bias detection probabilities were listed by Hofmeester *et al.* (2019): day movement rates, directionality and speed of movement, and resource availability. All are known to be related to two important life-history traits, animal diet and body mass (Carbone *et al.* 2005, Rowcliffe *et al.* 2016), which can easily be integrated into a modelling approach of CT data (Hofmeester *et al.* 2019). The semi-arboreal or fossorial behavior of some species might also lead to disparities in the detection process according to the time these species spent on the ground (Hofmeester *et al.* 2019). Often marginalized in CT surveys, the limited availability of these species could be addressed by quantifying their activity levels and accounting for it in the computation process (Rowcliffe *et al.* 2014). Because of these specificities, adapted protocols might therefore be preferred for specific taxa, as already implemented for wild cats (see Henschel *et al.* 2014, Bahaa-el-din *et al.* 2016) and pangolins (Willcox *et al.* 2019).

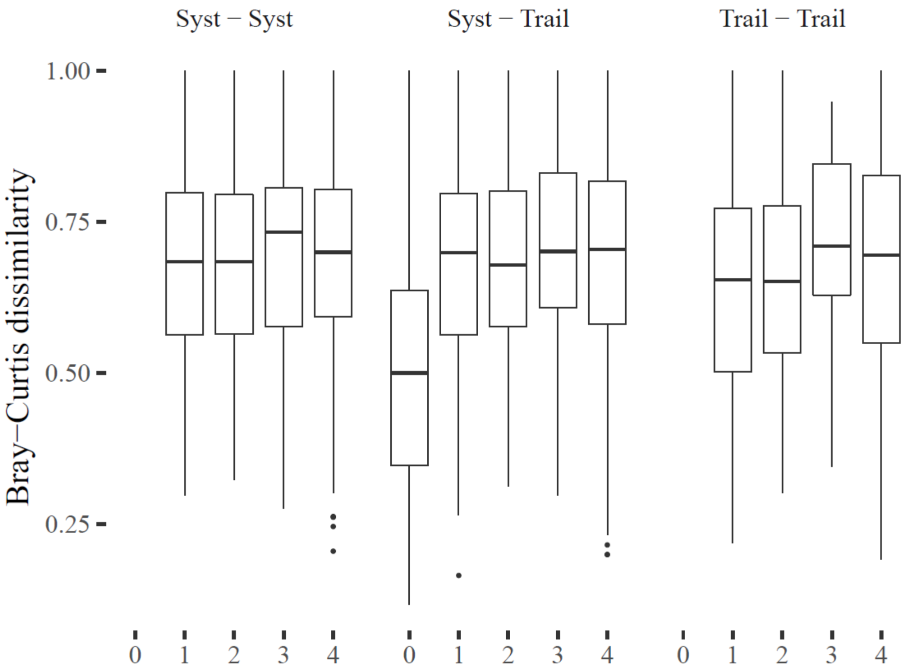
5 Conclusion

While multi-species monitoring is challenging, especially in tropical forests, camera trapping constitutes a non-invasive and efficient inventory method. Several factors influence the detection process, and systematic CTs undoubtedly provide a more robust sampling strategy when inferences at larger scales are of prime concern, especially since the travelling patterns of most tropical species remain unknown. However, a trail-based approach is still commonly used, and complete random placement is frequently discarded for fear of no/few detections. A major conclusion of this study is that species detection and capture rates are only barely influenced by the CT placement when the wildlife populations are abundant and the associated network of wildlife trails is dense. It might not be necessarily true in depauperate areas, and accounting for differences in study design and detection bias in CT data analysis might be required for multi-site comparisons.

6 Appendices



Appendix A Species average relative abundance index (RAI) of species in each placement strategy (systematic versus wildlife trail) for each area. One point represents one species, see Table 3.1 for species ID. Axes of RAI were square-root transformed to better visualize infrequent species, highlighting that all areas are dominated by a few species. The bootstrap Pearson correlation coefficient (r_{btp}) is also displayed for each grid.



Appendix B Dissimilarity in species composition (Bray–Curtis dissimilarity index) among camera traps (CTs) within and between placements with respect to geographic distances separating CTs in the field (0 = paired CTs, 1 = <1 km, 2= 1–2.5 km, 3= 2.5–5 km, 4= 5–10 km). 'Syst' and 'Trail' indicate systematic and trail-based placement, respectively.

4

Conservation value

Preamble

Relying on the results of **Chapter 2** & **3**, I used a standardized camera trap survey protocol to characterize the main determinants of the composition of mammal assemblages along a gradient of increasing anthropogenic pressure ranging from protected areas and production forest to hunted forests close to villages in two distinct zoogeographic districts, southeastern Cameroon (**Chapter 4**) and eastern Gabon (**Chapter 5**). In **Chapter 4**, camera trap data obtained during my MSc thesis were combined with pitfall trap data dedicated to study dung beetle assemblages along the same anthropogenic gradient (MSc thesis of Laetitia Delbeke) and are presented in the following chapter.

- Paper 3: published -

Conservation value of tropical forests: distance to human settlements matters more than management in central Africa

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This paper is published in *Biological Conservation*, 241, 108351

Abstract

Tropical forests in central Africa host unique biodiversity threatened by human degradation of habitats and defaunation. Forests allocated to conservation, production and community management are expected to have different conservation values. Here, we aimed to identify the determinants of the conservation value of tropical forests in southeastern Cameroon, by disentangling the effects of forest allocations, proximity to human settlements, and local habitat. We inventoried two taxonomical groups: mammal species with camera traps (3464 independent detection events) and dung beetle species with pitfall traps (4475 individuals). We used an integrated analytical approach, examining both species richness and composition. For both mammals and dung beetles, species richness decreased from the protected area to the community forests, and the logging concession showed intermediate richness. Species richness of both groups was negatively correlated to the proximity to human settlements and disturbance, with a decreasing gradient of body mass and the loss of the most threatened species. The replacement (*i.e.*, spatial turnover) of both mammal and dung beetle species among forest allocations suggest an integration of conservation initiatives to a large number of different sites, with a priority on protected and remote areas of high biodiversity. These results confirm the high conservation value of protected areas and their essential role in conservation strategies, ecologically connected with well-managed production forests with variable conservation value mainly depending on accessibility. Community forests located close to villages are much more degraded but not totally defaunated and still provide bushmeat to local populations.

Keywords: Biodiversity, Conservation value, Tropical forest, Mammal, Dung beetle, Forest allocation

1 Introduction

Tropical forests host at least two thirds of the Earth's terrestrial biodiversity (Gardner *et al.* 2009), while covering only 6 to 7% of the land surface (Dirzo & Raven 2003). But intensified anthropogenic activities lead to deforestation (loss of forest cover) and forest degradation (loss of ecosystem services). These threats induce an irreversible and drastic biodiversity loss across tropical ecosystems (Gardner *et al.* 2009) with major ecological consequences (Poulsen *et al.* 2013, Malhi *et al.* 2014).

In explicit geographical zones, planning and zoning processes define several forest allocations with different allowed practices (Oyono *et al.* 2014). The area allocated to biodiversity conservation has increased since the middle of the twentieth century (Watson *et al.* 2014). Despite these efforts, protected areas in the tropics are subjected to an erosion of biodiversity (Laurance *et al.* 2012, Tranquilli *et al.* 2014) associated with a rapid human population growth at protected area edges (Wittemyer *et al.* 2008). Covering a major proportion of tropical areas, production forests may also play a buffering role for biodiversity conservation (Clark *et al.* 2009, Gibson *et al.* 2011, Nasi *et al.* 2012, Putz *et al.* 2012). Responsibly managed production forests (with a management plan and under reduced-impact selective logging) can harbour a level of biodiversity that is similar to those observed in undisturbed or protected forests (Gibson *et al.* 2011, Putz *et al.* 2012, Edwards *et al.* 2014). But all production forests are not managed equally: companies certified by responsible management standards (*e.g.*, Forest Stewardship Council, FSC, or Programme for the Endorsement of Forest Certification, PEFC) are relatively scarce, especially in central Africa, and many production forests are managed under conventional logging. Engaging local populations in management has also been suggested as an alternative to state-managed conservation in protected areas (Berkes *et al.* 1994, Kellert *et al.* 2000, Duguma *et al.* 2018, Minang *et al.* 2019). As an alternative to industrial logging in central Africa, community forests have been shown to contribute to social and economic development with livelihood improvement (Lescuyer *et al.* 2019). The participation of local communities can improve sustainability if they are aware of the risks of unsustainable management for the long-term provision of goods and services (Ribot 2003, Maryudi *et al.* 2012, Blomley 2013). Different forest allocations pose different threats and opportunities for biodiversity conservation. Thus, the effects of different forest allocations on biodiversity needs to be evaluated (Panlasigui *et al.* 2018), specifically in central Africa, among protected areas, production forests, and community forests (Poulsen *et al.* 2011). Besides forest management, the influence of human settlements on biodiversity also needs to be quantified since intensified human activities, such as hunting, agriculture or artisanal logging, are directly associated to proximity to villages (Beirne *et al.* 2019) and roads (Kleinschroth *et al.* 2019). These disturbances modify forest ecosystems at the landscape-scale and at the local-scale of species habitat. Decoupling the effects of these different drivers on different groups and at different scales is of high importance for designing adequate conservation strategies (Poulsen *et al.* 2011).

Quantifying forest conservation value implies considering taxonomic groups sensitive to environmental disturbance and contributing to major ecological processes, such as mammals and insects (Nichols *et al.* 2009). On the one hand, mammal species are the main target of hunting, leading to a massive defaunation in central Africa (Abernethy *et al.* 2016, Ziegler *et al.* 2016) and many species of iconic megafauna (such as the chimpanzee, *Pan troglodytes*) are classified as endangered on the IUCN Red List (www.iucnredlist.org). The extirpation of hunted species leads to empty forests that still appear structurally intact but where most ecological functions are altered: trophic webs are disrupted, seed dispersal is limited hampering tree recruitment and forest regeneration, and other cascading effects (Redford 1992, Terborgh *et al.* 2008, Abernethy *et al.* 2013, Poulsen *et al.* 2018). On the other hand, insects are key components of tropical forest ecosystems (Nichols, Spector, *et al.* 2008). Specifically, dung beetle species are reported as excellent cost-effective ecological indicators in tropical biodiversity surveys at various scales (Klein 1989, Gardner *et al.* 2008, Cajaiba *et al.* 2017). They are sensitive to even small disturbances such as reduced-impact or selective logging (Nummelin & Hanski 1989, Nichols *et al.* 2007, Bicknell *et al.* 2014). Dung beetles contribute to a variety of important ecological processes including nutrient cycling and fertilization, plant growth, and seed dispersal (Nichols, Spector, *et al.* 2008, Nervo *et al.* 2017).

Our objective was to identify the determinants of the conservation value of tropical forests in southeastern Cameroon. We specifically aimed to disentangle the effects of (i) forest allocation (protected area, FSC-certified logging concession, and community forest), (ii) proximity to human settlements (roads and villages), and (iii) local habitat (forest degradation, canopy openness and distance to the nearest river) on the richness and uniqueness of local biodiversity. We hypothesized that conservation value is mainly driven by human activities rather than by local habitat characteristics, and specifically by forest management and proximity to human settlements. In northern Republic of Congo, Poulsen *et al.* (2011) indeed showed a higher influence of human disturbance (hunting, logging) at landscape-level on animal populations than local-scale effects (forest structure, canopy cover, fruit abundance, topographic and floristic changes). Here, we examine the variation in species richness between and within forest allocations (alpha and gamma diversities) for two taxonomic groups inventoried and sampled using appropriate methods: mammal species with camera traps and dung beetle species with pitfall traps. We also examine the uniqueness of species assemblages by (i) partitioning beta-diversity (Baselga 2010) into its turnover component (spatial replacement of species between sites of completely different compositions) and its nestedness component (loss of species between sites), and by (ii) conducting multivariate analysis (ordination) that integrates information on species traits and conservation status. Based on an integrated and comparative analysis of forest biodiversity in the specific landscape of the Dja area, we discuss the lessons learned for reconciling tropical forest conservation and management at a larger scale, in central Africa.

2 Material and Methods

2.1 Study area

The study was conducted in southeastern Cameroon (latitude varying from 2°49’ to 3°44’ N, longitude from 12°25’ to 14°31’ E, mean altitude of 743 meters). Forests in this area are assigned to Moist Central Africa (Fayolle *et al.* 2014). The annual rainfall is approximately 1640 mm with two distinct rainy seasons and a mean annual temperature of 23.1°C (Hijmans *et al.* 2005).

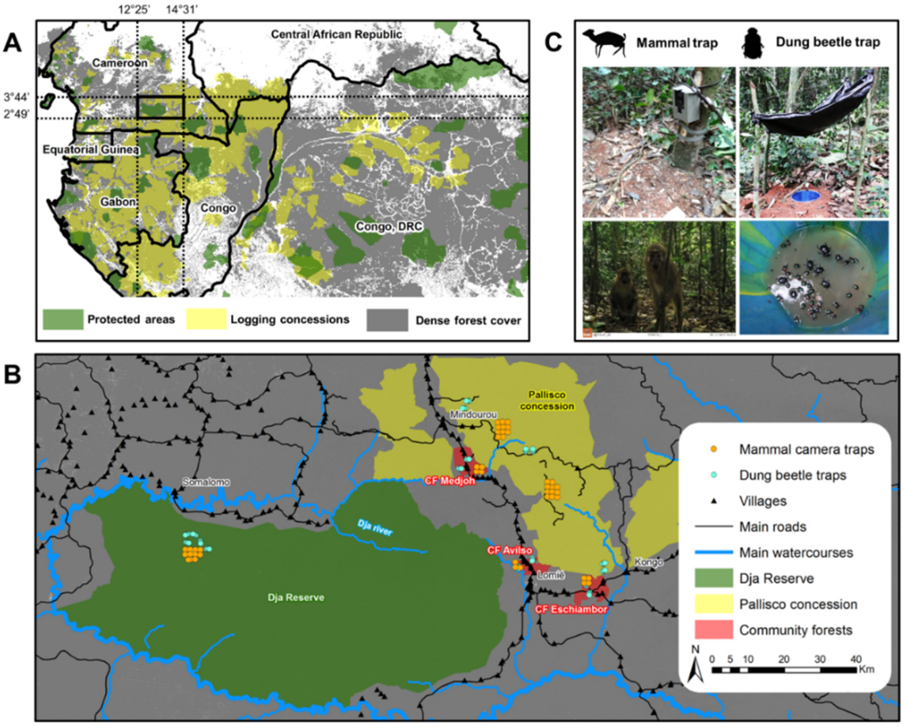

Figure 4.1 (A) Location of the study area among logging concessions and protected areas in central Africa. The grey background corresponds to "Dense forest cover" and includes lowland, submontane, montane, and swamp forests as defined by Mayaux *et al.* (2004). (B) Study area in southeastern Cameroon. Sampling sites of mammals (camera traps) and dung beetles (pitfall traps) in the three forest allocations are shown as orange and cyan points, respectively. (C) Illustration of a camera trap (with an example of a picture of *Cercocebus agilis*) and a pitfall trap (with an example of the individuals collected in a trap after 48 hours of trapping).

Cameroon was the first country in central Africa to implement a national zoning plan and to impose management plans for logging concessions and community forests after the 1994 Cameroonian Forestry Law. Three forest allocations (protected area, logging concession, and community forest) are well represented in Cameroon (88% of the National Forest Estate) and in central Africa (**Figure 4.1 A** and **Appendix A**), and are adjacent to each other in the study area (**Figure 4.1 B**). These areas are diversely affected by industrial and artisanal logging, hunting, and slash-and-burn agriculture activities (Poulsen *et al.* 2011, Abernethy *et al.* 2016).

The Dja Biosphere Reserve is the largest protected area in the country, managed for biodiversity conservation and listed as a Habitat/Species Management Area under

IUCN's Protected Area Categories System. It has been listed as a “Man and Biosphere Reserve” since 1981 and as a UNESCO World Heritage site since 1987. In the core area (526 000 hectares), agriculture, gathering and hunting are prohibited. In the buffer zone (approximately 200 000 hectares but not precisely delimited yet), local populations can engage in non-industrial sustainable activities (**Appendix A**).

The logging concession granted to the PALLISCO Company is managed since 2004 under 30-year forest management plans. Timber harvest is highly selective: on average in 2018, only 0.65 stems and 9.6 m^3 were cut per hectare. Out of the 388 949 hectares granted to the company, 341 708 hectares were certified by the Forest Stewardship Council (FSC) in 2008, committing to best practices for: (i) the economic effectiveness and viability of forest management, (ii) the ecological integrity of the forests through reduced-impact logging, protection of wildlife, protection against pollution, and (iii) the social equity for workers and local populations. User rights are given to bordering populations for deadwood and NTFP collection. Hunting activities are highly regulated (see details in **Appendix A**).

The community forests (CF) of Medjoh (4964 ha), Avilso (3433 ha) and Eschiambor (5069 ha) are located between the logging concession and the protected area (**Figure 4.1 B).** CFs are small forest areas situated along roads and villages and are dedicated to the exclusive use by local communities for timber harvesting, deadwood collection, NTFP gathering, hunting, and agriculture (**Appendix A**). They are managed via a ‘Simple Management Plan’ written by the communities themselves and under the supervision of the Forest administration.

2.2 Biodiversity inventory

We inventoried mammals and dung beetles using respectively camera traps (Ahumada *et al.* 2013) and pitfall traps (Larsen & Forsyth 2005). Sampling sites were distributed in the three forest allocations, at a distance of at least 500 meters from forest edge. In the logging concession, areas with different logging histories were evenly sampled to consider biodiversity recovery after logging. In the protected area, all sampling sites were located in the northwestern part of the Reserve (**Figure 4.1 B**), where vegetation types are the most similar to the logging concession and community forests (Sonké 1998).

Mammal species were inventoried using a total of 44 camera traps (model ‘Trophy Cam HD Aggressor’) set up during the rainy season from February to June 2017 and distributed as follows: one grid of 11 cameras in the protected area, two grids of 11 cameras each in the logging concession (one in a zone logged 23 to 27 years before and the other in a zone logged 17 years before), and one grid of 11 cameras distributed among the three community forests (**Figure 4.1 B**). Distances between two camera grids were between 9.3 and 112.3 km. Cameras were installed at a density of one camera per 2 km^2 according to the recommendations of the TEAM Network (2011). We placed cameras on trees at 30-50 cm above ground level and oriented in the direction of animal trails with a sufficient field of view to capture full-body images of mammals. The camera-based monitoring lasted 87-99 days and we standardized the data acquired by each camera to the first 87 inventory days. Herbaceous vegetation was systematically cleared in a radius of 4 meters around the camera, insuring comparable detection probability among all cameras. All cameras were set to take three consecutive shots per trigger. After the inventory, we only used the images acquired by 29 cameras (nine in the protected area, five in the zone logged 20-30 years before, nine in the zone logged 10-20 years before, and six in the community forests) because 15 cameras were either stolen/broken or did not operate properly during the entire inventory period. Images obtained from camera traps were analyzed with the Camera Base software linked to Microsoft Access (Tobler 2015). Detection events separated by at least 10 minutes were considered independent. We identified mammals to species when possible and recorded the number of individuals for each independent detection event. Based on the independent detection events, we produced occurrence and abundance matrices (with species as columns, and either cameras or dates as rows). The mean adult body mass (mean of the body mass given for males and females in Kingdon *et al.* 2013) and the IUCN status were collated for all inventoried species.

Dung beetles were inventoried using 72 baited pitfall traps from February to April 2016 and distributed along transects of four traps as follows: six transects in the protected area, six transects in the logging concession, and six transects in the community forests (two transects in each community forest). The six transects in the logging concession were distributed as follows: two transects in a zone logged 20 to 26 years before, two transects in a zone logged nine years before, and two transects in a zone logged three years before. To avoid interferences between traps on the same transect, we separated two traps by 250 meters, which is four times the distance recommended by Larsen and Forsyth (2005). Distances between two transects were between 1.4 and 116.9 km. Each pitfall trap consisted of a bucket (280 mm diameter and 270 mm deep) buried flush to the ground, containing one litre of odourless soaped water and baited with 16 grams of human faeces, and protected from rain by a plastic tarp of ~1 m^2. We collected dung beetles after 48 hours and preserved them in 70% ethanol. We identified dung beetles to species when possible and we assigned a unique morphospecies number when identification was uncertain. After having generated a list of all individuals collected, we produced occurrence and abundance matrices (with species as columns and traps as rows). The mean adult body length was computed for all inventoried species and morphospecies.

2.3 Correlates of biodiversity

The values of eight variables were collated for each sampling site, comprising three variables for forest allocations, two variables for proximity to human settlements, and three variables for local habitat. We tested the degree to which these eight variables influenced mammal and dung beetle species richness and composition. For forest allocations, we created three distinct dummy binary variables (i) “protected area”, (ii) “logging concession”, and (iii) “community forests”. We gave a value of one to the forest allocation to which the sampling site belongs, and null values for the two other forest allocation variables. The proximity to human settlements was computed by: (iv) the distance to the nearest road, and (v) the distance to the nearest village. In terms of habitat variables, we used: (vi) the forest degradation (proportion of pixels classified as degraded forest in the surroundings of each sampling site based on Sentinel-2 satellite imagery and supervised classification; see **Appendix B** for methodological details), (vii) the percentage of canopy openness above dung beetle traps (mean of five values obtained around each trap with hemispherical photographs; see **Appendix B** for methodological details), and (viii) the distance to the nearest river. All distances were computed in meters, with the 'Near' tool in ArcGIS software.

2.4 Biodiversity analysis

All analyses were performed within the R environment (R Core Team 2018). We used individual-based rarefaction curves (Gotelli & Colwell 2001) for each sampling site (camera traps for mammals and pitfall traps for dung beetles) to visualize the variation in species richness within and between sampling sites. We also generated sample-based rarefaction curves (Gotelli & Colwell 2001) to identify any differences in species richness among forest allocations (package "vegan", Oksanen *et al.* 2019). We extracted the species richness (alpha diversity) of each sample-based rarefaction curve for a common number of 435 camera-days for mammals and 24 traps for dung beetles for comparison among forest allocations. We also extracted 10 values of species richness for each sampling site from individual-based rarefaction curves, for a number of individuals (or independent detection events for mammals) equal to 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 (for the curves that reached these numbers of individuals). The consideration of ten values of species richness extracted for ten different numbers of individuals allowed to consider the overall shapes of individual-based rarefaction curves rather than only one value of species richness extracted for only one subjective number of individuals. Then, the relationships between the ten values of extracted species richness (response variables) and the eight variables defined above (correlates of biodiversity for mammal and dung beetle sampling sites separately, predictor variables) were analyzed using the sparse Partial Least Squares method (sPLS, using package "mixOmics", Lê Cao *et al.* 2009). This method identifies the best predictor variables for species richness of mammals and dung beetles, based on the criterion of the highest Variable Importance in the Projection (VIP). The main advantage of the method consists in the integration and variable selection combined simultaneously in a one-step analysis. In addition, tested variables can be correlated and can contain NA values. Then, Pearson's correlations were computed to further quantify the individual associations between species richness and relevant predictor variables identified by the sPLS.

Based on the occurrence matrix for both mammals and dung beetles, codifying the presence (1) or absence (0) of species (columns) in forest allocations (rows), we partitioned beta-diversity into turnover and nestedness components to compare the whole of forest allocations (multiple-site dissimilarities), and pairs of forest allocations (pairwise dissimilarities) using the package "betapart" (Baselga & Orme 2012). Whereas the 'turnover' component represent a spatial replacement of species among sites, 'nestedness' and specifically 'nested' sites indicate that some sites constitute a subset of other species assemblages, where some species were lost or are just absent (Baselga 2010). For mammals, the same number of camera traps were deployed in each forest allocation but ended into slightly unbalanced design because some cameras were stolen or broken in the field. We then developed a bootstrap approach with 1000 iterations to deal with the unbalanced sampling in the camera trap data. For each iteration, we randomly subsampled for each forest allocation five cameras out of the total number of retrieved cameras (up to nine), and we considered the detected species by these five cameras as present in the forest allocation (whatever the number of detections). This allowed generating an occurrence matrix with four lines, corresponding to the forest allocations, and with 26 columns, corresponding to the mammal species. On this occurrence matrix, we computed the multiple-site dissimilarity (among all forest allocations) and the pairwise dissimilarities (among pairs of forest allocations) with their turnover and nestedness components. We finally computed the average for the two beta-diversity components (nestedness and turnover) for the two approaches (multiple-site and pairwise) across the 1000 iterations.

In order to visualize the differences in species composition among forest allocations, we performed a Nonmetric Multidimensional Scaling (NMDS), for mammals and dung beetles separately, based on abundance matrices and Bray-Curtis distances (package “vegan”,(Oksanen *et al.* 2019). Abundance data were square root transformed and submitted to Wisconsin double standardization, due to large and highly variable abundance values. We plotted sites as triangles (with colors corresponding to forest allocations) and species as points (with size proportional to the mean adult body mass for mammals, and mean adult body length for dung beetles), as well as the IUCN conservation status for mammal species. The eight correlates of biodiversity previously mentioned were also plotted as supplementary variables describing sampling sites.

3 Results

3.1 Species richness

For mammal species, we obtained 3464 independent detection events and identified a total of 26 species (gamma diversity) including iconic species, such as the chimpanzee (*P. troglodytes*) and the giant pangolin (*Manis gigantea*). For dung beetle species, we collected and identified 4475 individuals and identified a total of 71 species (gamma diversity) belonging to 21 genera.

Individual-based and sample-based rarefaction curves for both mammals and dung beetles showed a decrease of species richness from the protected area to the community forests, the logging concession being intermediate between the two (**Figure 4.2**). Sample-based rarefaction confirmed the slight differences in richness among forest allocations (**Figures 4.2 B & D**). Individual-based rarefaction curves of the logging concession overlapped with those of the other forest allocations, showing that the logging concession could locally be as rich as the protected area or as depauperate as the community forests. For mammals, the alpha diversity of each forest allocation was 23 species in the protected area, 17 species in the zone logged 20-30 years before, 21 species in the zone logged 10-20 years before, and 18 species in the community forests. For dung beetles, the alpha diversity of each forest allocation was 58 species in the protected area, 49 species in the logging concession, and 41 species in the community forests.

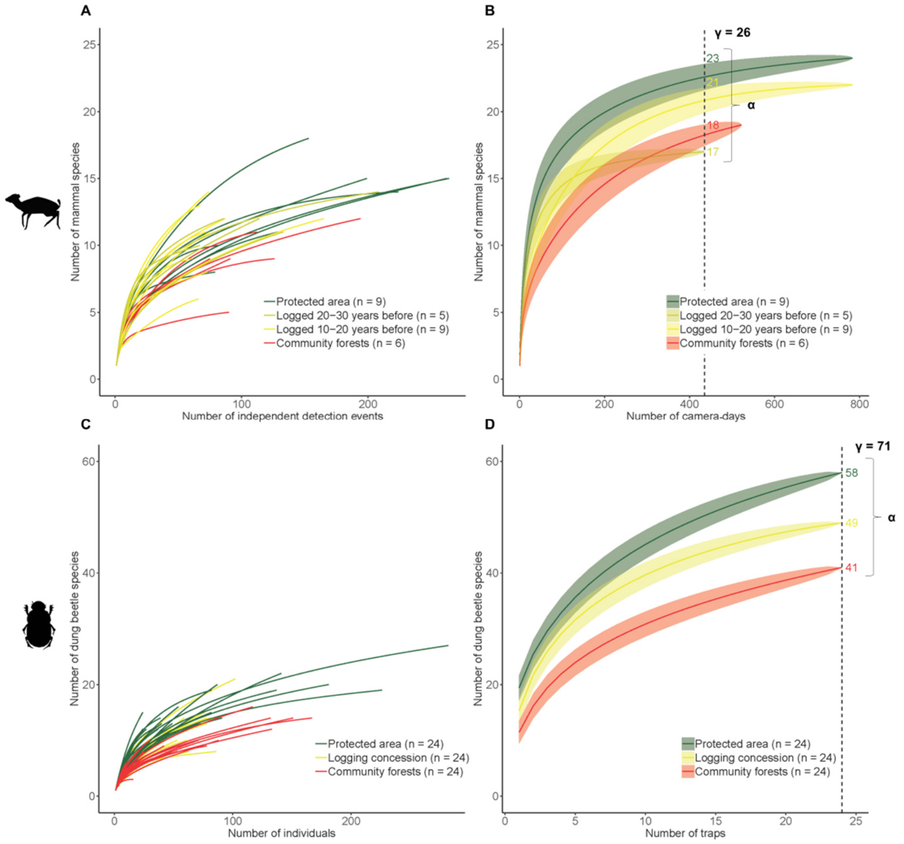

Figure 4.2 Individual-based and sampled-based rarefaction curves for mammals (A and B) and dung beetles (C and D). For mammals, the individual-based rarefaction curve considered individuals as the independent detection events (A) and the sampled-based rarefaction curve used camera-days on the horizontal axis (B). The alpha diversity at the scale of each forest allocation is provided for 435 camera-days (B) and for 24 pitfall traps (D). The gamma diversity is also provided and comprises the variety of inventoried species for mammals (B) and for dung beetles (D). The colored shaded areas on sampled-based rarefaction curves (B and D) correspond to the rarefied species richness ± its standard deviation.

For both mammals and dung beetles, sPLS quantified the relationships between the eight correlates of biodiversity and species richness values derived from individual-based rarefaction curves for 10 to 100 individuals. The most important predictors of species richness were "community forests" (VIP = 1.74, negative correlation) and the distance to the nearest village (VIP = 1.48, positive correlation) for mammal species; the distance to the nearest road (VIP = 1.65, positive correlation) and "protected area" (VIP = 1.58, positive correlation) for dung beetle species (**Table 4.1** and **Appendix C**).

Table 4.1 Values of VIP (Variable Importance in Projection) obtained from the sPLS explaining mammal and dung beetle species richness with correlates of biodiversity. The two highest VIP values are shown in bold for each taxonomic group. The sign in brackets indicate the direction of the effect of each predictor variable on species richness.

	Species richness (Y)	
Correlates of biodiversity (X)	**Mammals**	**Dung beetles**
Distance to the nearest road	0.66 (+)	**1.65 (+)**
Distance to the nearest village	**1.48 (+)**	0.80 (+)
Distance to the nearest river	0.24 (+)	0.44 (-)
Forest degradation	0.24 (-)	0.50 (-)
Canopy openness	/	0.34 (-)
Protected area	0.43 (+)	**1.58 (+)**
Logging concession	1.02 (-)	0.37 (+)
Community forests	**1.74 (-)**	1.21 (-)

3.2 Species composition

Beta-diversity was partitioned among forest allocations for both mammal and dung beetle species (**Figure 4.3**). Among both mammal and dung beetle species, a strong turnover component was revealed, indicating a replacement of species among sites (for mammals, $\beta = 0.25$ with turnover component = 0.15; for dung beetles, $\beta = 0.36$ with turnover component = 0.25). We observed proportionally higher nestedness patterns for mammal species (40% of beta-diversity) than for dung beetle species (31% of beta-diversity). For mammals, the species composition in the zone logged 20-30 years before the inventory was nested to the species composition in the three other forest allocations, with various levels of turnover. The species composition of the community forests was nested to that of the zone logged 10-20 years before, which was nested to that of the protected area, but showing simultaneously some turnover among forest allocations (list of species in **Appendix D**). For dung beetles, the species composition of the community forests was nested to the logging concession, which was nested to the protected area, showing a proportionally higher turnover among forest allocations than mammals (list of species in **Appendix E**).

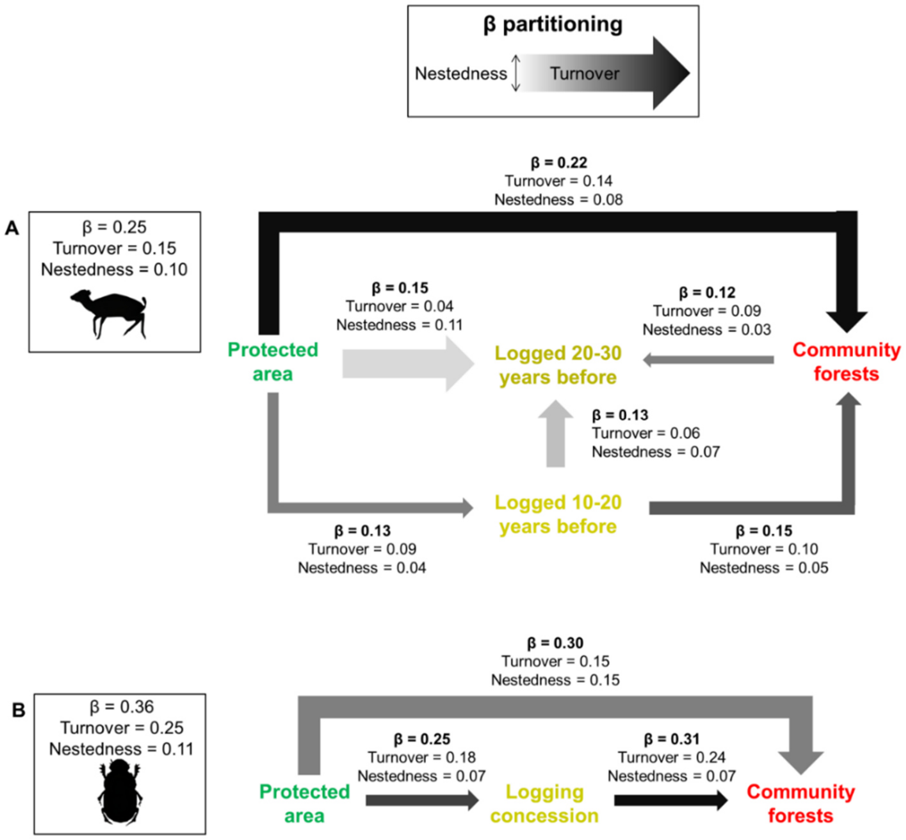

Figure 4.3 Beta-diversity partitioning in turnover and nestedness components for mammal species (A), and for dung beetle species (B). The total beta-diversity, turnover, and nestedness values given in the boxes correspond to multiple-site dissimilarities (overall comparisons among forest allocations), whereas other values represent pairwise dissimilarities between two particular forest allocations. The arrows are oriented in the direction of nested sites, with the arrow thickness proportional to the nestedness component, and the arrow darkness proportional to the turnover component.

A clear distinction in species composition between the protected area and the community forests was identified for both mammals and dung beetles, with an intermediate and heterogeneous composition in the logging concession (**Figure 4.4**). The NMDS for mammal species (**Figure 4.4 A**) showed a clear gradient from degraded community forests associated with mainly rodents and small-bodied species (negative scores on NMDS 1) to richer sites with bigger animals in the protected area and in remote areas from villages (positive scores on NMDS 1). A similar gradient was found for dung beetle species along the first axis (**Figure 4.4 B**), going from degraded forests with high canopy openness (mainly community forests) to remote areas in the logging concession and in the protected area. NMDS stress value was 0.22 for mammals and 0.24 for dung beetles.

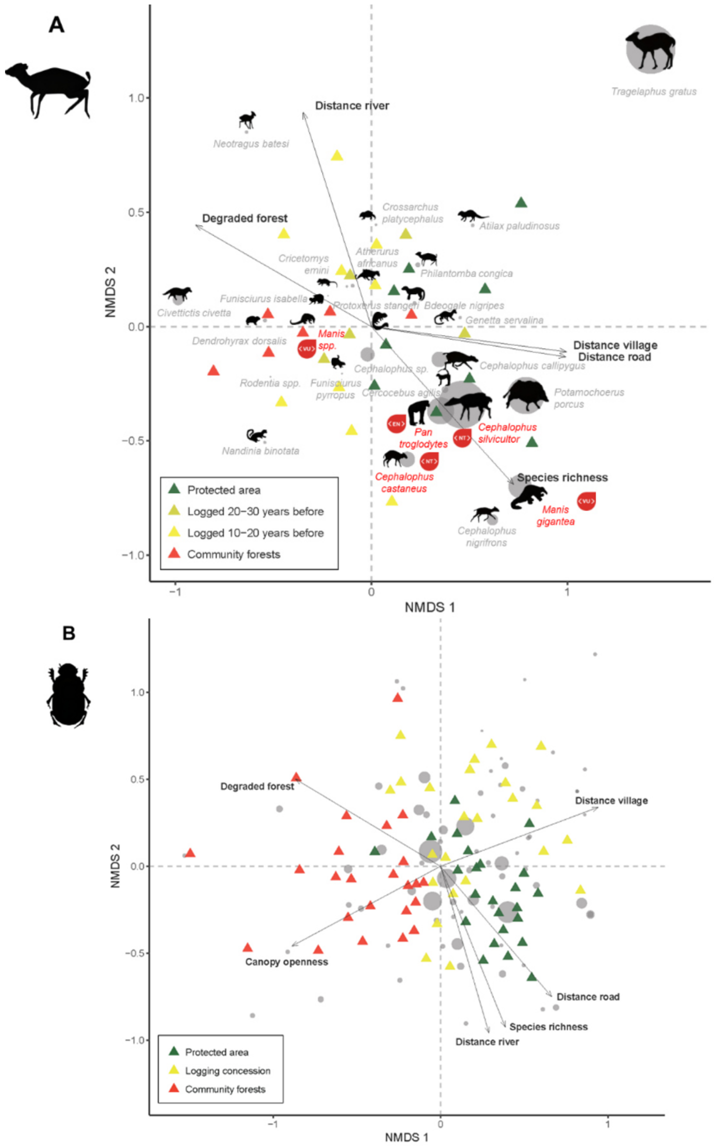

Figure 4.4 Nonmetric Multidimensional Scaling of the abundance matrix for mammal species (A) and dung beetle species (B). Colored triangles correspond to sampling sites in different forest allocations. Gray points correspond to species, with point size proportional to the mean adult body mass for mammals (A) or the mean adult body length for dung beetles (B). Arrows show the projection of supplementary variables: distance to the nearest road, distance to the nearest village, distance to the nearest river, forest degradation, canopy openness (only for dung beetles in B), and species richness. In A, mammal species names written in red are listed in the IUCN Red List of Threatened Species as "Near Threatened" (NT), "Vulnerable" (VU), or "Endangered" (EN), others being assessed as "Least Concern". Images of mammal species in A are extracted from Kingdon *et al.* (2013).

4 Discussion

Here, we conducted the first cross-taxonomic assessment of the conservation value of diverse forest allocations in central Africa, using an integrated framework for biodiversity analysis at the landscape scale. We identified an influence of forest allocation on biodiversity patterns. However, proximity to human settlements and disturbance was the main determinant of forest conservation value. We also found differential responses to forest disturbance across mammals and dung beetles.

4.1 Limitations of the study

Due to logistical and financial field constraints, we only sampled a single protected area and a single logging concession and our study design was thus pseudoreplicated (Hurlbert 1984). Therefore, our results should only be considered and interpreted at the local scale of our study system in its particular social-environmental context in southeastern Cameroon, without any generalization (Cottenie & De Meester 2003).

The sampling sites were spatially aggregated in grids (camera traps) and transects (pitfall traps) and were not distributed across the entire protected area and logging concession. Then, our sampling sites could not be totally representative of the overall spatial diversity of these two forest allocations. However, it is worth mentioning that we identified a total of 26 mammal species, which is the exact same number of species reported by Bruce *et al.* (2018) in a larger camera trap grid in the Northern Sector of the Dja Reserve. This protected area is reported to host 109 different mammal species of which 35 species are terrestrial and have a body mass higher than 0.5 kg (Kingdon 2015): we missed some species and some of them are extremely rare and possibly locally extinct.

Our mammal and dung beetle inventory protocols did better detect some species than others, as most inventory techniques do. The ability of camera traps to detect animals is correlated with species body size (Tobler *et al.* 2008, Rowcliffe *et al.* 2011). Abundances of small mammal species might have been underestimated, but detection events of mammal species of body mass lower than 1 kg, including mice, rats and squirrels, represented not less than 61% of all detection events. Concerning pitfall traps, we also used a standardized sampling design which can be used in a wide variety of contexts (Larsen & Forsyth 2005). All sampling sites were evenly distributed among forest allocations (same sample coverage) with the same sampling protocols and similar conditions. We hypothesized comparable detection probability under closed canopies, though slight differences in forest structure and composition. There is no element in our knowledge that was supposed to modify detection probability among forest allocations and we did everything we could not to influence it. For instance, cameras were oriented toward animal trails, with a clear angle, and with cleared herbaceous vegetation, according to the TEAM Network's recommendations (2011). Thus, we consider that the observed differences among forest allocations revealed true differences in mammal and dung beetle species diversity.

4.2 Differential response of mammals and dung beetles

For mammal species composition, our results showed a loss of species with proximity to human settlements. It was related to a gradient of decreasing body mass and conservation value, with less large and threatened species remaining near villages. As shown by Beirne *et al.* (2019), distance away from villages is directly correlated to hunting pressure. The community forests and the zone logged 20-30 years before were composed of a subset of species present in the more diverse sites and were more strongly impacted by hunting practices because of their proximity to villages. The highly detrimental effect of proximity to hunters' access points (*i.e.*, settlements and roads) has been previously demonstrated up to 40 kilometers inside the forest (Benítez-López *et al.* 2017), as have the impacts on mammal populations (Laurance *et al.* 2006, Clark *et al.* 2009, Benítez-López *et al.* 2017, Koerner *et al.* 2017). In the logging concession, the distribution of mammal populations is much more influenced by the development of the logging road network and increased accessibility to hunters and poachers than by the direct effects of logging (Robinson *et al.* 1999, Van Vliet & Nasi 2008, Brodie *et al.* 2015). Increasing hunting pressure induces a steady decline in total biomass of all vertebrates, with a particularly rapid decline of large-bodied preferred game species such as primates and ungulates (Poulsen *et al.* 2011, Koerner *et al.* 2017), as found here. Only small rodents (Kurten 2013) and other small generalist species (Van Vliet & Nasi 2008) could be more resilient to hunting pressure (Wright 2003, Benítez-López *et al.* 2017, Koerner *et al.* 2017). Here, and as also observed by Laurance *et al.* (2006) in Gabon, the pangolin and small rodents are more abundant in logged forests and forests close to villages than in undisturbed forests. This can be due to the density compensation phenomenon resulting from the extirpation of competitive species (Peres & Dolman 2000).

Each of the three forest allocations showed distinct dung beetle species composition, indicated by the high turnover component of beta-diversity among sampled areas. Large dung beetle species were more abundant in the protected area than in the two other forest allocations. As revealed by our results, several studies also showed that human-driven forest disturbances impact dung beetle species composition, particularly by reducing the abundance of large-sized species (Nichols *et al.* 2013, Edwards *et al.* 2014). Our analyses showed the high local influence of proximity to roads and associated logging, agricultural and habitat disturbances on dung beetle species composition. Dung beetle species have been identified as indicators of closed-canopy forests (Watkins *et al.* 2017). Impoverished samples of the communities are obtained in any clearings created for road construction, largely degrading dung beetle habitat quality (Hosaka *et al.* 2014). Dung beetle community composition is also affected by forest fragmentation (Nichols *et al.* 2007), as seen here in degraded community forests impacted by agriculture and with relatively higher canopy openess. In contrast to mammals, dung beetles are known to be particularly sensitive to the environmental effects of selective logging (Bicknell *et al.* 2014). As shown here, a negative influence of roads on dung beetle populations has already been demonstrated up to 170 meters into the forest interior due to micro-habitat variation, with associated declines of ecological functions (Hosaka *et al.* 2014, Edwards *et al.* 2017) such as dung and seed removal (Andresen 2003, Slade *et al.* 2011).

4.3 Conservation value of forest allocations

In the face of major environmental issues in central Africa (Abernethy *et al.* 2016), our results confirmed the importance of protected areas in the conservation of large-bodied and threatened mammal species, as well as most forest dung beetle species (as also shown by Davis and Philips, 2005). Even if many protected tropical forests experience alarming biodiversity losses (Laurance *et al.* 2012), the long-term presence of conservation activities can reduce threats (Tranquilli *et al.* 2014). In the Dja Biosphere Reserve, conservation activities include law enforcement through anti-poaching patrols and awareness campaigns, scientific research, and tourism, which together can lower threats in African protected areas (Tranquilli *et al.* 2014). Additionally, in the northern sector of the Reserve motor vehicles cannot easily cross the Dja River reducing accessibility for commercial poachers.

We found that production forests can harbour similar species richness and composition to that of protected areas. Vulnerable pangolin species (*Manis* spp.) were even found more frequently in the logging concession than in the two other forest allocations (**Appendix D**). It has already been demonstrated that selective logging has modest impacts on most taxonomic groups (*e.g.*, species richness of birds, mammals, invertebrates, and plants according to Putz *et al.* 2012) and only slightly reduces biodiversity levels (Clark *et al.* 2009, Gibson *et al.* 2011). In particular, Burivalova *et al.* (2014) suggested that most taxonomic groups would be resilient to selective logging at intensities lower than 10 m^3 ha^{-1}, as applied in the FSC-certified concession studied here. However, here we reported high spatial heterogeneity of biodiversity in the logging concession that we related to local disturbances induced by roads. Indeed, as a side effect of logging, the road network can make some areas highly accessible and deeply impacted by human activities (logging, hunting and poaching), whereas remote areas remain nearly intact (Poulsen *et al.* 2009).

Community forests were found to be particularly depauperate, with a dominance of small-sized mammal species and poor dung beetle communities. The low conservation value of these forests is due to the high proximity to villages and roads (Beirne *et al.* 2019). Human presence is associated with hunting pressure, fire, and forest fragmentation induced by slash-and-burn agriculture. Yet some mammal species were found to be more abundant in these young secondary forests, such as the African palm civet (*Nandinia binotata*) that lives in umbrella trees (*Musanga cecropioides*). Community forests cannot yet be considered as totally defaunated, even though human populations intensively use them for a multitude of ecosystem services, including bushmeat provision (Lhoest *et al.* 2019).

4.4 Conservation implications

Our results confirm that the road network and associated forest accessibility have major detrimental effects on biodiversity. The area damaged by logging roads typically reaches 0.6 to 8.0% of forest area in tropical countries (Kleinschroth & Healey 2017) and 1.26% in the studied logging concession in 2018. Roads are a financially costly element of logging activities, and both concession holders and biodiversity conservation would benefit to improve the design and planning of logging roads (Edwards *et al.* 2017). It has been previously suggested to: (i) implement strategic planning and long-term spatial prioritization (Kleinschroth *et al.* 2019) in order to limit the size and expansion of logging road networks (Putz *et al.* 2008, Laurance *et al.* 2009); (ii) define a minimum volume of timber extracted per unit length of logging road to justify road construction (Edwards *et al.* 2017); (iii) close logging roads after timber extraction to facilitate forest recovery and discourage hunters from penetrating the forest (Clark *et al.* 2009, Bicknell *et al.* 2015, Kleinschroth *et al.* 2016); and (iv) avoid building any roads suitable for motor vehicles inside protected areas (such as in the Dja Biosphere Reserve) and only planning appropriate pedestrian access where needed.

Our study identified a strong decline of mammal species richness in proximity to villages in southeastern Cameroon. The hunting pressure surrounding rural communities is known to be extremely high in Cameroon. Several effective solutions must be implemented to halt the defaunation crisis in central Africa, including: (i) law enforcement (Critchlow *et al.* 2017) comprising anti-poaching operations (Benítez-López *et al.* 2017) and a better control of access in logging concessions and protected areas (Van Vliet & Nasi 2008); (ii) participatory repressive enforcement program (Clark *et al.* 2009, Vermeulen *et al.* 2009, Beirne *et al.* 2019); (iii) ban of hunting of sensitive species (according to the IUCN status) and regulation of hunting of the most resilient and locally abundant species such as the blue duiker (*Philantomba monticola*) or the African brush-tailed porcupine (*Atherurus africanus*) (Van Vliet & Nasi 2008, Nasi *et al.* 2011); (iv) provision of alternative sources of proteins (local fish farming, aviculture, supply of butcher's meat, vegetal proteins, edible insects) at affordable prices, with a minimization of their negative environmental impacts (Wilkie *et al.* 2005, Rentsch & Damon 2013).

Conservation strategies have to be designed and coordinated at a large scale (landscape, national or continental scale) in balance with the need for economic development and bushmeat provision (Poulsen *et al.* 2011). High values of turnover among forest allocations for both mammal and dung beetle species in our results support a devotion of conservation initiatives to a large number of different sites, with a priority on protected and remote areas of high biodiversity. Production forests in the surroundings of protected areas have a crucial buffer role to play. In particular, adapted management aimed at minimizing the degradation of high conservation value forests is an important requirement of FSC certification. If strictly protected forest patches are not connected with production forests in a larger forest matrix, no conservation intervention is likely to be sufficient (Edwards *et al.* 2014). Connected to protected areas, production forests offer the chance to conserve many ecosystem services, functions, and species (Clark *et al.* 2009). They cover a high proportion of forest lands and show lower opportunity costs than protected areas. It is vital for biodiversity that protected and production forests be maintained as forest lands rather than being converted to agriculture or plantations characterized by much lower conservation values (Chazdon *et al.* 2009).

5 Appendices

Appendix A Characteristics of forest allocations in the study area. Area of each zone was calculated with existing polygons (World Resources Institute 2012) or using planning documents in order to manually digitize polygons (buffer zone of the protected area). Mean forest cover in 2000 was quantified based on Hansen *et al.* (2013)

	Land allocation types						
	Protected area		Logging concession				Community forests
	Core area	Buffer zone	Production	Conservation	Protection	Agroforestry	
Area (hectares)	526,155	207,584	287,533	45,594	6,789	856	13,466
Mean forest cover (%)	89.6	89.5	90.7	90.2	89.9	90.9	89.7
Deforestation rate (%)	0.0	0.2	0.1	0.1	0.1	1.5	1.5
Hunting	Prohibited	Regulated*	Regulated*	Regulated*	Prohibited	Regulated*	Regulated*
NTFP	Prohibited	Allowed	Allowed	Allowed	Prohibited	Allowed	Allowed
Deadwood	Prohibited	Allowed	Allowed	Allowed	Prohibited	Allowed	Allowed
Living wood	Prohibited	Allowed	Prohibited	Prohibited	Prohibited	Allowed	Allowed
Agriculture	Prohibited	Allowed**	Prohibited	Prohibited	Prohibited	Allowed**	Allowed

*Authorized for self-consumption only, with traditional selective techniques, only for non-protected species

**Current agricultural occupation zone, but prohibition to extend agricultural areas beyond

Appendix B Quantification of habitat variables “forest degradation” and “canopy openness”

In order to quantify forest degradation in the surroundings of mammal and dung beetle sampling sites, we performed a supervised classification with the maximum likelihood method based on satellite imagery. We used the blue, green, red, and near infrared bands of two Sentinel-2 images, mosaicked in a sole one, acquired on the 25 January 2016, with a 10 meters pixel size. Reference data (9640 reference points) were defined from a combined visual interpretation of the Sentinel-2 image and Google Earth data for better spatial resolution. Four classes were identified: (i) dense forest matrix (comprising dense forest stands and swamp forests), (ii) degraded forests (comprising forest visually impacted by both logging and slash-and-burn agriculture) and crops, (iii) bare soil (roads and villages) and (iv) water surface (rivers). We later used a majority filter with a sliding square window of 3 x 3 pixels to smooth the resulting raster. The classification performance was assessed based on the Kappa statistic derived from the confusion matrix. We defined buffer zones around biodiversity sampling points to compute a metric of forest degradation based on the classification raster. Around each camera trap, we considered a 700 meters buffer zone to potentially influence the detection of mammals, considering the recommended distance of 1.4 kilometers between two cameras for mammal inventories in tropical regions (international protocol of TEAM Network 2011). Around each dung beetle trap, we considered a 75 meters buffer zone, considering that the traps could influence these insects up to 50-100 meters (Larsen & Forsyth 2005). We computed the proportion of pixels classified as degraded forest in those circular windows around each biodiversity sampling site.

To estimate canopy openness above dung beetle pitfall traps, we took five hemispherical photographs per trap, at 1.5 meters of height and at sunrise: one photo directly above the trap and four photos at 10 meters from the trap in the direction of the four cardinal points. Vegetation below 3 meters of height was cleared beforehand. The percentage of canopy openness is the percentage of open sky seen from beneath a forest canopy and was calculated with GLA software (Frazer *et al.* 1999). The percentage of canopy openness associated to each trap was the mean of the five values obtained for each trap.

Appendix C Pearson' s correlation matrices of extrapolated species richness, and environmental variables, for mammals (A) and dung beetles (B)

A

Environmental variables	Y for X = 10	Y for X = 20	Y for X = 30	Y for X = 40	Y for X = 50	Y for X = 60	Y for X = 70	Y for X = 80	Y for X = 90	Y for X = 100
	Mammal species richness (Y) extracted from individual-based rarefaction curves for different numbers of detection events (X)									
Distance to the nearest road	-0.04	0.29	0.25	0.25	0.34	0.28	0.27	0.40	0.48	0.33
Distance to the nearest river	0.49	0.31	0.22	0.22	0.33	0.14	0.20	0.12	0.16	0.16
Distance to the nearest village	0.40	0.50	0.32	0.32	0.43	0.27	0.42	0.41	0.49	0.33
Forest degradation	0.05	-0.16	-0.30	-0.30	-0.26	-0.31	-0.20	-0.35	-0.36	-0.30
Protected area	0.06	0.35	0.38	0.38	0.37	0.39	0.33	0.49	0.49	0.42
Logging concession	0.30	0.05	-0.12	-0.12	-0.02	-0.16	0.03	-0.15	-0.09	-0.13
Community forests	-0.40	-0.46	-0.32	-0.32	-0.41	-0.29	-0.42	-0.41	-0.49	-0.35

B

Environmental variables	Y for X = 10	Y for X = 20	Y for X = 30	Y for X = 40	Y for X = 50	Y for X = 60	Y for X = 70	Y for X = 80	Y for X = 90	Y for X = 100
	Dung beetle species richness (Y) extracted from individual-based rarefaction curves for different numbers of individuals (X)									
Distance to the nearest road	0.68	0.65	0.67	0.57	0.59	0.58	0.57	0.57	0.53	0.55
Distance to the nearest river	-0.24	-0.17	-0.25	-0.25	-0.22	-0.20	-0.23	-0.20	-0.14	-0.20
Distance to the nearest village	0.44	0.48	0.61	0.59	0.58	0.60	0.58	0.60	0.52	0.56
Canopy openness	-0.47	-0.40	-0.50	-0.47	-0.52	-0.54	-0.57	-0.53	-0.52	-0.53
Forest degradation	-0.29	-0.36	-0.37	-0.34	-0.33	-0.27	-0.24	-0.28	-0.25	-0.29
Protected area	0.60	0.57	0.60	0.51	0.51	0.52	0.51	0.51	0.48	0.49
Logging concession	0.09	0.20	0.29	0.38	0.39	0.39	0.42	0.44	0.41	0.43
Community forests	-0.67	-0.71	-0.82	-0.79	-0.81	-0.82	-0.82	-0.84	-0.79	-0.81

Appendix D List of mammal species inventoried

Species	Mean number of independent detection events per camera working during 87 days				IUCN status
	Protected area	**Logged 20-30 years before**	**Logged 10-20 years before**	**Community forests**	
Atherurus africanus	12.6	13.4	5.8	5.7	Least Concern
*Atilax paludinosus**	3.4	1.2	0.3	0.2	Least Concern
Bdeogale nigripes	1.7	0.4	0.2		Least Concern
Cephalophus callipygus	8.2	2.0	1.9	0.3	Least Concern
Cephalophus castaneus	3.2	2.4	1.3	0.3	**Near Threatened**
Cephalophus nigrifrons	0.1				Least Concern
Cephalophus silvicultor	7.0	1.4	0.4	0.3	**Near Threatened**
Cephalophus sp.	0.3		0.3	0.2	/
Cercocebus agilis	0.2	2.6	1.1	0.8	Least Concern
Civettictis civetta				0.2	Least Concern
Cricetomys emini	30.0	21.2	34.3	48.0	Least Concern
Crossarchus platycephalus	1.6	0.8	0.8	0.5	Least Concern
Dendrohyrax dorsalis			0.1	0.2	Least Concern
Funisciurus isabella	22.9	30.8	9.6	24.5	Least Concern
Funisciurus pyrropus	1.2	7.6	0.6	0.7	Least Concern
Genetta servalina	3.6	2.4	0.3	0.8	Least Concern
Manis gigantea	0.6				**Vulnerable**
Manis spp.	0.3	1.0	1.1	0.5	**Vulnerable**
Nandinia binotata	0.4	0.2	0.7	1.2	Least Concern
Neotragus batesi	0.1		0.6		Least Concern
Pan troglodytes	0.3		0.3		**Endangered**
Philantomba congica	49.4	7.2	9.7	2.8	Least Concern
Potamochoerus porcus	1.6		0.3		Least Concern
Protoxerus stangeri	4.2	16.8	3.3	7.3	Least Concern
Rodentia spp.	5.0	10.2	9.1	20.2	/
Tragelaphus gratus	0.7				Least Concern

*The detection events recorded for *Atilax paludinosus* (Marsh Mongoose) also include the detection events of *Xenogale naso* (Long-nosed Mongoose), but we were not able to distinguish the two species on acquired images.

Appendix E List of dung beetle species inventoried and references for the identification

	Number of individuals collected (24 pitfall traps in each forest allocation)		
Species	**Protected area**	**Logging concession**	**Community forests**
Alloscelus combesi			1
Amietina larochei		13	
Caccobius elephantinus	1		
Catharsius gorilla	78	33	65
Catharsius gorilloides	1	2	5
Catharsius lycaon	44	52	12
Chalconotus cupreus	1		
Copris phungae subsp. *Gabonicus*	16	2	3
Diastellopalpus conradti	4	15	11
Diastellopalpus laevibasis	8		1
Diastellopalpus murrayi	3	4	3
Diastellopalpus noctis	10	7	15
Diastellopalpus sulciger	29	18	23
Garreta cf *diffinis*	1		
Heliocopris coronatus	6	3	3
Heliocopris helleri	2	3	1
Heliocopris mutabilis	2	6	3
Lophodonitis carinatus	4	1	
Milichus inaequalis			1
Milichus merzi	6		
Mimonthophagus apicehirtus	2		
Neosaproecius trituberculatus	1		1
Neosisyphus angulicollis	10	17	30
Onthophagus atronitidus	162	1	2
Onthophagus barriorum			2
Onthophagus biplagiatus		3	
Onthophagus cf picturatus		1	
Onthophagus densipilis	78	27	204
Onthophagus denudatus	2	6	
Onthophagus depilis	2	2	
Onthophagus dorsuosus	1		
Onthophagus erectinasus	1	9	1
Onthophagus fuscidorsis	633	562	577
Onthophagus graniceps	2		
Onthophagus intricatus	79	22	3
Onthophagus justei	42	9	18
Onthophagus laminosus	1		6
Onthophagus macroliberianus	2		
Onthophagus montreuili	6	3	29
Onthophagus orthocerus	65	51	1
Onthophagus pilipodex	1	1	

Onthophagus pseudoliberianus	3	2	2
Onthophagus rufipodex	1		3
Onthophagus strictestriatus	6	1	
Onthophagus sulcatulus	11	15	1
Onthophagus umbratus	36	14	13
Onthophagus vesanus	2		
Onthophagus sp. 1		6	
Onthophagus sp. 2	1	4	1
Onthophagus sp. 3		2	
Onthophagus sp. 4	1	2	
Onthophagus sp. 5	6	2	
Onthophagus sp. 6	3	1	
Onthophagus sp. 7		6	
Onthophagus sp. 8	1	2	
Onthophagus sp. 9		2	
Onthophagus sp. 10		2	1
Onthophagus sp. 11	11		1
Onthophagus sp. 12	2		
Onthophagus sp. 13	2		3
Onthophagus sp. 14	1		
Pedaria ovata	24	16	7
Pedaria spinithorax	7		
Proagoderus semiiris	142	131	282
Pseudopedaria grossa	33	6	8
Pseudosaproecius validicornis		1	8
Sisyphus arboreus	76	42	1
Sisyphus bayanga	4	8	
Sisyphus sp.	4	1	
Sisyphus walteri	182	109	9
Tomogonus crassus			1

Dung beetle species were identified using the following references:

Branco, T., 1990. Essai de révision des genres du "groupe" stiptopodius : le genre *Neosaproecius* nov. (Coleoptera : Scarabaeidae). *Annales de la Société Entomologique de France (N.S.)*, 26(4) : 595-599.

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Josso, J-F & Prevost, P., 2015. Révision du genre *Pedaria* Laporte, 1832. *Magellanes, Collection Systématique*, 26 : 1-160.

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Montreuil, O., 2016. Nouveaux *Sisyphus* Latreille, 1807, du groupe *seminulum* : le complexe *arboreus* (Coleoptera, Scarabaeidae, sisyphini). Bulletin de la Société entomologique de France, 121(2) : 167-174.

Moretto, P., 2010. Les Scarabéides coprophages de Bayanga en République Centrafricaine (Coleoptera, Scarabaeidae). *Bulletin de la Société entomologique de France,* 115(4) : 455-477.

Moretto, P., 2017. *Heliocopris eryx* (Fabricius, 1801) et ses formes. Description d'une espèce et de 2 sous-espèces nouvelles. (Coleoptera, Scarabaeidae, Coprini). *Catharsius, La Revue,* 14 : 23-40.

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5

Response to hunting

Preamble

In **Chapter 4**, we argued that forest accessibility, a common proxy of hunting pressure, better predicts the alteration of terrestrial mammal assemblages than forest management. This assumption might be valid at the landscape scale but in hunting territories that generally extend over smaller areas, hunting pressure is more disparate and does not simply radiate from the village centers. In **Chapter 5**, we (SWM Gabon team & I) therefore implemented a comparable camera trap survey protocol surveying a gradient of increasing anthropogenic pressure ranging from remote and protected forests up to potentially highly defaunated village forests across eastern Gabon. To refine our understanding of the alteration patterns within hunted forests, we additionally measured hunting pressure through the monitoring of hunting bag and hunter GPS self-follows.

- Paper 4: draft -

Mammal assemblages' alteration under increasing hunting pressure in eastern Gabon

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This chapter is drafted for a publication in *Conservation Biology*

Abstract

Background Hunting is the most important threat on mammal diversity in central Africa.

Aim While specific studies have reported a general trend of wildlife decline but contrasted resistance to hunting between species, we still fail to accurately describe the response of the whole species assemblages to increasing hunting pressure, and detailed analyses of these responses over a complete defaunation gradient to identify tipping points and ecological indicators to guide sustainable hunting management and conservation actions.

Location Eastern Gabon.

Methods We profiled the mammal assemblages along a gradient of increasing hunting pressure, ranging from remote areas deemed not hunted to more disturbed and potentially impoverished areas in the vicinity of three different villages, combining wildlife population data from camera trap (CT) surveys with a detailed quantification of hunting pressure (offtake monitoring and GPS tracking of hunting activities).

Main results and discussion Important changes in community composition were identified within and between forest land allocations and hunting regimes. In the Ivindo NP and in the logging concession, the communities are diversified and include large bodied species such as apes and forest elephants. With increasing hunting pressure, assemblages are becoming less speciose and specifically depauperate in large bodied species and offtake composition tended to be dominated by rodents.

Conclusion and perspectives Practical implications were finally derived to guide further wildlife monitoring and conservation actions.

Keywords: Terrestrial mammals, Species diversity, Species composition, Hunting regime, Offtake pressure, Sustainable management, Camera traps

1 Introduction

The hunting of wild animals and the consumption of wild meat is the major driver of animal diversity loss in the tropics, and especially in west and central Africa (Fa *et al.* 2002, Ripple *et al.* 2016). At the same time, bushmeat remains of extreme importance for the livelihoods and the nutrition of millions of people (Nasi *et al.* 2011, Ingram *et al.* 2021). When considering both hunting pressure (Benítez-López *et al.* 2019) and forest integrity (Grantham *et al.* 2020), only little forest areas remain intact in central Africa, and most mammal assemblages are highly threatened by hunting pressure (see **Chapter 2**) which is widespread across the region (Ziegler *et al.* 2016).

Hunting-induced changes in the structure and composition of forest wildlife communities have been well documented locally (*e.g.* in Nigeria, Effiom *et al.* 2013; in Cameroon, Lhoest *et al.* 2020 [**Chapter 4**]; in Gabon, Beirne *et al.* 2019, Koerner *et al.* 2017; in Republic of Congo, Marrocoli *et al.* 2019; in Democratic Republic of Congo, Hart 2000). The same pattern emerges with species assemblages dominated by small-sized species and rodents and depleted in most large-bodied mammals nearby human settlements and accessible areas. The extraction of large-bodied species, and the release of their top-down control, disrupts plant-animal interactions and forest functioning, potentially initiating trophic downgrading of the entire ecosystem (Estes *et al.* 2011). Herbivory, seed dispersal and predation, and seedling/sapling recruitment are some of the processes that are particularly altered in heavily hunted sites (Wright *et al.* 2000, Wright 2003, Vanthomme *et al.* 2010, Poulsen *et al.* 2013), compromising other critical services such as long-term carbon sequestration and resilience to global change (Abernethy *et al.* 2013, Bello *et al.* 2015).

While specific studies have reported a general trend of wildlife decline but contrasted resistance to hunting between species (*e.g.*, Van Vliet *et al.* 2007, Van Vliet & Nasi 2008), we still fail to accurately describe and formalize the response of the whole species assemblages to increasing hunting pressure (Marrocoli *et al.* 2019). Refine information on hunting pressure is, however, logistically challenging to acquire, and thus rarely available, and even less for long time periods. In this study, we tackled this challenge by profiling the mammal assemblages along a gradient of increasing hunting pressure in eastern Gabon, ranging from remote areas deemed not hunted to more disturbed and potentially impoverished areas in the vicinity of villages, combining wildlife population data from camera trap (CT) surveys with a detailed quantification of hunting pressure. We specifically addressed the two following research questions:

1) How can variation in species composition inform the alteration state of mammal assemblages? While providing a benchmark for what a relatively intact megafauna assemblage looks like in the region might be done by valuing old wildlife populations assessments, characterizing the continuum of alteration, potentially involving local extirpation of vulnerable species (nestedness) and species replacement within or between guilds (turnover) remains challenging and hard to capture (Bruce *et al.* 2017).

2) Does the spatial distribution of the hunting pressure explain the change in species composition better than forest accessibility? As hunters are generally assumed

to act as central-place foragers radiating from human settlements (Abrahams *et al.* 2017, Koerner *et al.* 2017, Beirne *et al.* 2019, Marrocoli *et al.* 2019), hunting pressure is often proxied by accessibility indices such as distance from the village center, whereby the most accessible areas are deemed to be the most altered, reflecting the combined effects of current and past hunting strategies (Rist *et al.* 2009). This assumption might be valid at the landscape scale (see **Chapter 4**) but in hunting territories that generally extend for about ten kilometers from the village (Froese *et al.* 2022), and up to 25 km (Abernethy *et al.* 2013), hunting pressure is more disparate (Mockrin *et al.* 2011, Fa *et al.* 2021, Froese *et al.* 2022) and accurate, spatially explicit measure of hunting pressure might refine the understanding of the alteration patterns.

2 Material and Methods

2.1 Study area

The study was conducted in the bushmeat supply area of Lastoursville, the chief town of the Mulundu department in eastern Gabon, where 43% of the population of the department (~ 28,000 inhabitants, MEFEPA & WRI 2017) is concentrated. The majority of the population remains essentially rural, settled along the main roads, railways and river routes, leaving vast areas of forest largely uninhabited, mostly granted to logging companies apart from the Ivindo National Park at the north-west boundary of the department, being protected since 2002 (**Figure 5.1**). The population density is therefore quite low, at around 1,8 inhabitants per km² (Direction Générale de la Statistique 2015). Climate in the region is characterized by mean annual rainfall and temperature of 1,702 mm and 24.4°C, respectively (Fick & Hijmans 2017). Though the distribution of rainfall is bimodal, with two rainy seasons (peaks in March and October) and two dry seasons, including a short (January-February) and a long dry season (midJune-midSeptember), wet evergreen forest prevails in the area (Fayolle *et al.* 2014, Réjou-Méchain *et al.* 2021).

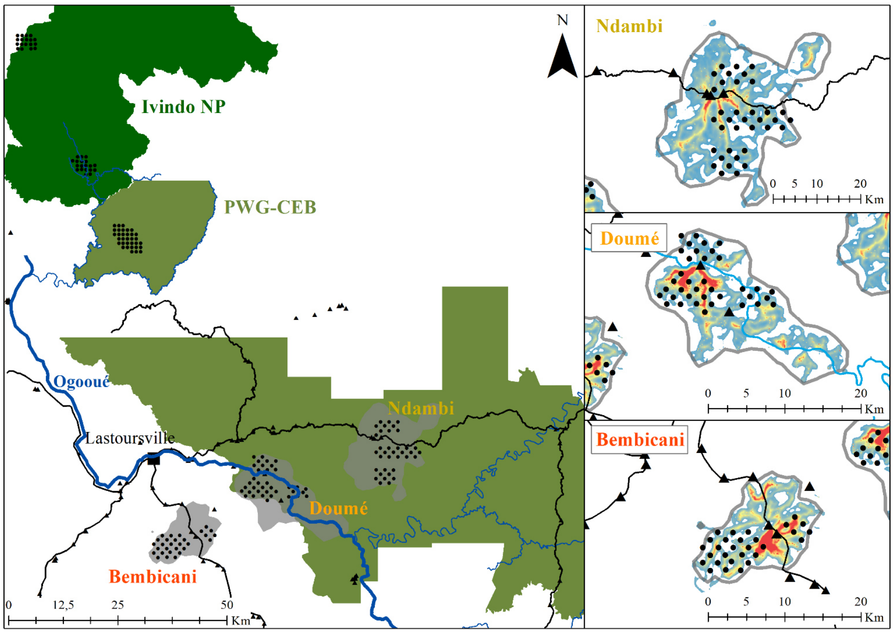


Figure 5.1 Location of the camera traps (black dots), the villages (black triangles), the national road (black line) and the Ogooué (blue line) across the study area as well as zoom on the utilization distribution (UD) within the hunting territory of each surveyed village (Ndambi, Doumé & Bembicani). UD was computed using a movement-based kernel method with a minimum smoothing parameter of 30 m and a diffusion coefficient of 500 m²/sec on a 50m x 50m quadrat grid (see Benhamou & Cornélis, 2010, for a complete description of the method). The grey contour corresponds to the 95% UD isopleth provided by the classical kernel method using the ad hoc smoothing parameter.

2.2 Hunting and offtake monitoring

As part of the Sustainable Wildlife Management EU Program (https://www.swm-programme.info), a baseline diagnostic was first carried out in almost every village of the department, and the villages of Bembicani, Doumé and Ndambi were selected as pilot sites for wildlife and hunting monitoring (Cornélis *et al.* 2022). In each village, a household census combined with a stakeholder analysis was first conducted to identify all the individuals involved in the bushmeat system. Once identified, the hunters could volunteer to join the hunting and offtake monitoring in accordance with the Free, Prior and Informed Consent (FPIC) principle. Over the course of a full year (from the 1st May 2019 to the 30st April 2020), offtakes were monitored at least once a day, and preferably three times a day, when the hunters had returned to their village. For each hunting trip, the date and time of departure and return as well as the number of catches were recorded. Each catch was identified at the species level and weighed. If the animal had been cut up, each piece was weighed separately. When possible, the date and time of the catch, the sex, the age class (juvenile or adult), the preservation state and the capture method (gun, wire trap or hand-picked) were also recorded. On a voluntary basis, hunters could also be equipped with a GPS device (Garmin eTrex® 10) to record their hunting tracks, temporary or permanent hunting camps and catches. The GPS were scheduled to acquire locations at 2 minutes intervals. In the end, a total of 668 hunting trips were GPS tracked (5 473 km), recorded by 67 different hunters (33 in Bembicani, 17 in Doumé and 17 in Ndambi).

2.3 Camera trap survey

A CT survey was implemented in parallel to the hunting and offtake monitoring in order to characterize the ground-dwelling species assemblages in the hunting territory of each village. To ensure spatial congruence between hunting activities and camera records, we identified the main hunted areas using preliminary monitoring data on offtake and installed the CT grid in actively hunted sectors, at increasing distances from the village center. Each CT was left for at least one month (between April and June 2019) in the field. Regular grids of 29 - 36 CTs, with a density of one camera per 1 or 2 km², were deployed within the hunting territories of the three pilot villages and in two control sites deemed to be largely preserved from hunting: the southern part of the Ivindo NP, and adjacent and remote area of the FSC-certified logging company PWG-CEB that was logged more than ten years ago (**Figure 5.1**). The Bolyguard SG 2060X model (Boly, Victoriaville, QC, Canada) was used for all CT grids, except in the logged forest of PWG-CEB for which the Bushnell Trophy Cam HD model (Bushnell, Overland Park, KS, USA) was used. The CT were installed at 30–50 cm height, facing a small wildlife trail or a trail crossing according to the TEAM network (Jansen *et al.* 2014) and earlier work in the area (Fonteyn *et al.* 2021). Forest undergrowth was slightly cleared to reduce false triggers. CTs were parametrized to record five second videos with the minimum trigger delay (0.8 s). Wildlife videos were processed with the open access Timelapse Image Analysis system (Greenberg 2022). All terrestrial and semi-terrestrial species which might be hunted were considered for the analysis. Species taxonomy followed the IUCN Red List of Threatened Species. Because of challenging identification, some species were grouped for further analysis into four species complexes (*i.e.*, large-spotted genets, mongoose, forest squirrels, small pangolins) as detailed in Fonteyn *et al.* (2021). Successive detections of the same species or species complex were considered independent if they are at least 30 min apart (Meek *et al.* 2014).

2.4 Data analysis

First, we characterized the hunting regime (spatial extent, catches composition, meat use and hunting practices) derived from the offtake monitoring and the ground-dwelling mammal assemblages (richness and species composition) derived from the camera trap monitoring of each village. The spatial extent of the hunting territory at the village and at the individual hunter scale was computed from the GPS tracks of the hunting trips using a movement-based kernel (MBK) density estimation method (Benhamou & Cornélis 2010) and encompassed all the area comprised within the 95% utilization distribution (UD) isopleths. To be comparable between villages, space use density probabilities, *i.e.*, what we consider here as the current hunting pressure, were weighted by the total number of recorded GPS locations in the village, assuming that a representative and equal sample of all hunting trips was acquired in each village. For each village, we used the hunting bag data to derive the total number of hunted species and the proportion of rodents, artiodactyls, and primates in all catches, as well as the total biomass extracted over the study period and the resulting average catch weight. We also measured the mean biomass harvested during a hunting trip, including unsuccessful hunting trips. The CT data were used to evaluate the richness and composition of mammal communities in the forest. The detection rate, which corresponds to the mean number of independent events per sampling day and CT (Rovero & Marshall 2009) was calculated for each species and area. For both type of data, we also computed a duiker index (hereafter BlueDuiker%) representing the percentage of blue duikers against all duikers' (*Cephalophus* spp. and *Philantomba monticola*) catches and detections. This index is adapted from Marrocoli *et al.* (2019) and Yasuoka *et al.* (2015) but considers all duiker species rather than the restrictive category of 'red duiker' as it can be assumed that all medium-sized and large duikers are likely to be less resistant to higher hunting pressure due to their size-related life history traits.

Then, we assessed the species composition similarity between all camera pairs using the Bray-Curtis (dis-)similarity index and performed a non-metric multidimensional scaling to examine species composition gradient. We used an ANCOVA (Analysis of Covariance) to test the effect of site, current hunting pressure (average space use density probabilities computed at 100, 250, 500, and 1000 m around the CT) and two accessibility indices (distance of each CT to the village center and to the nearest communication axis, *i.e*, the national road network and the navigable river of the Ogooué) on species composition, specifically using dissimilarity with the control area, here after called 'compositional alteration'.

All analyses were performed in the R software using the "adehabitatHR" package (Calenge 2006) to estimate hunter space use and the "vegan" package (Oksanen *et al.* 2019) for diversity analyses (richness and dissimilarity-based approaches).

3 Results

3.1 Hunting regime and wildlife populations

Over the year, we recorded a total of 2,874 hunting trips conducted by 114 different hunters and the capture of 5,007 animals (~71,094 kg), mostly caught with 12-gauge shotguns (**Table 5.1a**). Hunting trips lasted on average 14-15 hours [$CI_{0.95}$, 14.12 – 15.43] with a mean harvesting rate all villages considered of 14.4 kg per hunted trip. Most hunting activities were confined within a 10 km radius around the village, except for the riverside village of Doumé where some hunters benefitted from the Ogooué river to travel up to 25 km upstream (**Figure 5.1**). The total extracted biomass was roughly the same between the three villages but the hunting patterns in the Bembicani and Ndambi villages reflect two contrasted situations, while Doumé village represents an intermediate state (**Table 5.1a**). In Bembicani, the most populated village, hunting was carried out exclusively for commercial purposes and extended over a very small area (78 km^2), largely inferior to the hunting territories observed for the two other villages and the total time spent hunting in Bembicani was two times higher than in the two other villages. This echoes the two-fold decrease in average biomass per offtake observed from Bembicani to Ndambi, suggesting a depletion of the large game species in the most hunted territory. The strong pressure on the mammal communities and the strong alteration level in Bembicani, and to a lesser extent in Doumé, is also demonstrated by the shift in offtake species composition with a decrease in the proportion of artiodactyls at the expense of other orders such as rodents and primates in hunting bag data, and a higher proportion of blue duiker in all duikers catches as well.

The wildlife population metrics derived from the CT survey are consistent with the results derived from offtake data (**Table 5.1b**). The gradient in hunting pressure and the community alteration are reflected by the average biomass of a detection event which strongly declined from the control areas (Ivindo NP and CEB logged forests) to the villages, even after the removal of elephants and great apes' detections, which can strongly skew the metric. Though estimates of species richness were comparable between sampled areas since species detection accumulates over the monitoring period, the overall species composition recorded by CT strongly differed along the gradient. The percentage of rodent and artiodactyl detections increased and decreased respectively from the control areas to the villages, and with increased hunting pressure between the villages from Ndambi to Bembicani, following the trend observed in offtake data. Rodents, for instance, accounted for more than 70% of the detections in the Bembicani village, while this proportion did not exceed 17% in control areas. Contrastingly to offtake data, the BlueDuiker% index derived from CT data presented high values in control areas and the lowest value in Bembicani, the village under the greatest pressure.

Table 5.1 Characteristics of the hunting pressure and wildlife community in the three study villages (Bembicani, Doumé and Ndambi) and in the two control areas (CEB and Ivindo NP) ordered in terms of hunting pressure, from the most intense hunting regime to the most preserved areas

	Bembicani	Doumé	Ndambi	CEB	Ivindo
a) Hunting pressure					
Population size (>18 y)	259	84	67		
Number of hunters included in the offtake monitoring*	52	20	25		
Village hunting territory in km² (MBK 95%)	137	247	268		
Mean average hunter territory in km²	2.32	9.88	8.93		
Number of species hunted	32	24	25		
% of pieces** marketed	88%	91%	48%		
% of individuals catched by gun, trap and machete	65/29/5	97/3/<1	95/4/<1		
Estimated annual biomass harvested (kg)***	16 894	14 843	9 636		
Average catch weight (kg)	6.6	8.5	13.7		
Mean harvested biomass per hunting trip (kg)****	10.03	19.90	21.75		
% Rodents/ %Artiodactyls / %Primates	27/44/9	17/70/4	2/83/9		
BlueDuiker%	54%	56%	32%		
b) Wildlife community					
Survey effort in camera.days (Number of CT)	963 (29)	1224 (36)	1155 (36)	1312 (22)	2263 (37)
Observed species richness	25	26	31	26	31
Estimated richness at 900 camera.days and the 95% LCL & UCL	25 [20-29]	25 [23-27]	30 [28-32]	26 [24-27]	30 [29-31]
Average detection biomass$_{\text{all sp/all sp- elephant \& great apes}}$ (kg)	5.6/5.6	20.8/9.7	54.2/14	341.7/ 19.6	140.7/ 17.1
Proportions of rodents and artiodactyl detections	71/15	40/46	26/63	8/78	13/72
BlueDuiker%	28.8%	42.2%	35.3%	32.5%	42.8%

* hunters with at least 5 hunting trips registered during the surveyed year

** piece corresponds to a whole individual or body part of an individual

*** one forest elephant has been reported during the surveyed year and was removed from this analysis

**** including unsuccessful hunts and considering trap, gun and mixed hunts together

3.2 Alteration of mammal assemblages in response to hunting

When considering the detected community at the scale of a CT, a significant shift in mammal assemblages is evidenced along the hunting pressure gradient, from the CT located in the control areas (in green tones) to that installed in the villages (in yellow, orange and red with increasing hunting pressure, **Figure 5.2**). This means that though the CT grids detected roughly the same number of species over the survey period (**Table 5.1b**), each individual CT detected mammal assemblages composed of vastly different species with varying detection rates. The first ordination axis described this species turnover with the increasing detection of rodents *(e.g.*, *Atherurus africanus*) and small predators (*e.g.*, genets and mongoose) in hunted sites contrasting with medium-sized and large species clustered on the opposite side of the axis and pairing up with cameras in control areas. The species assemblage of the Bembicani village appeared extremely altered in comparison with the control sites, while that of Ndambi, and to a lesser extent of Doumé, displayed average species detection rates closer to those found in control sites, particularly for commonly hunted species such as duikers and red river hogs (barplots in inset **Figure 5.2**). The species composition of the two control sites remains very similar overall, with slight variations in the detection rate for some species (*e.g.*, forest elephants).

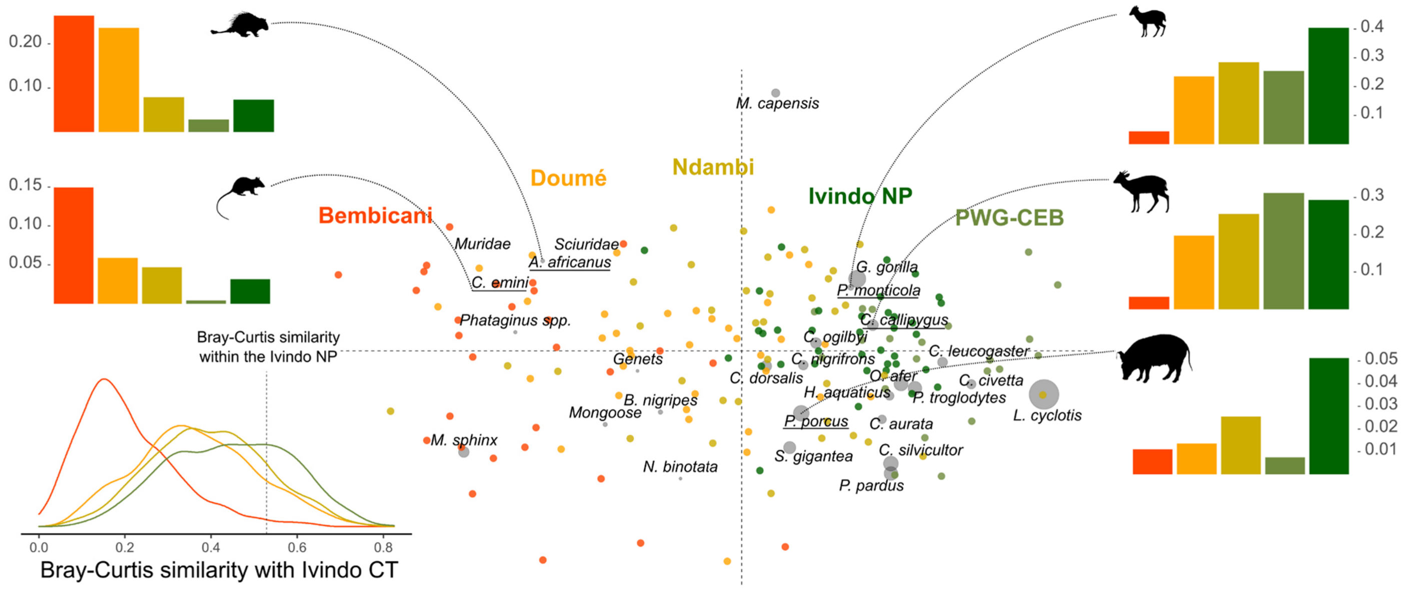


Figure 5.2 *Main graph*: Faunistic similarity (Bray-Curtis index, from no similarity “ 0” to similar composition “ 1”) between camera traps (1 camera trap = 1 point) along the studied gradient displayed on a non-metric multidimensional scaling, from the most hunted village (Bembicani) to the “ intact” Ivindo National Park. *Histograms*: Mean detection rates in each site (three villages, the PWG-CEB logging company and the Ivindo National Park) of five species showing a contrasted trend along the gradient. *Bottom left*: the Bray-Curtis similarity of each camera trap compared to each camera trap in the Ivindo National Park, *i.e.*, the compositional alteration, presented in the form of smoothed histograms.

To synthetize species assemblage's alteration in the villages in comparison with what can be considered an intact mammal assemblage, we computed the (dis)similarity between the CTs located in the villages with those located in the Ivindo NP (smoothed histograms in inset in **Figure 5.2**). We further tested whether this dissimilarity in species composition is related to indices of hunting pressure and to spatial factors and we found that the alteration in species composition was largely explained by current hunting regime, and notably the spatial distribution of hunting pressure, but we found significant differences between villages (a significant village effect, **Table 5.2**). Species assemblages were more altered in areas more densely used by hunters (significant slopes of the linear model considering all CT), and this tendency was still significant when adjusting for the interaction with the sampled village (ANCOVA, **Table 5.2**). In contrast, distance from the village center and from the nearest communication axis poorly explained the compositional alteration of each CT.

Table 5.2 Determinants of mammal assemblage alteration. Analysis of covariance (ANCOVA) depicting the influence of direct hunting pressure (mean UD considering a buffer of increasing radius; 100, 250, 500 and 1000 meters around the CT) on species composition similarity with the nearest distance to human settlements and road on species composition similarity with the Ivindo National Park.

	Village effect	Hunting Effect	Distance to village	Distance to road	Interaction	R^2	F-statistic
Sim. ~ UD_{100} * village	***	**	/	/	NS	45%	15.86
Sim. ~ UD_{250} * village	***	***	/	/	NS	46%	15.93
Sim. ~ UD_{500} * village	***	***	/	/	NS	46%	16.03
Sim. ~ UD_{1000} * village	***	***	/	/	NS	46%	15.97
Sim ~ $Dist_{village}$ * village	***	/	NS	/	NS	43%	14.32
Sim. ~ $Dist_{road}$ * village	***	/	/	NS	NS	45%	15.62

4 Discussion

4.1 A dissimilarity-based approach to better grasp mammal assemblages' alteration in space and time

Overhunting is one of the most widespread and pervasive components of tropical forest degradation in central Africa, undermining forest integrity and resilience as well as human livelihoods and food security for decades (Fa & Brown 2009, Abernethy *et al.* 2016). As a consequence of the size-selective behavior of hunters (Benítez-López *et al.* 2019, Bogoni *et al.* 2020), hunted mammal communities are becoming largely downsized and populations of sensitive species are either drastically reduced or locally extirpated as hunting pressure increases (Marrocoli *et al.* 2019). By integrating the whole variation in species composition, the dissimilarity-based approach implemented here provides a comprehensive and refine tool to formalize the continuum of alteration species assemblages might experience while facing increasing hunting pressure. Building on this approach, we showed that the compositional alteration of hunted territories was highly variable between villages and largely explained by the ongoing hunting pressure. Under low hunting pressure, as in the village of Ndambi, the composition of the terrestrial mammal assemblage was comparable to that in the control areas, but with greater local variation. At the opposite, the terrestrial mammal assemblages of the very hunted Bembicani village, and to a lesser extent Doumé village, are strongly downsized and largely dominated by rodents, presenting consequently very limited overlap with the controls on the ordination. Interestingly, offtake composition derived from hunting bag data mirrors this process, with a 2-fold decrease in average catch weight from the Ndambi to Bembicani villages. Beyond informing the alteration state of mammal assemblages as a baseline assessment, the analytical approach proposed here also allows for the spatial prioritization and the monitoring of short- and long-term impacts of management and restoration initiatives, particularly when compared to business-as-usual scenario in unmanaged hunting systems.

One of the main strengths of our approach relies in the concurrent monitoring of so-called control sites. Because of its remoteness and controlled forest access, the study site within the PWG-CEB forest permit, though disturbed by logging activities more than a decade ago, exhibited a ground-dwelling mammal assemblage very similar to the one found in the adjacent protected forests of the Ivindo NP, restating the conservation potential and the buffer role responsibly managed logged forest could play at the periphery of protected areas. Yet, using a control either in protected areas or in remote and almost undisturbed sites is not always possible in every study design. We therefore tested a comparable but simplified approach that only accounts for species presence or absence rather than species detection rates, considering the feasibility to easily list the species potentially present in a given study area, in this case the ones retrieved in Ivindo National Park. Compositional alteration is, however, more fine-grained than a simple local extirpation of species and the trend using only presence/absence data was less robust in profiling alteration patterns along the surveyed gradient (**Appendix A**).

4.2 Determinants of community alteration

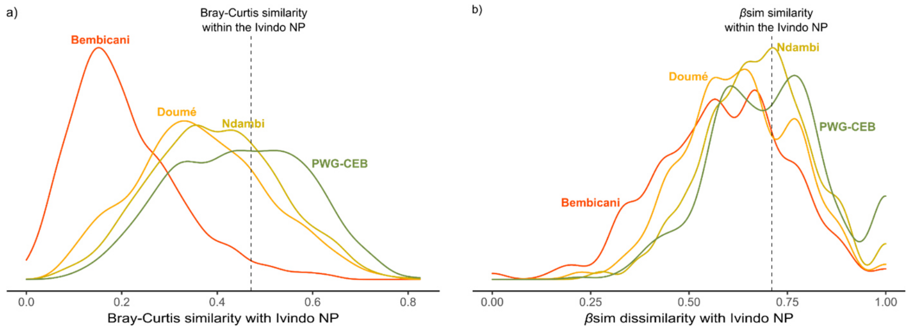
While forest accessibility is generally assumed to well proxy hunting pressure and has been related to depleted and highly altered mammal assemblages (see **Chapter 4** in the Dja area in Cameroon; Koerner *et al.* 2017 in north-eastern Gabon), our results confirmed that hunters do not roam their territory blindly and follow a wide network of hunting trails to move through the forest, conditioning a highly spatialized hunting pattern which differentiated from a halo of influence that simply radiates around the village (**Figure 5.1**, Froese *et al.* 2022; Van Vliet *et al.* 2010). The spatial arrangement of customary hunting territories is indeed not only dependent on the current location of the villages, but also a legacy of their ancestral location, in a context where many villages formerly scattered in the forest were moved along the main roads under the colonial administration (Vermeulen & Karsenty 2001). Spatial disparities in hunting pressure within the hunting territory also exist as a result of an heterogeneous distribution of micro-habitats preferred by hunters and no-take zones (Van Vliet *et al.* 2010, Mockrin *et al.* 2011), a context difficult to grasp without an in-depth knowledge of the history and hunting practices of each village.

Our results showed that hunter's space use distribution largely explained the compositional alteration of each CT. This stresses the relevance of this indice as a predictor of abundance and corroborates the results of previous studies in central Africa (Rist *et al.* 2009). This tendency, though less strong, was also apparent inside each hunting territory. Conversely, both accessibility indices (distance to the village center and to the nearest communication axis) did not perform well for explaining this compositional alteration, either between or within hunting territories. Despite the influence of current hunting pressure, we also found a significant effect of the site, that was even more important, the dissimilarity with the control being always greater for Bembicani, the most highly hunted village. This local effect may reflect the cumulative impact of many years of hunting, *i.e.*, the ghost of past hunting. Rist *et al.* (2009) also supported this hypothesis to explain the abundance responses exhibited by some primates to distance from the village center, but not to ongoing hunting. Beyond hunting history, environmental conditions such as forest types or the encroachment of rural areas on the surrounding forest matrix may also cause a differentiated response between villages, providing more suitable conditions for certain guilds such as rodents.

5 Conclusion

In this study, we implemented a dissimilarity-based approach to profile changes in the species composition of terrestrial mammal assemblages along a gradient of increasing pressure in the eastern tropical forests of Gabon, as well as to identify the main determinants of their alteration state. We showed that the current space use distribution of the hunters within the hunting territory is a much more effective predictor than classical accessibility indices based on euclidian distance to characterize the continuum of alteration mammal assemblages experienced along the studied gradient, but that other factors might also drive local differences such as habitat modification and past hunting regimes.

6 Appendix



Appendix A (a)The Bray-Curtis similarity (accounting for species abundance) and (b) the βsim similarity (accounting for species presence, Koleff *et al.* 2003) of each camera trap compared to each camera trap in the Ivindo National Park, *i.e.*, the compositional alteration, presented in the form of smoothed histograms.

6

General discussion

1 Major findings and research perspectives

In this thesis, I implemented a β-diversity approach to describe the composition and the distribution of mammal assemblages across central African forests, as well as to identify their determinants, both patterns and determinants being of increasing precision from **Chapter 2** to **Chapter 5**. An overview of the results, chapter by chapter, is presented in **Figure 6.1**.

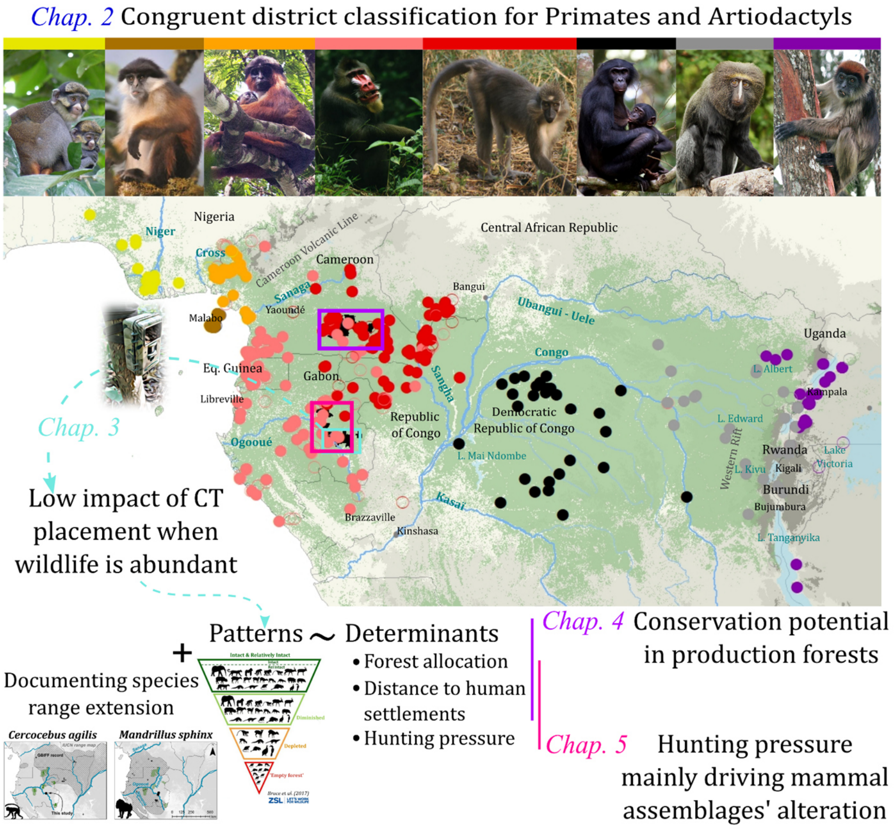


Figure 6.1 Schematic overview of thesis' results, chapter by chapter.

Using species lists from over 500 survey locations (presence/absence data), I first established a spatially congruent classification of mammal assemblages across the region, consisting of eight primate and six artiodactyl zoodistricts respectively (**Chapter 2**). Major rivers, *i.e.*, the Congo-Ubangui River system and the Cross and Sanga Rivers, proved to be of central importance in structuring the zoodistricts of both groups, with a secondary role of insularity and precipitations for primate assemblages. This classification goes beyond the coarse and hardly informative regionalizations produced in the past and fills an important knowledge gap in this particular data-deficient and understudied region (Gardner *et al.* 2009, Billand 2010, Gibson *et al.* 2011, Verbeeck *et al.* 2011, White *et al.* 2021**, Figure 6.2)**.

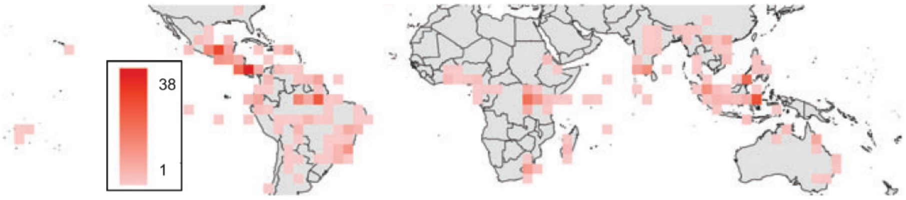


Figure 6.2 Research effort on biodiversity in human-modified tropical forest landscapes from Gardner *et al.* (2009) depicting significant differences in research attention between tropical regions with very few studies in central Africa.

More importantly, the districts' map complements regional conservation efforts of the last two decades by consolidating the landscape approaches adopted by international organizations with species assemblage data from field studies (USAID/CARPE landscapes, Key Landscape for Conservation of the EU's strategy to wildlife conservation in Africa, **Figure 6.3**). By combining maps of predicted defaunation (Benítez-López *et al.* 2019) and forest integrity across the region (Grantham *et al.* 2020), I showed that most mammalian districts face a high level of threats and contrasted levels of protection. I also unveiled large and relatively intact areas, especially in DRC, that could be used to expand the protected area network in line with international standards and targets – the 17% threshold of the Aichi Target 11 (UN CBD, 2010) and the "30 by 30" target pledged by numerous countries ahead of the COP 15. Such top-down identification must nevertheless be confirmed by ground data, both on the state of animal populations and on the socio-economic context prevailing in these potential areas of high conservation value as political instability (Davies *et al.* 2022) and the lack of local participation and compliance with conservation policies may hinder these initiatives (Andrade & Rhodes 2012). Compiling these sleeping data across the region has also pinpointed huge understudied areas, some of them holding high discovery potential (Moura & Jetz 2021). This calls for extensive funds and ground surveys (White *et al.* 2021) in these remote and enigmatic parts of central African forests such as the central Congo Basin peatland complex and the Congo-Kasaï interfluve region of DRC, where new species have still very recently been discovered (Hart *et al.* 2012). Another research perspective would consist in integrating local variations of species abundance into these clustering analyses, possibly better informing ecological responses and vulnerability to environmental and human disturbances as recently illustrated for tropical trees in central Africa (Réjou-Méchain *et al.* 2021). However, this refinement can only be achieved under the condition of strictly similar data collection protocols, a constraint, which if considered in our current dataset, would considerably reduce the number of surveys and thus the power of the analysis. Such standardization initiative has, however, proved to be a source of unique and reliable information allowing to track wildlife population trends and changing state in animal communities on sometimes very large scales (*e.g.*, the TEAM network, Ahumada *et al.* 2011, Rovero *et al.* 2020).

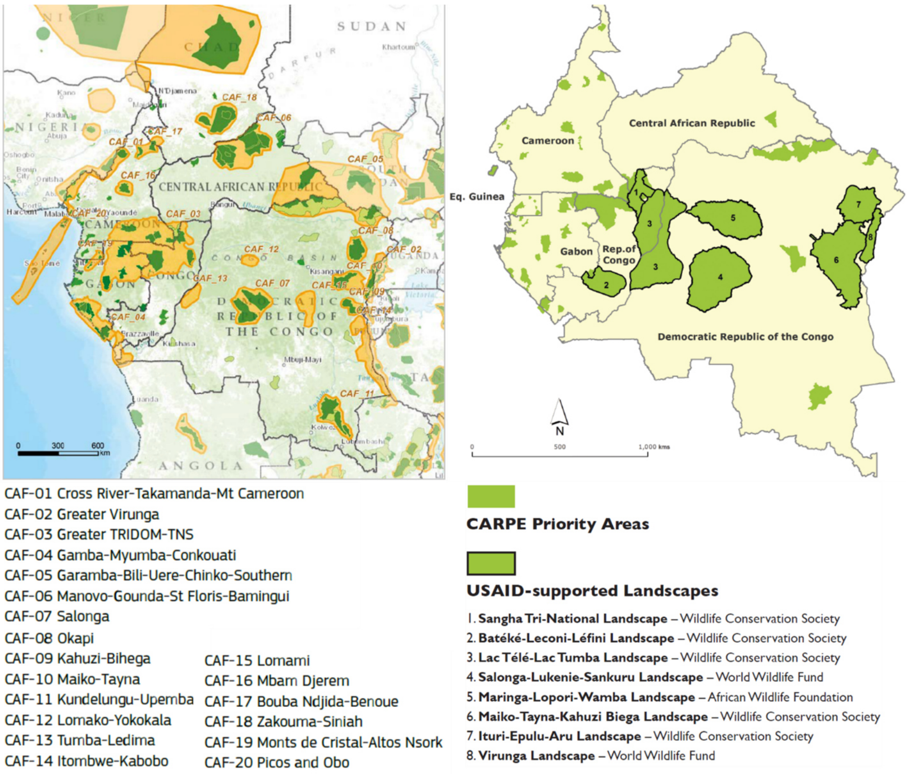


Figure 6.3 *Left panel*: the 20 Key Landscapes for Conservation of central Africa, as part of the European Union's conservation strategy plan presented in "Larger than Elephants" (European Comission 2017). *Right panel*: the Central Africa Regional Program for the Environment (CARPE) priority areas and the supported landscapes.

Having identified how mammalian assemblages differentiate and structure themselves at the regional scale, I sought to document the compositional changes these assemblages may undergo along gradients of human disturbance, ranging from protected areas and nearby production forests to more disturbed and highly hunted forests in the vicinity of villages.

In dense and structurally complex environments such as tropical forests, it has been amply demonstrated that camera traps are a particularly relevant tool for inventorying animal populations (Silveira *et al.* 2003, Srbek-Araujo & Chiarello 2005, Moore, Pine, *et al.* 2020, Zwerts *et al.* 2021). We therefore adopted this technique as the backbone survey method for assessing terrestrial mammalian assemblages in this thesis. Prior to any survey and to fill an important scientific knowledge gap, source of intense debate in the camera trapping literature, I initially tested the impact of camera trap placement on the remotely sensed mammal diversity of a particularly rich and well-preserved tropical forest of eastern Gabon (**Chapter 3**). From species richness to individual species detection rates and overall community composition, I evidenced little impact of camera trap placement strategy on diversity estimates. Though highly specific, methodological contributions such as the one presented in this thesis are essential for reaching consensual recommendations and optimizing survey protocols for secretive and elusive rainforest species communities using camera trap devices. Further investigations might consider how detectability can vary between species, sampling designs and individual camera traps, an important issue that can introduce unmodeled heterogeneity in detection probability across camera locations as revealed by recent field tests and simulations in temperate environments (Kays *et al.* 2021). The influence of home range and territorial behavior on the detectability of species would also deserve greater attention from the scientific community, as territory sharing is variable between as well as within species.

Using standardized camera trap surveys, I then confirmed that hunting largely determines the alteration state of ground-dwelling mammal communities of central African forests in the context of two distinct zoogeographic regions (southeastern Cameroon and eastern Gabon), well beyond other determinants such as forest management or habitat heterogeneity. I restated that selectively logged forests under responsible management with integrated wildlife management and strict control of forest access present high conservation value and provide an ecologically relevant alternative for forest management in the region, complementary to the established protected areas network.

In southeastern Cameroon (**Chapter 4**), we showed that the Dja faunal reserve held the most preserved terrestrial mammal assemblages along the surveyed gradient although some iconic species were not detected like the leopard and the forest elephant, even if they are known to occur in the reserve from other studies (Bruce *et al.* 2018). Rather than logging history, the conservation value of nearby production areas was largely determined by forest accessibility, a commonly used proxy deemed to capture the full range of hunting intensities at the landscape scale (Fragoso *et al.* 2016, Koerner *et al.* 2017, Roopsind *et al.* 2017, Beirne *et al.* 2019). Remote selectively logged areas were holding similar species richness and composition to that of protected areas, while community forests, which stretch close to the villages and at the interface between agricultural land and dense forest, exhibited deeply impaired mammal assemblages dominated by certain guilds of species such as rodents. The local extirpation of most large-bodied mammals in hunted forests nearby human settlements and the shift in species composition towards more resistant species is a common pattern that has been well documented across the region (*e.g.* in Nigeria, Effiom *et al.* 2013; in Gabon, (Beirne *et al.* 2019, Koerner *et al.* 2017); in Republic of Congo, Marrocoli *et al.* 2019; in Democratic Republic of Congo, Hart 2000).

A comparable gradient of human disturbance was also surveyed across eastern Gabon using a similar camera trap methodology in addition to a dedicated monitoring of offtake and hunter activities (**Chapter 5**). Once again, sustainably managed forests support a wide range of species, including rare and threatened taxa, and maintain nearly intact mammal assemblages, very similar to those found in the Ivindo National Park. On the other hand, the hunting territories, which can extend over several hundred square kilometers as confirmed by other survey results in the region (Delvingt 2001a, Vermeulen & Karsenty 2001, Fa *et al.* 2021, Froese *et al.* 2022), evidenced contrasted levels of alteration. Though habitat degradation by agricultural activities possibly impacts animal communities, the species turnover observed in hunting territories is largely explained by hunting regimes, and the possible combined influence of current and past harvesting practices (Abernethy *et al.* 2013). Highly hunted territories exhibit highly depleted mammalian assemblages with sensitive species being replaced by species more tolerant to hunting such as rodents (Van Vliet & Nasi 2008, Marrocoli *et al.* 2019). This compositional shift is also visible to some extent within each hunting territory, resulting in greater variability in species composition and highly localized alteration patterns as a consequence of the heterogeneous distribution of hunters and the resulting hunting pressure (Van Vliet *et al.* 2010, Froese *et al.* 2022).

Figure 6.4 Emblematic mammal species of central Africa from left to right: the common chimpanzee (*Pan troglodytes*), the bongo (*Tragelaphus eurycerus*), the forest elephant (*Loxodonta cyclotis*), the lowland gorilla (*Gorilla gorilla*), the giant pangolin (*Smutsia gigantea*), the okapi (*Okapia johnstoni*) and the mona monkey (*Cercopithecus mona*).

While survey data presented in this thesis seemed to confirm the buffer role production forests might play in landscape conservation strategy, especially in the periphery of protected areas, and the varying alteration levels within hunted village forests, it is worth remembering that ground camera trap surveys are restricted in their species coverage, only documenting the largest semi-terrestrial and terrestrial species, and thereby ignoring population trends of other groups of taxa. Coupling ground and canopy camera traps in joint protocols (Hongo *et al.* 2020) and using complementary surveys methods such as environmental- or insect-derived DNA (Rodgers *et al.* 2017, Gogarten *et al.* 2020), live traps (Mena *et al.* 2021) and acoustic devices (Wrege *et al.* 2017, Zwerts *et al.* 2021, 2022) might surely expand and refine our understanding of the whole mammal populations response to disturbance gradients (Whitworth *et al.* 2019). Furthermore, although comprising many emblematic species (**Figure 6.4**) that are particularly impacted by threats as diverse as poaching, overhunting, zoonotic risks, pet trade, and habitat degradation and loss, mammals still represent only a small fraction of the species diversity that inhabits the tropical forests of central Africa and therefore can only partially inform their structure and alteration state as not all taxonomic groups are equally affected by each type of disturbance (Gibson *et al.* 2011, Burivalova *et al.* 2014). Specific census methods for birds, bats and arthropods such as beetles or butterflies have already provided a bigger picture of differential, and sometimes idiosyncratic, responses to human disturbances, especially to logging and hunting activities (Bicknell & Peres 2010, Bicknell *et al.* 2014, 2015, Benítez-López *et al.* 2017 and in **Chapter 4**).

2 Beyond assemblages, species response to hunting

Following the results highlighted in **Chapter 4** and **Chapter 5**, I reasserted that bushmeat hunting more than any other factors determines the degree of alteration of large mammal assemblages across central African forests. Hunted forests surveyed in this thesis were typified by contrasting levels of alteration and a clear shift in species composition in the most degraded hunting territories which we formalized using a beta-diversity approach. Here, I would like to pave the way for a conceptual framework describing the differential response of species to hunting that lies behind this species turnover in order to discern which species are unlikely to withstand low and moderate harvesting pressure (hereafter referred to as “losers”) from those that can prosper or even increase in population size although hunted (hereafter referred to as “winners”). The so-called density compensation experienced by winners has been suggested to arise from interacting factors such as predator release, reduced competition for food resources within guilds as well as indirect influence of habitat modification (Fa & Brown 2009, Abernethy *et al.* 2013, Van Vliet *et al.* 2016). First documented for primate assemblages in neotropical forests (Peres & Dolman 2000), a similar process is potentially occurring also in hunted sites across central African forests, where large rodents seemed to particularly benefit from it (Effiom *et al.* 2013, Koerner *et al.* 2017, Van Vliet *et al.* 2017, Lhoest *et al.* 2020). Other species like the blue duiker (*Philantomba monticola*) are also suspected to be resistant to hunting as well (Van Vliet & Nasi 2008) but the lack of knowledge on their life-history traits (Van Vliet & Nasi 2019) and the large uncertainties around densities estimates make it difficult to accurately assess the sustainability of current harvesting levels (Van Vliet & Nasi 2008). Yet, identifying the loser and winner species of current hunting regimes is essential for designing sustainable harvesting practices in the near future and an essential step in maintaining productive forests around human settlements, a vital source of food and income in rural areas where employment activities non-detrimental to forest integrity are scarce.

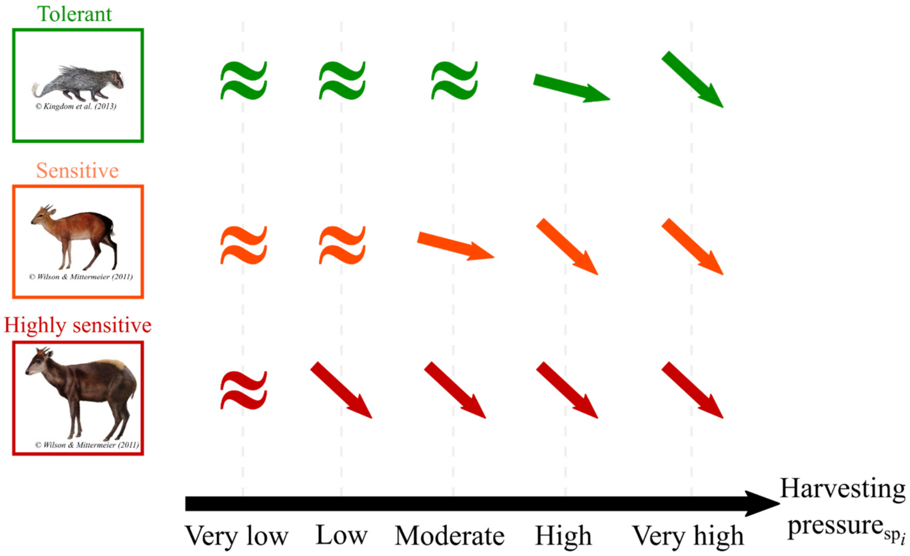


Figure 6.5 Distinguishing population trend of highly sensitive species (in red), sensitive species (in orange) and tolerant species (in green) to increasing species-specific harvesting pressure in single-species hunting context.

Depending on habitat requirements (*e.g.*, home range size, diet) and life history traits (*e.g.*, the rate and timing of reproduction, age of sexual maturity), species are expected to show a different response to hunting (**Figure 6.5**). Among hunted species, and based on accumulated evidence (Delvingt 2001b, Wright 2003, Fa & Brown 2009, Marrocoli *et al.* 2019, Lhoest *et al.* 2020), we recognize three possible cases: highly sensitive species to hunting, sensitive species and tolerant species. Of all hunted taxa, large mammals are facing the greatest threats (Poulsen *et al.* 2013, Ripple *et al.* 2016, Benítez-López *et al.* 2017). Usually present at low densities, they are quickly extirpated by hunters, and their long generation time and low population growth rate prevent quick recovery (Cardillo *et al.* 2005, Fa *et al.* 2005, Fa & Brown 2009, Mysterud 2011, Poulsen *et al.* 2011). Therefore, they seem to particularly fit the pattern of our "highly sensitive species" scenario, showing a systematic and quick decline in abundance even for low harvesting levels; their resistance threshold being easily overpassed, resulting ultimately in their local extirpation. Some species of small or medium size or with particularly high reproductive rate can be considered less sensitive to some extent ("sensitive species" in **Figure 6.5**). Such species display smaller and slower decreases in population size when harvesting levels stay moderate but drop rapidly when harvests soar. In contrast, other small-sized species can show resistance to hunting ("tolerant species" in **Figure 6.5**), exceeding their ability to resist only under very high harvesting levels. The key question here, essential for any species-based management strategy, is to understand which harvesting level exceeds the resistance threshold of each species.

The different species response to increasing harvesting pressure presented in **Figure 6.5** must be understood in the theoretical context of single-species hunting with no direct or indirect interspecific interactions (*e.g.*, predator-prey relationship, density compensation). Under real conditions, this situation rarely occurs as species interact and hunters usually target several prey species simultaneously (Rowcliffe *et al.* 2003). Understanding which species are the "losers" and "winners" in these highly dynamic and interconnected multi-prey systems remains however a challenge.

There are two ways to assess if a species loses or gains under certain harvesting regime. One is to track the species population size over time in a spatially defined area as species harvest increases. The other one involves a Space-for-Time substitution assuming different sites, each characterized by its own hunting regime, to be representative of different states in the response trajectory. Because ecological responses are typically long, especially when dealing with taxa such as large mammals, obtaining the entire chronosequence of species response to harvesting is hard to achieve and requires long-term and logistically challenging surveys. Space-for-Time study design is therefore generally preferred, resulting in the survey of a spatial gradient covering a part and preferably the whole range of hunting levels from remote, less disturbed protected forests, assumed to approach a reference state where species abundance is at environmental carrying capacity (K), up to heavily hunted and depleted forests near human settlements. This logic has long been applied in community ecology (Pickett 1989) as well as in studies investigating the evolution of game diversity along a forest degradation gradient (*e.g.*, Gillet *et al.* 2016) but has never been formalized and tested with empirical data.

I therefore propose a conceptual framework (**Figure 6.6**) to describe the evolution of species populations under a certain harvesting pressure regime, which for ease of understanding will correspond to a harvesting level considered as very high for the three types of species (*i.e.*, the final state in **Figure 6.5)**.

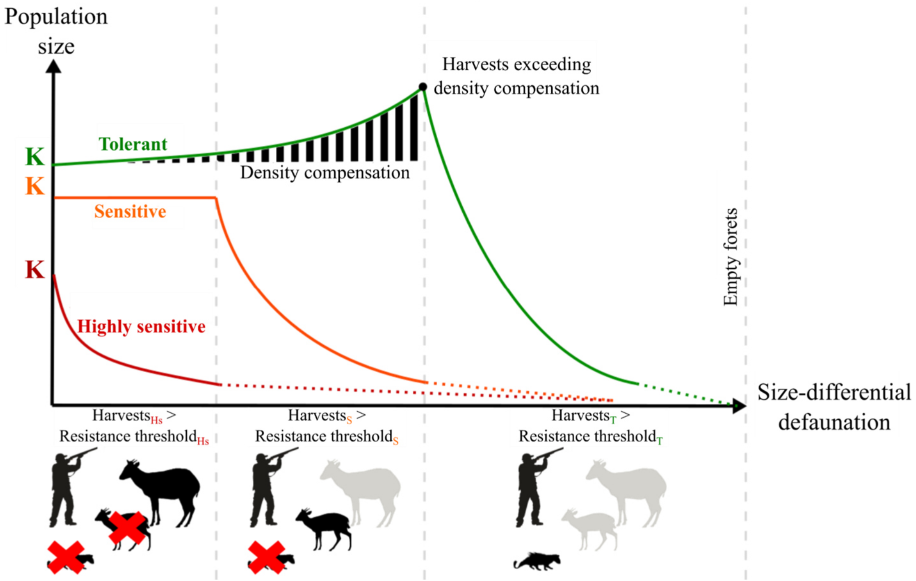


Figure 6.6 Size-differential defaunation and evolution of species population size experienced under very high harvesting pressure showing the differing response between each category of species (highly sensitive, sensitive and tolerant). As long as the larger species remain in the hunting area, the other species, crossed out in red here, are not preferentially targeted by hunters which hunt them opportunistically as they offer little benefit. They, however, become targeted when the abundance of the larger species is so reduced that they are no longer economically interesting to pursue, shaded in grey in the figure. K corresponds to carrying capacity of the species which can be surrogated by species abundance retrieved in control area without hunting, in a protected or remote areas for instance.

A first important consideration of this model is that hunters are theoretically assumed to follow the optimal foraging theory during their muti-species hunts, targeting the most profitable species, which are often the largest, to maximize their economic return. (Mithen 1988, FitzGibbon 1998, Sirén & Wilkie 2016, Wilkie *et al.* 2016). Although this theory does not address all the factors involved in hunters' decision-making process, it does provide insights for explaining the delayed response of some species to hunting induced by the size-based prey selection, the less profitable species being actively pursued once the more valuable species reach such a low level of abundance that it is no longer cost-effective for the hunter to actively pursue them (*i.e.*, opportunistic search).

A second point concerns the course of species population size under overharvesting scenario. It is commonly accepted to liken population growth in natural environment to a logistic model dynamic, depicting the highest growth rate of the population when the species population size reaches about half of the carrying capacity (K/2) (Salo *et al.* 2013, **Figure 6.7a,b**). Harvest can be part of such dynamic, the species population being at equilibrium only if harvests equal natural growth and at maximum sustained yield (MSY) when population density reaches half of the carrying capacity (**Figure**

6.7c). However, considering that the decline of hunted populations due to overharvesting (*i.e.*, when harvest exceed the natural growth rate) follows a similar trend remains to be proven. In the proposed framework (**Figure 6.6**), the curve translating the drop in species abundance remains purely theoretical and would merit simulation to better capture the biological reality of this response based on estimates of hunting territory size, species density as well as species productivity (number of offspring per time unit) and harvesting rates (number of individuals killed per time unit).

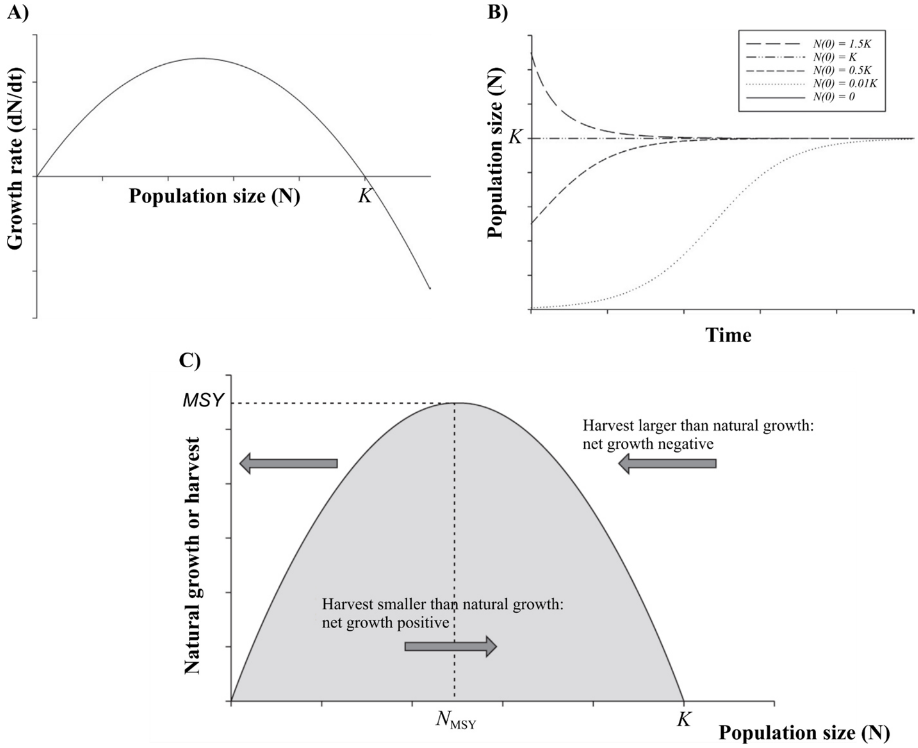


Figure 6.7 A) Relationship between population size and absolute growth rate, according to the logistic model. **B**) Logistic growth in time, with different sizes of the initial population. As long as the initial size is greater than zero, the population asymptotically approaches the carrying capacity, *K*. **C**) Population decrease if harvest rates exceed the equilibrium according to the logistic model. In contrast, if harvest rates are under the curve, the population grows. Figures and legends extracted from Salo *et al.* (2013).

Then, I confront the assumptions and framework presented above with the survey data collected in eastern Gabon and partly presented in **Chapter 5**. By sampling a gradient ranging from the remote and protected forests of the Ivindo National Park up to hunting territories with contrasted levels of hunting pressure, I could test the "winner/loser" theory following a Space-for-Time substitution. I used the species detection rates derived from the camera trap grids to surrogate species population size.

Relying on detection rates to assess species population state has important caveats since other factors apart from the true abundance might influence species detectability. This issue has already been largely discussed in **Chapter 3**, but here I assume that the number of sampling units was large enough (> 29 camera traps in each study sites) and that the survey protocol was well standardized between study sites to be able to rely solely on detection rates to surrogate population size.

Applying our conceptual framework of species response to hunting has evidenced that most species are "highly sensitive" to hunting, either directly or indirectly, and can be identified as losers in current hunting regimes (**Figure 6.8**). Furthermore, it seems that most species have already passed their resistance threshold along the surveyed gradient, with a drastic drop in their detection rates in hunted forests. The tipping point seems to occur for most species between the harvesting pressure levels found at Ndambi and at Doumé, although it would require long-term monitoring data to verify this hypothesis. This is the case for instance for the Peter's duiker (*Cephalophus callipygus*), which has a much lower detection rate in hunted areas than in the control, especially in Bembicani. The blue duiker (*Philantomba monticola*), the most frequently hunted species in the studied systems, seems to withstand a certain degree of exploitation before a rapid decline takes place which contradicts the usual claims about this species. However, as for most tropical species, estimating a sustainable harvesting rate for this species is a challenge as information on its life-history traits is particularly deficient (Van Vliet & Nasi 2019). Blue duikers densities, whether in undisturbed or hunted areas, remains unclear, particularly as estimates differ greatly among survey methods and areas (Kamgaing *et al.* 2018, Barychka *et al.* 2020, Poulain 2021). In Ndambi, 150 individuals were killed in a hunting territory that covers 268 km², which corresponds to a harvesting rate of 0.6 blue duiker km^{-2} yr^{-1}. This rate rises to 2.4 blue duikers km^{-2} yr^{-1}in Doumé and 4 blue duikers km^{-2} yr^{-1} in Bembicani. Because the offtake sampling was not exhaustive, these rates should be regarded as minimum values reflecting a sizeable general trend. According to the most conservative estimates (*i.e.*, 5 individuals per km², Kamgaing *et al.* 2018), hunting territories would roughly contain 1300, 1200 and 650 blue duikers in Ndambi, Doumé and Bembicani respectively, but this number could be multiplied by 5, 10 or even 20 according to other estimates derived from nocturnal direct observations and camera traps (Julve Larrubia 2005, Kamgaing *et al.* 2018, Amin *et al.* 2021, Poulain 2021). The uncertainties surrounding these measurements have led scientists to develop modelling approaches to guide harvesting policies that account for natural heterogeneity in hunting effort and in game populations dynamic (Van Vliet *et al.* 2010, Barychka *et al.* 2020). Optimal harvesting rate, *i.e.*, sustaining a survival probability superior to 0.90 over 100 years, has been estimated up to 2 blue duikers km^{-2} yr^{-1}, whereas it increases to 4-5 blue duikers km^{-2} yr^{-1} when hunting yields are maximized, at the expense of the survival probability (Barychka *et al.* 2020). The low availability of life-history traits and the large disparities in the few existing estimates explain the remaining uncertainties around the potential response of game populations (Van Vliet *et al.* 2010, Barychka *et al.* 2020). However, these results seem to confirm that the blue duiker offtake levels observed in Ndambi and Doumé, which are much lower than the actual reported offtakes across central Africa (14-25 blue duikers km^{-2}

yr^{-1}, Barychka *et al.* 2020), may be sustainable in light of the small differences in detection rates obtained between these villages and the control area (**Figure 6.8**).

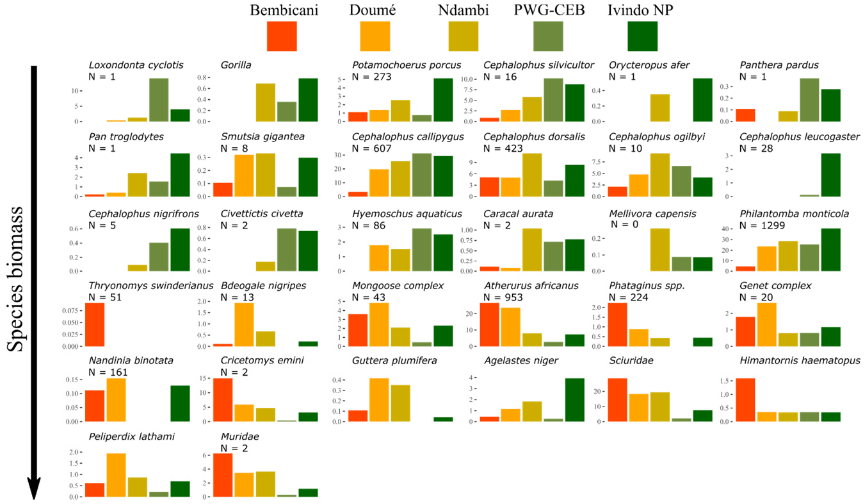


Figure 6.8 Species detection rates (Number of independent detections over 100 camera.days) from villages (Bembicani in red, Doumé in orange and Ndambi in khaki) to control areas (PWG-CEB logged forest in light green and Ivindo National Park in dark green) displayed by decreasing biomass. For each species, the total number (N) of hunted individuals reported by hunters during the one-year survey is also displayed.

Some species appeared relatively 'tolerant' to hunting including the African brush-tailed porcupine, but also, more surprisingly the bay duiker (*Cephalophus dorsalis*) and the small pangolin species complex. The bay duiker is a widely consumed species in central Africa (Van Vliet *et al.* 2012, Batumike *et al.* 2021) which has been shown to be less resistant to hunting than the blue duiker, either using long-term monitoring data or through modelling (Van Vliet *et al.* 2007, Barychka *et al.* 2020). Here, detection rates of the bay duiker in hunted sites did not substantially deviate from the one recorded in the Ivindo NP and offtake rates were also lower than the ones registered in other bushmeat-harvesting systems, exceeding optimal yields only in Bembicani village (Barychka *et al.* 2020). With no knowledge of past offtake and potential changes in hunting behavior, and with little information on the carrying capacity of the surrounding forests, this situation may reflect a long-term hunter/prey trade-off through source-sink dynamic or obscure an incoming collapse in bay duiker populations. Like many other species in central Africa, pangolins are elusive species, notoriously difficult to census and limited knowledge is available about their biology (Willcox *et al.* 2019), yet they are particularly threatened owing to international trafficking of their scales (Mambeya *et al.* 2018). Here, we did not evidence a dedicated hunting strategy towards pangolins species, most of the catches being handpicked during recorded hunting trips, although some trafficking requests were informally reported by hunters. As already shown in Gabon and Cameroon (Laurance *et al.* 2006, Lhoest *et al.* 2020), pangolins, but also rodents, seem to easily thrive closer to human settlements. Here we also showed that the detection rates of these species are much higher when compared to the control area, especially as offtake increases. One might assume varying detectability between villages and control areas, but all CT were placed in a standardized way, far enough in the hunting territories to avoid old fallow lands. Apart from the natural variability of food resources (*e.g.*, more abundance of ants for myrmecophagous species such as pangolins) which is difficult to quantify, it can be suggested that the alteration of the community due to current and past hunting may have released or partially reduced predation pressure and competition for resources allowing density compensation for these species.

The red river hog (*Potamochoerus porcus*) is one of the most appreciated species by bushmeat consumers in the studied region and therefore has a high market value, making it a favorite target for hunters. This gregarious species, whose herds can number several dozen individuals, seems however to be becoming rarer in the most hunted village areas. This decrease is even more marked when comparing to the detection rates found in the Ivindo NP and could be even more accentuated if the average number of individuals per group was considered. Empirically, we often credited this suidae species of high reproductive rates but very little data on their population dynamics exists.

Alongside widely hunted species, there is a whole range of species that also seem to be impacted more indirectly by hunting. This is the case for small carnivores such as genets and mongooses, which surprisingly have higher detection rates in village areas than in control areas despite some capture by hunters. The trend seems to be reversed for carnivores with a higher biomass, the civet (*Civettictis civetta*), the golden cat (*Caracal aurata*) and the leopard (*Panthera pardus*). One could argue that small carnivore species may benefit from the increased abundance of small rodents in hunted forests. Yet, the low detection rate of carnivores as a whole makes the interpretation of these trends risky, especially for large home range species for which the chosen sampling design may not be appropriate.

Beyond these factors, other confounding variables associated with the consensus required by multi-species monitoring, such as the trap density (grid size) or the sampling effort, might have impacted detectability (Hofmeester *et al.* 2019). The selected CT spacing may be optimal for certain target species but not for others (Foster & Harmsen 2012). Here, we followed the grid size recommended by the TEAM Network, which represents a compromise for ground-dwelling vertebrates in the tropics. However, highly mobile species with large home ranges (*e.g.*, forest elephants) and occurring sometimes at low densities (*e.g.*, leopards) might be missed or underestimated with such a design.

Following the trend analysis of detection rates, we can see that the hunting pressure, both present and past, in the surveyed hunted territories has had a strong impact on most game species. This trend is even more pronounced in Bembicani, where harvesting levels have resulted in drastic drops for many species. To avoid the spread of the empty forest syndrome (Wilkie *et al.* 2011), even in sparsely populated areas such as eastern Gabon, only a concerted hunting management by and for rural communities could yield sustainable game exploitation.

As in other hunting management systems like in Europe, simple monitoring tools and indicators should be provided to locally inform stakeholders regarding management decisions and hunting regulation. By cross-referencing hunting bag data and camera traps, I could highlight which species seem to poorly withstand harvesting pressure and need dedicated regulation strategy in the context of three specific hunted territories in eastern Gabon. Such expert-based intensive monitoring seems, however, unrealistic to implement in a long-run routine and over extended spatial scales, given the time required to collect and analyze the data. Upcoming studies should focus on the design of simplified management indices, weighing up the cost-benefit ratio of reducing the quality and quantity of data while maintaining the indices' ability to accurately detect changes in game populations and hunting patterns (Danielsen *et al.* 2009). Cost-effective and sufficiently powerful indices have already been achieved from locally based monitoring schemes (Rist *et al.* 2010) and it is reasonable to assume that a combination of well-chosen, low-detail indices could be as informative as fine-grained indices. The offtake composition, notably the proportion of rodent catches, and easy-to-record catch per unit effort (CPUE) indices could be potential diagnostic standards for assessing and monitoring the degree of alteration of hunted forests. Relying on CPUE indices for monitoring species-specific populations trend is however more challenging. Indeed, in multi-species hunting systems, the only way to ensure a proportional relationship between hunting productivity indices such as CPUE and species population size is to assess the real hunting effort experienced by the monitored species. If one relies on the measurement of overall hunting effort (*e.g.*, the number of active hunting hours), variations of the index can be triggered both by a change in species population size or by a change in hunting practice (*i.e.*, the hunter allows more prospective effort to find the species during a hunt of similar duration). Only actively hunted species can therefore be monitored through such CPUE ~ abundance relationship approach.

The temporal and spatial organization of hunting should also be a central element in community-led hunting projects. A quota-based harvest is undoubtedly the easiest hunting policy to implement in regulated hunting systems. Theoretically, proportional harvests (*i.e.*, a constant percentage of the population) largely outperform the quota-based approach as it is a more conservative strategy, adaptable to natural variation in game populations, and has proven to be much more robust in models for species with poorly known life history traits (Barychka *et al.* 2020). However, adjusting these proportions each hunting season requires a great deal of effort to monitor the species game stock, which largely prevents this model from thriving. Identifying the presence of areas neglected by hunters, *i.e.*, no-take zones, and critically analyzing their size and distribution should also be considered as they are assumed to play a key role in the dispersal dynamic and the protection of resident game populations (Mockrin & Redford 2011).

Finally, in view of the many unknowns, both in terms of the biological characteristics of the game species and the behavior of hunters and their hunting practices, adaptive management remains a necessary step prior to the implementation of any strict regulatory policy, which will inevitably involve many restrictions on current hunting practices, will have to be negotiated on a community-by-community basis, and will involve external control by the state administration. The adaptive nature of this type of management is both a strength and a weakness, as changes in management actions need to be clearly and explicitly reported to stakeholders who may become weary of repeated changes.

3 Other research outputs and practical tools

Practical outputs and tools of particular interest for forest managers and more broadly to wildlife ecologists can be derived from the results of this thesis.

In the regional analysis (**Chapter 2**), I listed the potential pool of species each zooregion may host, an easy benchmark to gauge the level of defaunation in newly sampled sites by highlighting undetected species as well as a target to reach in restoration and rewilding initiatives. Beyond species lists, I also proposed a way to describe and quantify the level of defaunation using refine species composition data (**Chapter 5**). By integrating control areas in the survey protocol, the dissimilarity-based approach I employed allows for a comprehensive overview of the alteration state of mammal assemblages and, as part of adaptive management, can be directly used by wildlife practitioners and managers to assess how the species assemblage and its state of alteration vary over space and time, pinpointing for example the priority territories to restore as well as the impact of management measures such as hunting regulations over time.

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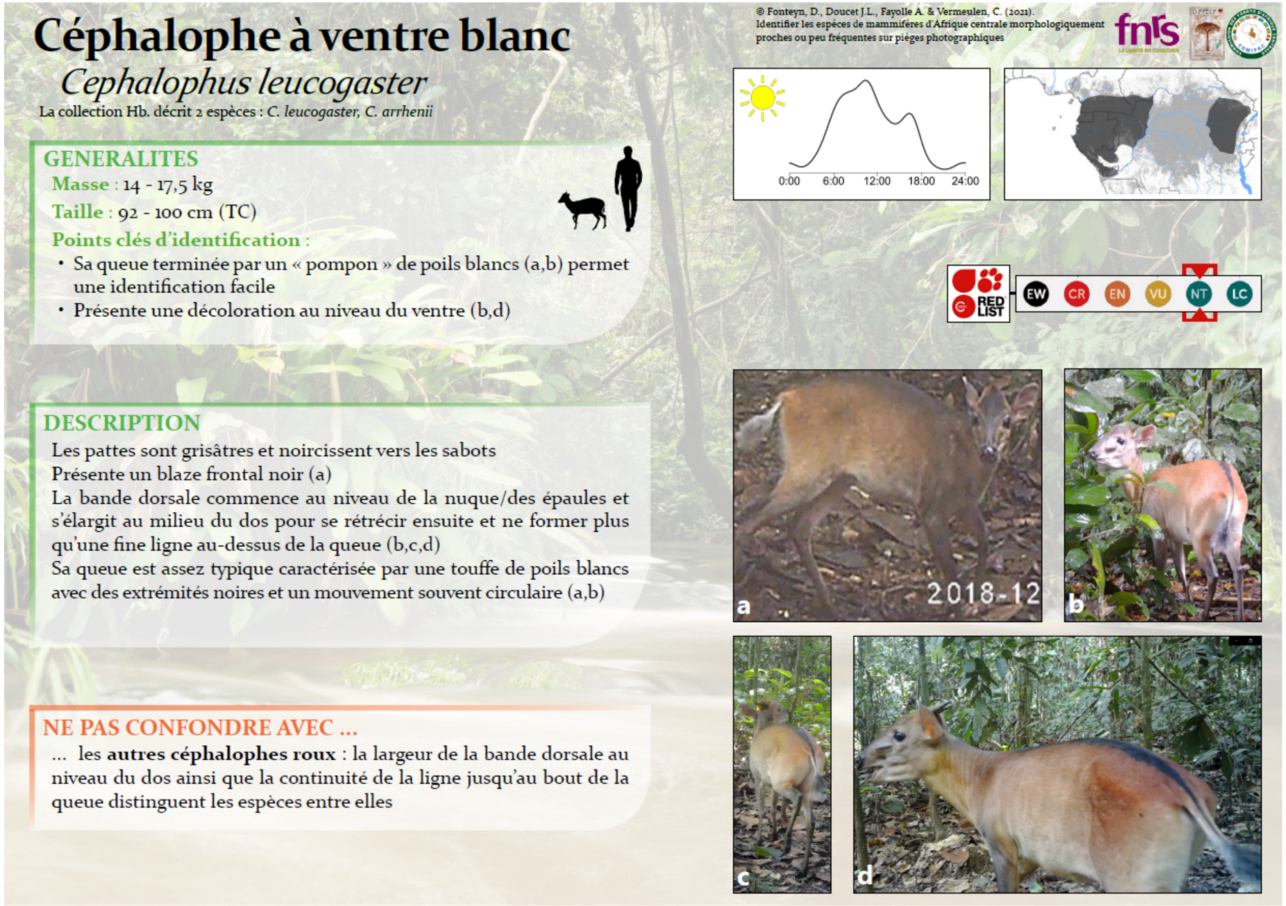
ÉLABORATION ET MISE EN ŒUVRE D'UN PLAN DE GESTION DE LA FAUNE - GUIDE TECHNIQUE À DESTINATION DES GESTIONNAIRES DES FORÊTS DE PRODUCTION D'AFRIQUE CENTRALE

Barbara Haurez, Davy Fonteyn, Sarah Toint, Charles Bracke, Jean-Louis Doucet, Kasso Daïnou, Stéphane Kéhou, Cédric Vermeulen

Figure 6.9 Structure of the web interface FAUNEFAC and front page of the technical guide dedicated to wildlife management plan in logging concession.

Understanding the zoogeographic context and the alteration state of a surveyed forest is important, but having guidance on how to survey forest animal population is equally crucial. In addition to the thorough methodological contribution undertook in **Chapter 3**, we have also produced a methodological toolbox dedicated to camera trap surveys, called FAUNEFAC (https://www.gembloux.ulg.ac.be/faunefac/) to help all kinds of practitioners and managers working with wildlife-related issues. This didactic web interface comprises different sections (**Figure 6.9**) that aim to: (1) describe the technology of camera traps and guide managers to the appropriate equipment; (2) establish the sampling protocol based on a GIS tutorial; (3) calibrate the cost and manpower of camera trap installation and recovery missions; (4) describe the camera trap installation in the field step by step using user-friendly drawings to assist practitioners; (5) manage the data transfer and archiving; (6) identify the species through a video gallery containing 35 species and a practical guide listing the most difficult species to identify including 19 freely available identification sheets (https://orbi.uliege.be/handle/2268/263954, **Figure 6.10**). Finally, a Shiny application to help automatic processing of camera trap data is also proposed (7) to facilitate data reporting in accordance with forest certification standards.



Céphalophe à ventre blanc

Cephalophus leucogaster

La collection Hb. décrit 2 espèces : *C. leucogaster, C. arrhenii*

© Fonteyn, D., Doucet J.L., Fayolle A. & Vermeulen, C. (2021).
Identifier les espèces de mammifères d'Afrique centrale morphologiquement proches ou peu fréquentes sur pièges photographiques

GENERALITES

Masse : 14 - 17,5 kg

Taille : 92 - 100 cm (TC)

Points clés d'identification :

- Sa queue terminée par un « pompon » de poils blancs (a,b) permet une identification facile
- Présente une décoloration au niveau du ventre (b,d)

DESCRIPTION

Les pattes sont grisâtres et noircissent vers les sabots
Présente un blaze frontal noir (a)
La bande dorsale commence au niveau de la nuque/des épaules et s'élargit au milieu du dos pour se rétrécir ensuite et ne former plus qu'une fine ligne au-dessus de la queue (b,c,d)
Sa queue est assez typique caractérisée par une touffe de poils blancs avec des extrémités noires et un mouvement souvent circulaire (a,b)

NE PAS CONFONDRE AVEC …

… les **autres céphalophes roux** : la largeur de la bande dorsale au niveau du dos ainsi que la continuité de la ligne jusqu'au bout de la queue distinguent les espèces entre elles

Figure 6.10 An example of an identification sheet for the white-bellied duiker (*Cephalophus leucogaster*) from the FAUNEFAC toolbox.

This toolkit is part of a larger work that I co-authored that consists of a review of inventory methods and wildlife management measures in order to identify the most relevant practices in the context of forest concessions. This includes a review of the grey and scientific literature, as well as diagnostics, based on interviews, for different concessions that are certified or in the process of certification. The management measures identified were transcribed into an operational technical guide made available to forest operators (https://orbi.uliege.be/handle/2268/253115). A model wildlife management plan was also integrated into this guide.

Finally, I also showed the ancillary but critical information you can derived from camera trap surveys. The extensive camera trapping surveys implemented in this thesis has indeed allowed to document range extension for two primate species across eastern Gabon, the agile mangabey (*Cercocebus agilis*) and the mandrill (*Mandrillus sphinx*) (**Figure 6.11**). Although these areas were not considered understudied in our regional analysis, these unexpected detections show that a great deal of basic ecological information remains to be understood for most species in central Africa, even for species that are widely hunted and significantly contribute to the bushmeat sector in the sub-region such as the blue duiker (Van Vliet & Nasi 2019). These records have been published in African Journal of Ecology (IF=0.92) (**Annex**, and at https://doi.org/10.1111/aje.13061).

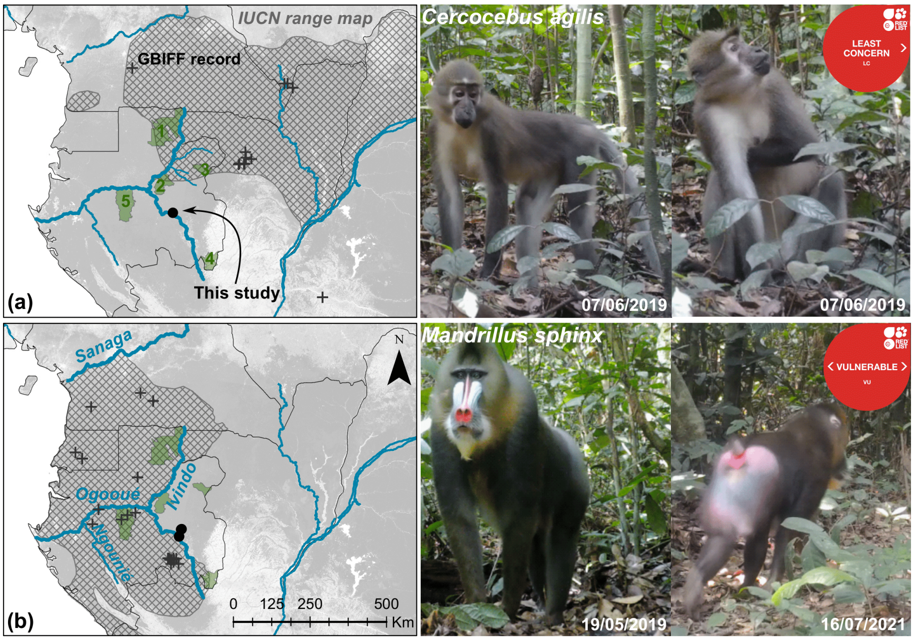


Figure 6.11 New camera trap records for *Cercocebus agilis* (a) and *Mandrillus sphinx* (b) in eastern Gabon. The background map corresponds to tree cover (Hansen *et al.* 2013). Species range (cross-hatched) from the International Union for Conservation of Nature (IUCN) and occurrence (cross) from the Global Biodiversity Information Facility (GBIF) repository (occurrence dataset: https://doi.org/10.15468/dl.d47asp, https://doi.org/10.15468/dl.p5qf62 accessed via GBIF.org on 2021-03-31) are also shown. The Minkébé National Park (NP) (1), Ivindo NP (2), Mwagna NP (3), Batéké Plateau NP (4) and Lopé NP (5) are highlighted in green.

4 Conclusion

This thesis provided a unique opportunity to explore the main determinants of the distribution of mammalian assemblages within the world's second largest tropical forest. From a regional biogeographic classification that showed the severe lack of conservation and knowledge in some areas of the region to an assessment of the degradation of mammalian assemblages along gradients of human pressure, this thesis highlighted the rising threats that central African forest mammals face.

Central African forests are expected to face enormous environmental and human-driven changes in the coming years (Abernethy *et al.* 2016, Réjou-Méchain *et al.* 2021), putting their long-term conservation at risk. The results of this thesis nevertheless reassert that conservation of large mammalian fauna is still possible outside of strictly protected areas, as long as the human population growth in the region has not reached the predicted peaks. I reasserted that selectively logged forests under responsible management provide an ecologically relevant alternative for forest resource management in the region, particularly in the periphery of protected areas where their buffering role can be crucial in maintaining large tracts of poorly disturbed forest. As long as integrated wildlife management is safeguarded and coupled with a strict control of forest access, these production forests have been shown to retain nearly intact mammal assemblages and high conservation value, a trend also confirmed in other tropical regions (Putz *et al.* 2012). The expansion of this management model into national forestry policies is even being considered in some countries of the region such as Gabon. Support and capacity building for forest operators, whose core expertise remains purely related to timber extraction and trade, must be considered if such national strategies are to be implemented and the tools and approaches developed in this thesis can provide such guidance.

While such practical outputs of my thesis can improve the capacity building of wildlife manager teams and enhance the conservation efforts conceded by forest permit holders, it is also necessary to provide tools rural communities can easily handle to reduce the impact of their hunting practices on the most sensitive species. Moving towards a sustainable use model of game species in these currently neglected forests represents a priority action that may be hampered by the lack of knowledge of even the most commonly hunted species. Experimental models of adaptive community-based hunting management such as those supported under the SWM Program, coupled with extensive ecological and demographic studies of the principal hunted species, could provide new perspectives for species conservation in the region. Yet, the “conservation by sustainable use” model, which could potentially be aligned with international standards such as those of the OECMs, still needs to remain a complementary strategy to maintaining and enhancing protection within the current protected area network.

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Annex

Received: 5 April 2022 | Revised: 4 July 2022 | Accepted: 30 August 2022
DOI: 10.1111/aje.13061

RESEARCH NOTE

African Journal of Ecology WILEY

Range extension of the agile mangabey (*Cercocebus agilis*) and of the mandrill (*Mandrillus sphinx*) in eastern Gabon evidenced by camera traps

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Funding information
Commission des Forêts d'Afrique Centrale; Fonds pour la Formation à la Recherche dans l'Industrie et dans l'Agriculture; Programme de Promotion de l'Exploitation Certifiée des Forêts

Keywords: agile mangabey, camera trap, mandrill, range extension

1 | INTRODUCTION

The agile mangabey (*Cercocebus agilis*) is a medium-sized, omnivorous Old World monkey from the large *Cercopithecidae* family that inhabits the dense humid tropical forests of central Africa. Although mainly arboreal, the species is often found on the ground in groups of highly variable size, from 10 to 50 individuals to over 200 individuals (Devreese et al., 2013; Quris, 1975). The geographical distribution of the species is vast, ranging from western Cameroon to the Central African Republic and north-eastern Democratic Republic of Congo, but its limits are unclear, particularly for its westernmost isolated populations (Maisels et al., 2020). In Gabon, the species is believed to occur only in the north-eastern part of the country, in the Minkébé National Park (NP) area and possibly in the Ivindo NP and Mwagna NP (Maisels et al., 2020; see IUCN range map in Figure 1). Shah (2003, 2013) reports personal communications of experienced scientists in this region but the only documented observations date back more than 50 years along several tributaries of the Ivindo River, on its left bank specifically (Quris, 1975). Since then, *C. agilis* has no longer been reported in the region (Maisels et al., 2020).

The mandrill (*Mandrillus sphinx*) also belongs to the *Cercopithecidae* family. It is an omnivorous semi-terrestrial forest-dwelling species that live in large groups characterised by a multi-levelled social structure where females generally occupy a central position (Abernethy et al., 2002; Bret et al., 2013; Brockmeyer et al., 2015). The mandrill hordes can reach spectacular numbers, up to over 800 individuals, especially in areas where they are not hunted (Abernethy et al., 2002). Social organisation within mandrill hordes is still debated, particularly concerning the potential seasonal presence of males in the cohesive group of females and offspring (Abernethy et al., 2002; Brockmeyer et al., 2015). In contrast to the agile mangabey, a strong sexual dimorphism exists, distinguishing the larger and more coloured males, especially on the snout and the genitalia, from the smaller, greyish-brown females (Abernethy & White, 2013; Zinner & Gadsby, 2013). Mandrill distribution extends along western central Africa, south of the Sanaga River, in Cameroon, mainland Equatorial Guinea and Gabon, and down to

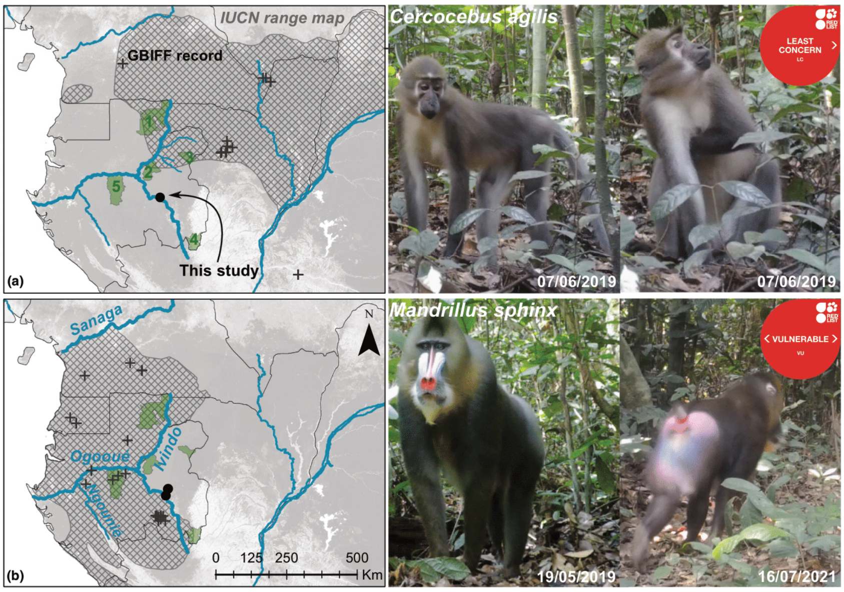

FIGURE 1 New camera trap records for *Cercocebus agilis* (a) and *Mandrillus sphinx* (b) in eastern Gabon. The background map corresponds to the tree cover (Hansen et al., 2013). Species range (cross-hatched) from the International Union for Conservation of nature (IUCN) and occurrences (cross) from the global biodiversity information facility (GBIF) repository (occurrence dataset https://doi.org/10.15468/dl.d47asp, https://doi.org/10.15468/dl.p5qf62 accessed via GBIF.org on 2021-03-31) are also shown. The Minkébé National Park (NP) (1), Ivindo NP (2), Mwagna NP (3), Batéké Plateau NP (4) and Lopé NP (5) are highlighted in green. Species videos and coordinates of the record localities are available in Video S1.

the Mayombe forest and the Massif du Chaillu in the Republic of Congo (Figure 1). In Gabon, its distribution is limited to the east by the Ogooué and Ivindo Rivers, although its presence has been documented on two occasions in north-western Congo (Abernethy & Maisels, 2019; Zinner & Gadsby, 2013).

In this note, we present new observations of these two primate species in eastern Gabon evidenced by camera traps (Figure 1). These records suggest a potential range extension of *Cercocebus agilis* by 100 km to the south and reassert its presence in Gabon, which had not been documented for 50 years. Mandrill detections were also obtained for the first time on the right bank of the Ogooué in this area, in 2019 and in 2021, supporting the potential long-term establishment of at least one and possibly a few individuals on this side of the river.

2 | METHODS

Species records were obtained from extensive camera trap surveys conducted in 2019 (May–June) and in 2021 (June–October) in different hunting territories around Lastoursville as part of the ongoing EU Sustainable Wildlife Management programme (https://www.swm-programme.info/; Figure 1). The study area is essentially covered by wet evergreen forest (Fayolle et al., 2014; Réjou-Méchain et al., 2021) and the mean annual rainfall and temperature reach, respectively, 1702 mm and 24.4°C (Fick & Hijmans, 2017). The camera traps (Bolyguard SG 2060X, Boly, Victoriaville, QC, Canada) were installed in the forest undergrowth at 30–50 cm height, oriented towards a small wildlife trail or trail crossing according to our early work in the area (Fonteyn et al., 2021). When triggered, camera traps recorded high-quality 5-s videos with the minimum reset time (0.8 s).

3 | RESULTS AND DISCUSSION

In June 2019, we detected the agile mangabey on five consecutive videos (available in Video S1), all included in the same detection event (i.e. detected within 30 min). The date, time and exact location of the camera trap records are available in Table S1. The recorded location was 2.5 km north of the Ogooué River (location 1, Figure 2), consistent with the habitat preferences of the species for seasonally-flooded

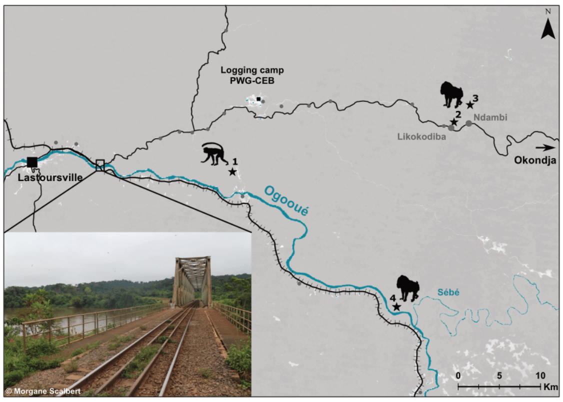

FIGURE 2 Map of the study area and exact locations of the camera trap records of *Cercocebus agilis* (location 1) and *Mandrillus sphinx* (locations 2, 3, 4) shown on a background map of tree cover (Hansen et al., 2013). The road and railway networks are also displayed in black. A photograph of the railway bridge crossing the Ogooué River is also shown in inset.

and swamp forests and riparian habitats (Gautier-Hion et al., 1999; Shah, 2013; Zinner, 2013). The detection was made <50 m from an old logging road of the Precious Woods Gabon—Compagnie Equatoriale des Bois (PWG-CEB) logging company, as the area was logged 5 years prior to the camera trap survey. Unfortunately, the sex of the individual could not be determined in the videos. Prior records of the species in Gabon date back to 1974, when Quris (1975) reported sightings of several bands in the riparian environments of the Njadié, Liboui and Mounianghi rivers, which all flow into the Ivindo River (see Figure 1) more than 130 km north from our study area, suggesting an extension of the species range of more than 100 km southwards.

Two mandrill detections were recorded in May 2019 (locations 2, 3, Figure 2 and in Supporting information) along the Lastoursville-Okondja road (R19) close to the villages of Likokodiba and Ndambi. A third detection was recorded 23 km south in July 2021 (location 4, Figure 2). These three detection events (with a total of four videos) evidenced the presence of at least one and potentially two adult males in the area. Natural crossing of a river as wide as the Ogooué remains a difficult hypothesis to consider, and where mandrill populations do occur on both banks in other sites, two genetically distinct populations have been found, suggesting that the Ogooué River potentially forms an important barrier to gene flow (Telfer et al., 2003). Even smaller rivers, such as the Ngounié (Figure 1), seem to be an insurmountable obstacle for mandrills (C. Orbell, pers. obs.). Hedwig et al. (2018), however, reported a camera trap record of a young male mandrill, east of the Ogooué River, in the Batéké Plateau NP, 150 km south of our recorded location. The authors suggested that this individual is a transient emigrant who may have either crossed the river or bypassed it south of the park at its source. In our case, the two scenarios may be considered. Crossing of the Ogooué River could have occurred via the road or railway bridges on the outskirts of Lastoursville (Figure 2), the railway bridge being probably the less frequented of the two communication routes. Solitary males leaving their cohesive horde and moving independently have already been documented in wild populations in the Lopé NP (Abernethy et al., 2002; White, 2007), as has the immigration of non-natal adult and sub-adult males in a released mandrill population in the Lékédi Park (Brockmeyer et al., 2015). We may thus assume that such exploratory behaviour could have ended in a crossing of the Ogooué River, though mandrills are reputed to usually avoid open habitats in undisturbed areas, especially adult males (Brockmeyer et al., 2015; White, 2007; White et al., 2010). Another possible scenario might also be the release of an individual by humans. Indeed, sometimes hunters temporarily keep young orphan monkeys as pets (Calattini et al., 2007). Once adolescents, these potentially aggressive individuals may escape or be released. In both cases, the different observations made 3 years apart indicate the ability of this (or these) individual(s) to survive in this area. If this event is not too rare and occurred again, with the arrival of additional congeners, especially mature females, it could lead to the establishment of a population in the forest area managed by the PWG-CEB logging company.

ACKNOWLEDGEMENTS

We are grateful to the National Centre for Scientific and Technical Research for providing Cirad and its partners the research authorization (n°AR002/I 9/MESRS/CENAREST/CG/CST/SCAR) on Gabonese territory. We are also grateful to the EU Sustainable Wildlife Management Programme Project staff in Gabon—particularly Samuel PEREIRA DIAS—for providing technical support. Acknowledgements are also due to the many students who implemented the camera trap surveys in 2019 and in 2021, especially Mexan YIA OKANABENE, Robin HORION and Jeff OSSELE. We also wish to thank the PWG-CEB company for providing access to the study area.

FUNDING INFORMATION

Davy Fonteyn benefitted from a FRIA grant of the Fonds de la Recherche Scientifique (FNRS) in Belgium and also received support from the 'Programme de Promotion de l'Exploitation Certifiée des Forêts' (PPECF) (contract C132) and the 'Commission des Forêts

d'Afrique Centrale' (COMIFAC) through the project 'De l'Inventaire au Plan de Gestion de la Faune, développement d'outils pour rencontrer les exigences des référentiels de certification' (IPGF).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Species videos and coordinates of the record localities are available in Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Fonteyn, D., Fayolle, A., Orbell, C., Malignat, R., Cornélis, D., Vanthomme, H., Vigneron, P., & Vermeulen, C. (2022). Range extension of the agile mangabey (*Cercocebus agilis*) and of the mandrill (*Mandrillus sphinx*) in eastern Gabon evidenced by camera traps. *African Journal of Ecology*, *00*, 1–4. https://doi.org/10.1111/aje.13061