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ABSTRACT

We tackle the potential impact of bushmeat markets (BM) and traditional medicine markets (TMM) on the functional diversity of mammalian communities in southern Benin, West Africa. A hybrid approach combining direct observations, DNA-typing and questionnaires allowed us to identify 94 species-level taxa across 11 mammalian orders, the greatest ever reported numbers for African wildlife markets. TMM sold species of high conservation concern or regulated by international conventions and sourced among all the taxonomic orders and bioclimatic zones of the country. BM were taxonomically and functionally 100% nested within TMM. However, functional richness was high in both markets, impacting nine diet specializations and five ecological functions, which included seed dispersion (frugivores, folivores and omnivores), prey regulation (carnivores and invertivores), browsing (folivores), grazing (omnivores) and fertilization (nectarivores). TMM likely jeopardized the regulatory, structural and production functions of the sourced ecosystems as they sold species with the greatest body weights and generation lengths, and smallest litter sizes, including large herbivores and keystone predators. BM, despite their restricted range, sourced among a non-selective taxonomic and functional spectrum and as such, also represent a significant threat to ecosystem functioning in southern Benin. The functional database that we provide can serve as a starting point to pursue the quantification of functional diversity in African mammals and further investigate the impact of wildlife markets on ecosystem functioning in tropical Africa. Overall, long-term surveys of the two types of wildlife markets are needed to accurately quantify the threat they constitute to mammalian biodiversity and the sustainability of ecosystem services.

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1. Introduction

Unsustainable wildlife hunting for bushmeat consumption and trade is one of the major threats to biodiversity conservation in the tropics (Cardoso et al., 2021). Although humans have been hunting in the West and Central African tropical forests for millennia, hunting for bushmeat has become unsustainable because of (1) increasing demand from a growing human population and lack of affordable alternative protein sources, (2) more efficient hunting and trading networks due to facilitated access to wildlife areas and markets, (3) high provisioning by hunters due to global poverty in rural areas and lack of alternative livelihoods in these areas, and (4) poor governance, state corruption and weak law enforcement (Kümpel et al., 2010; Matseketsa et al., 2022). The bushmeat trade in tropical Africa was estimated to affect approximately 500 species, especially mammals (Redmond et al., 2006). Extraction volumes reached about 4.9 M tons per year and were estimated highly unsustainable (Fa et al., 2002). In central Africa, where bushmeat may account for up to 80% of the animal protein consumed by rural communities (Pearce, 2005), the bushmeat markets (BM) constitute an important economy, generating 393 million US dollars per year in DR Congo alone (Valimahamed et al., 2017).

In western Africa, wildlife trade for traditional medicine –taking place at traditional medicine markets (TMM)– is an alternative trade to the bushmeat that fills traditional and cultural functions. Contrary to BM, TMM are entirely dedicated to religious and medicinal practices and sell live animals, skulls, skins and dried body parts that can stay for long periods on the stalls (Zanvo et al., 2021). Such type of wildlife trade is also expected to have a deleterious impact on biodiversity (Alves and Rosa, 2007; D'Cruze et al., 2020; Williams et al., 2013), especially since TMM target various protected species and can have a large trade network extending to foreign countries (Djagoun et al., 2013; Nikolaus, 2011). However, in comparison to BM, the global impact on biodiversity and monetary value that TMM represent remain largely unexplored.

Thus, wildlife –and more specifically mammals– in tropical Africa is threatened by two types of wildlife trade. The relative contributions of BM and TMM to hunting pressure and the connections that may link the two co-existing markets have rarely been investigated (Buij et al., 2016). Beyond the strict number of species and their volumes (taxonomic richness and biomass), one way of assessing the potential impact of human activities on biodiversity and ecosystems is to quantify trends in the diversity of functional traits, namely functional diversity (FD) (Cantera et al., 2022; Su et al., 2021). Predicting the long-term influence of wildlife trade on the FD of ecosystems remains challenging, but a few studies from the tropical forests have already demonstrated that reduced mammalian densities could lead to significant ecosystem changes and cascading effects along the food chain (Tagg et al., 2020). Because most ecosystem processes are driven by the combined effects of diverse functional groups (e.g., seed dispersers, prey regulators, grazers, etc.; Osuri et al., 2020), wildlife trade activities in western Africa, which are generally supplied by non-selective hunting (Newing, 2001), have the potential to negatively impact the FD of forest ecosystems (Tagg et al., 2020). Moreover, studying functional traits such as reproductive parameters could allow assessing more finely the sustainability of wildlife trade, depending on the species targeted and help support management decisions to mitigate the deleterious impact of the trade in wildlife.

The global objective of our study was to tackle the issue of two types of wildlife trades in western Africa through the prism of their potential impact on the FD of natural ecosystems, as measured from the hunted mammalian communities. Our specific objectives were to (i) establish a comprehensive list of the mammalian species sold in bushmeat and traditional medicine markets in southern Benin and discuss their regional conservation status, and (ii) assess the functional diversity represented by the mammalian communities sold in the two different markets to question the potential impact of wildlife trade on the ecosystems of the subregion. Finally, we discuss the conservation implications of our findings for mammalian species and ecosystems in western Africa and propose research perspectives that could improve the survey and management of the wildlife trade in southern Benin.

2. Material and methods

2.1. Study area

Benin is subdivided into three bioclimatic zones following a South-North gradient of desiccation: the Guinean zone (from the coast −6°25' N- to 7°30' N), the Sudano-Guinean zone (7°30' N - 9°45' N) and the Sudanian zone (9°45' N - 12°30 N'). The study was conducted across southern Benin (Fig. 1), where bushmeat and traditional medicine markets are predominant relative to the northern part of the country (Djagoun et al., 2013). The study area is nested within the Dahomey Gap, a region characterized by severely fragmented, patchily distributed forests, caused by the superimposed effects of long-term anthropogenic activities and drier environmental conditions (Alohou et al., 2017; Salzmann and Hoelzmann, 2005). The Lama Forest (LF) is the largest protected forest area (4777 ha) in southern Benin. Two types of wildlife markets are found scattered outside of the protected area, namely bushmeat and traditional medicine, and these markets are primarily or partially supplied by hunting activities that occur within or in the vicinity of the LF (Djagoun et al., 2013; Djagoun et al., 2022). The bushmeat markets (BM) represent the sites where fresh and smoked specimens of wildlife are sold for food consumption in a quick turnaround time, and are established along main roads. On the other hand, traditional medicine markets (TMM) –the most abundant market type in southern Benin– sell dry specimens often treated with chemical products for medicinal and cultural purposes with a longer turnaround time (Zanvo et al., 2021). They are generally integrated into regular market places.

2.3. Species identification

We used a hybrid approach combining direct observations (morphological identification), DNA-typing and questionnaires to

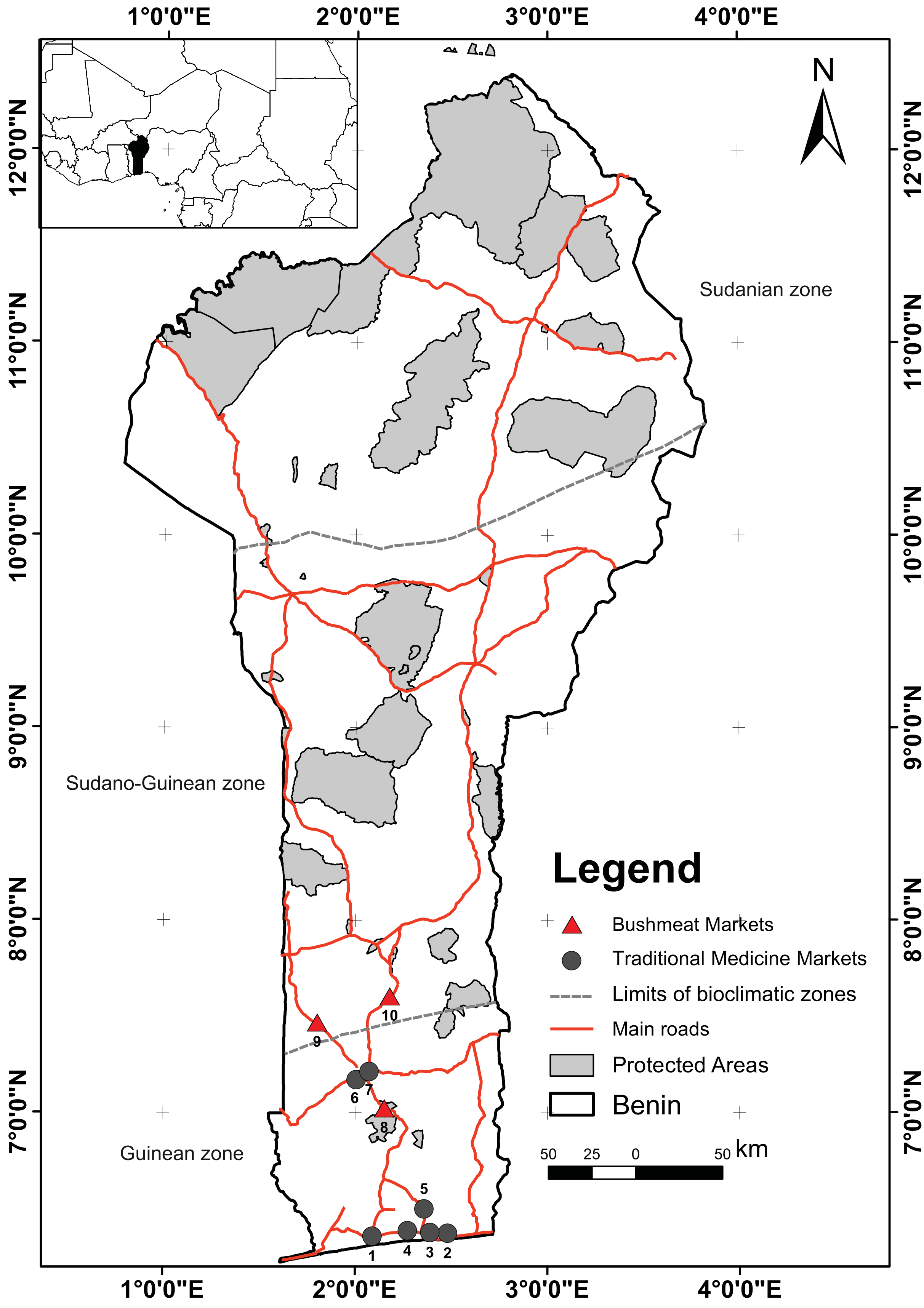

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Fig. 1. Distribution of the two types of wildlife markets surveyed across southern Benin. Traditional medicine markets: 1- Zobè ; 2- Dantokpa; 3- Vèdoko; 4- Godomey; 5- Calavi; 6- Gbèdagba; 7- Avogbannan. Bushmeat markets: 8- T è gon (at the vicinity of the Lama Forest); 9- Sèto; 10- Hounkpogon.

identify the species sold in the wildlife markets. Taxonomy and English common names followed the IUCN Red List of Threatened Species (https://www.iucnredlist.org/), whereas common names in *Fon* –the dominant ethnic group– were also recorded (see below).

2.3.1. Morphological identification from direct observations crossed with questionnaires

Given that many specimens sold in TMM are highly processed and carved, accurate taxonomic morphological identification can prove challenging. To improve species identification, we first conducted focus groups including 5–8 individuals in three large TMM from Cotonou (Abomey-Calavi, Dantokpa and Godomey; one focus group per market) where we recorded the local names of the species as listed in the Red List for Benin (Neuenschwander et al., 2011) and the Biodiversity Atlas of Benin (Sinsin and Kampmann, 2010). We then used this knowledge to implement the survey in the TMM, by setting up individual interviews where we would go through all the mammalian species listed in our *Fon-latin* names' table using a customized identification guide combining photos from internet and pictures from Kingdon (2015). Only the species actually present on the stalls of the interviewees were considered (Table 1 SI). In BM, the morphological identification of the carcasses was preliminary based on Kingdon (2015) and cross-checked with information provided by traders and hunters. Whenever possible, pictures of the specimens were taken in TMM and BM as digital vouchers to confirm species identification. Taxonomy followed that of the IUCN Red List of Threatened Species (hereafter, $IUCN_{RL}$).

2.3.2. Molecular identification

We collected 194 genetic samples of mammals in nine TMM and three BM from southern Benin (Fig. 1, Table 2 SI). Among those, three samples came from dry heads of "leopard" (*Panthera pardus*) and "wild dog" (*Lycaon pictus*) sold in TMM (Fig. 2). All the samples were stored in 95% EtOH before laboratory processing.

Genomic DNA extraction of the 111 fresh samples –mostly– collected from the BM was done with the NucleoSpin® Tissue Kit (MACHEREY–NAGEL, Hoerdt, France), following manufacturer's recommendations. Final elution step was repeated twice in 50 µl BE to maximize DNA yield and concentration. Genomic DNA was extracted from the 83 smoked tissue and dry skin samples collected from TMM in a degraded DNA-dedicated room using a modified CTAB procedure (Gaubert & Zenatello, 2009). Final resuspension was done in 100 µl RNAse-free water.

DNA-typing relied on the amplification and sequencing of four mitochondrial genes, as detailed in Gaubert et al. (2015), including cytochrome *b* (cyt *b*; 402 bp), cytochrome oxydase I (COX1; 658 bp) and the ribosomal subunits 12 S (361–394 bp) and 16 S (482–528 bp). Amplification and sequencing procedures together with post-processing validation of the nucleotide sequences are detailed in Appendix 1.

The taxonomic identity of the sampled carcasses was achieved through a platform dedicated to the DNA-typing of African forest bushmeat, DNAbushmeat (http://mbb.univ-montp2.fr/MBB/DNAbushmeat), where we searched for best matching sequence homologues. When percentages of similarity with the query were < 95% (cyt *b* and COX1) or < 97% (12 S and 16 S), we considered that the species was not represented in DNAbushmeat (Gaubert et al., 2015). In this case, we used Blastn (https://blast.ncbi.nlm.nih.gov/) to search the NCBI nucleotide database, optimizing for highly similar sequences (megablast; Ng and Pang, 2010). We applied the decision pipeline of Gaubert et al. (2015): Fig. 2), which relies on the taxonomic distribution of the best hit values, distance tree view of the query, assessment of NCBI database coverage and expert validation, as well as similarity threshold values, to taxonomically assign the sequences. Final molecular identification was determined on a 4-gene consensus-based approach, by choosing the most inclusive phylogenetic level (i.e. species or higher taxonomic categories) relative to the level of conflicting taxonomic identifications observed among the four genes (Gaubert et al., 2015).

2.4. Database

A database was established for all the species identified using both morphological and molecular approaches (Table 1 SI). We reported both global ($IUCN_{RL}$) and local (Red List for Benin; RLB) conservation status. The presence or absence of a species in Benin was cross-checked between the two references. Bioclimatic zone coverage was inferred from the $IUCN_{RL}$ range maps. Ecological and functional information on habitat, diet, litter size per year and mean body weight was extracted from Kingdon (2015) and the Mammals of Africa (Kingdon et al., 2013). Knowledge gaps were completed by taxon-specific search on Google and Google Scholar (see Table 1 SI). Generation length was extracted from the $IUCN_{RL}$. Missing data were completed by using the $IUCN_{RL}$ generation length calculator (https://nc.iucnredlist.org/redlist/content/attachment_files/Generation_Length_Workbook.xls). For this purpose, data on longevity and fertility were extracted from the sources referred to above, and completed using specialized databases (https://genomics.senescence.info/species/index.html; https://www.demogr.mpg.de/longevityrecords/0203.htm). Survival rate was arbitrarily fixed to 0.5 when unknown (most of the cases).

2.5. Descriptive statistical analyses

Descriptive statistics for comparing the biodiversity spectrum, conservation status and functional diversity between the species sold in TMM and BM were run in XLSAT 2021.4.1 (Addinsoft, 2022). We used the nonparametric Mann–Whitney U test (McKnight and

Najab, 2010) to test differences in distributions between TMM and BM for taxonomic richness, global and local conservation status, habitats, diet and functional categories. None of the differences proved significant (data not shown).

2.6. Functional diversity analyses

We used five traits related to ecology and reproductive biology to analyze the functional diversity of the species sold in wildlife markets: habitat preference, diet, mean litter size per year, generation length and mean weight (Table 1 SI). Functional diversity was quantified using the functional richness index (FRic) and the functional dispersion index (FDis) (see Laliberté and Legendre, 2010; Villéger et al., 2008). These two complementary FD indices rely on a multidimensional Euclidean space where the axes are functional traits (or factorial axes from a Principal Coordinates Analysis (PcoA) computed on these traits) along which species are placed according to their trait values (Mason and Mouillot, 2013). The FRic index measures the volume of functional space occupied by a given species assemblage by calculating the convex hull volume, defined by the species at the vertices of the functional space, that encompasses the entire trait space filled by all species of this assemblage (Villéger et al., 2008). The FDis ranging from 0 to 1 quantifies the mean distance of species to the centroid of the functional space, and consequently measures how species are functionally dissimilar within the functional space. It is worth noting that the FDis is unaffected by species richness (Laliberté and Legendre, 2010) which allows comparing species pools with different number of species. To calculate these two indices, we first computed the pairwise functional distances between species using the Gower dissimilarity index to build the functional space. This distance allows mixing different types of variables, which is the case in our study. Then, a PCoA was performed using this distance matrix to build a

Fig. 2. Dry heads of "leopard" (top) and "wild dog" (bottom) sold in the traditional medicine markets from southern Benin. DNA-typing showed that these artifacts were from domestic dogs (skull and skin). From top-left to bottom-right: [leopard] frontal view, occlusal view, [wild dog] frontal view, lateral view. White scale bar = 2 cm.

Table 1
List of the 94 mammalian species present in traditional medicine markets and bushmeat markets from southern Benin, together with their conservation status.

Name in *Fon*	Expert ID	English name	Order	TMM	BM	CITES	$IUCN_{RL}$	RLB
Adjidja-kouzin	*Atelerix albiventris*	Four-toed hedgehog	Eulipotyphla	present	present		LC	NE
Agbanlin	*Tragelaphus scriptus*	Bushbuck	Cetartiodactyla	present	present		LC	NT
Aluilui	*Nandinia binotata*	African palm civet	Carnivora	present	present		LC	VU
Aluilui	*Genetta pardina / "maculata"*	Large-spotted genets	Carnivora	present	present		LC	DD
Atchou-glinzin	*Cricetomys sp1*	–	Rodentia	present	present		–	–
Atchou-glinzin	*Cricetomys gambianus*	Gambian rat	Rodentia	present	present		LC	NE
Awassagbé	*Xerus erythropus*	Striped ground squirrel	Rodentia	present	present		LC	NE
Awi	***Felis silvestris catus***	**Domestic cat**	**Carnivora**	**present**	**present**		–	–
Awi-gbéton	*Felis silvestris*	Wild cat	Carnivora	present	present	II	LC	VU
Azui	*Lepus victoriae*	African savanna hare	Glires	present	present		LC	NE
Azui	***Oryctolagus cuniculus***	**European rabbit**	**Glires**	**present**	**present**		–	–
Djè	*Herpestes ichneumon*	Egyptian mongoose	Carnivora	present	present		LC	LC
Don	*Protoxerus stangeri*	Forest giant squirrel	Rodentia	present	present		LC	NE
Gbédja	*Arvicanthis niloticus*	African grass rat	Rodentia	present	present		LC	NE
Gbéglouza	*Potamochoerus porcus*	Red river hog	Cetartiodactyla	present	present		LC	VU
Gbozoun	*Philantomba walteri*	Walter's duiker	Cetartiodactyla	present	present		DD	NT
Hâ-zounvoun	*Dendrohyrax interfluvialis*	Benin tree hyrax	Hyracoidea	present	present		NE	EN
Hô	*Thryonomys swinderianus*	Greater cane rat	Rodentia	present	present		LC	NE
Houin	*Kobus sp.*	–	Cetartiodactyla	present	present		–	–
Klan-vè	*Erythrocebus patas*	Patas monkey	Primates	present	present	II	NT	LC
Lihoui	*Phataginus tricuspis*	White-bellied pangolin	Pholidota	present	present	I	EN	VU
T è -zouizon	*Sylvicapra grimmia*	Common duiker	Cetartiodactyla	present	present		LC	LC
Toloua	*Tragelaphus spekii*	Sitatunga	Cetartiodactyla	present	present		LC	EN
Wô	*Crossarchus platycephalus*	Flat-headed cusimance	Carnivora	present	present		LC	LC
Zin-wi	*Cercopithecus mona*	Mona monkey	Primates	present	present	II	NT	VU
Adjagbè	*Aonyx capensis*	African clawless otter	Carnivora	present		II	NT	EN
Adjagbè	*Hydrictis maculicollis*	Spotted-necked otter	Carnivora	present		II	NT	VU
Adjidja-hanon	*Hystrix cristata*	Crested porcupine	Rodentia	present			LC	NE
Adjinankou	*Loxodonta africana*	African savanna elephant	Proboscidea	present		I	EN	–
Aduoinglénon	*Dendromus melanotis*	Gray climbing mouse	Rodentia	present			LC	DD
Afiankou	*Hippotragus equinus*	Roan antelope	Cetartiodactyla	present			LC	VU
Afiankou	*Damaliscus lunatus*	Topi	Cetartiodactyla	present			LC	EN
Afin	*Steatomys jacksoni*	Jackson's fat mouse	Rodentia	present			DD	NE
Afluiflui	*Nycteris grandis*	Large slit-faced bat	Chiroptera	present			LC	NE
Afluiflui	*Myonycteris leptodon*	Sierra Leone collared fruit bat	Chiroptera	present			LC	NE
Afluiflui	*Megaloglossus woermanni*	Woermann's bat	Chiroptera	present			LC	VU
Agbogbéton	*Syncerus caffer*	Buffalo	Cetartiodactyla	present			NT	NT
Aluilui	*Genetta genetta*	Small-spotted genet	Carnivora	present			LC	LC
Aluilui	*Genetta thierryi*	Hausa genet	Carnivora	present			LC	DD
Ato	*Papio anubis*	Olive baboon	Primates	present		II	LC	LC
Awlégbè	*Lemniscomys zebra*	Heuglin's striped grass mouse	Rodentia	present			LC	NE
Awlégbè	*Lophuromys sikapusi*	Rusty-bellied brush-furred rat	Rodentia	present			LC	NE
Awlégbè	*Lemniscomys striatus*	Typical striped grass mouse	Rodentia	present			LC	NE
Dègbo	*Hippopotamus amphibius*	Hippopotamus	Cetartiodactyla	present		II	VU	VU
Démontchi	*Galagoides demidoff*	Demidoff's dwarf galago	Primates	present		II	LC	DD
Démontchi	*Galago senegalensis*	Northern lesser galago	Primates	present		II	LC	LC
Djè	*Vulpes pallida*	Pale fox	Carnivora	present			LC	VU
Djè	*Ichneumia albicauda*	White-tailed mongoose	Carnivora	present			LC	NT
Djê	*Atilax paludinosus*	Marsh mongoose	Carnivora	present			LC	VU
Don	*Heliosciurus sp.*	Sun squirrel	Rodentia	present			–	–
Donké ïkeï	*Funisciurus sp.*	African striped squirrel	Rodentia	present			–	–
Donké ïkeï	*Funisciurus substriatus*	Kintampo rope squirrel	Rodentia	present			DD	EN
Ganhouéganhoué	*Epomops franqueti*	Franquet's epauletted fruit bat	Chiroptera	present			LC	VU
Ganhouéganhoué	*Epomophorus gambianus*	Gambian epauletted fruit bat	Chiroptera	present			LC	NE
Ganhouéganhoué	*Nanonycteris veldkampi*	Veldkamp's dwarf epauletted fruit bat	Chiroptera	present			LC	NE
Gbédja	*Arvicanthis rufinus*	Guinean arvicanthis	Rodentia	present			LC	NE
Gbéglouza	*Phacochoerus africanus*	Common warthog	Cetartiodactyla	present			LC	NT
Gbévoun	*Canis adustus*	Side-striped jackal	Carnivora	present			LC	NT
Glanlan	*Caracal caracal*	Caracal	Carnivora	present		I	LC	NT
Glanlan	*Leptailurus serval*	Serval	Carnivora	present		II	LC	VU
Guidi soton	*Procavia capensis*	Rock hyrax	Hyracoidea	present			LC	VU

(*continued on next page*)

Table 1 (*continued*)

Name in *Fon*	Expert ID	English name	Order	TMM	BM	CITES	$IUCN_{RL}$	RLB
Héto-ha	*Malacomys longipes*	Big-eared swamp rat	Rodentia	present			LC	–
Hla	*Lycaon pictus*	African wild dog	Carnivora	present			EN	CR
Hla-y é ké	*Crocuta crocuta*	Spotted hyaena	Carnivora	present			LC	NT
Hôdjidja	*Atherurus africanus*	African brush-tailed porcupine	Rodentia	present			LC	NT
Houin	*Redunca arundinum*	Southern reedbuck	Cetartiodactyla	present			LC	–
Houin	*Kobus ellipsiprymnus*	Waterbuck	Cetartiodactyla	present			LC	VU
Kinikini	*Panthera leo*	Lion	Carnivora	present		I	VU	VU
Kpo	*Acinonyx jubatus*	Cheetah	Carnivora	present		I	VU	EN
Kpo	*Panthera pardus*	Leopard	Carnivora	present		I	VU	VU
Lâ	*Alcelaphus buselaphus*	Hartebeest	Cetartiodactyla	present			LC	VU
Loki	*Gorilla gorilla*	Western gorilla	Primates	present		I	CR	–
Loumon	*Orycteropus afer*	Aardvark	Tubulidentata	present			LC	EN
Sin	*Civettictis civetta*	African civet	Carnivora	present		[III - Ethiopia]	LC	VU
Sin	*Ictonyx striatus*	Zorilla	Carnivora	present			LC	VU
Tchoukou	***Canis lupus familiaris***	**Domestic dog**	**Carnivora**	**present**			–	–
T è -ahé	*Ourebia ourebi*	Oribi	Cetartiodactyla	present			LC	VU
T è -ahé	*Eudorcas rufifrons*	Red-fronted gazelle	Cetartiodactyla	present			VU	EN
T è -akli	*Cephalophus niger*	Black duiker	Cetartiodactyla	present			LC	EN
T è -vè	*Cephalophus rufilatus*	Red-flanked duiker	Cetartiodactyla	present			LC	NT
Toké	*Eidolon helvum*	African straw-coloured fruit bat	Chiroptera	present			NT	NE
Toké	*Rousettus aegyptiacus*	Egyptian fruit bat	Chiroptera	present			LC	VU
Toké -hé	*Hypsignathus monstrosus*	Hammer-headed fruit bat	Chiroptera	present			LC	VU
Toklan	*Cercocebus torquatus*	Red-capped mangabey	Primates	present		II	EN	EX
Toklan	*Colobus vellerosus*	White-thighed colobus	Primates	present		II	CR	EN
Ton	*Crocidura olivieri*	Olivier's shrew	Eulipotyphla	present			LC	NE
Wô	*Mungos gambianus*	Gambian mongoose	Carnivora	present			LC	NT
Wô / Ratel	*Mellivora capensis*	Honey badger	Carnivora	present			LC	VU
Wô-kuikui	*Herpestes sanguineus*	Common slender mongoose	Carnivora	present			LC	NT
Zin-abawé	*Chlorocebus tantalus*	Tantalus monkey	Primates	present		II	LC	LC
Zinblawawè	*Anomalurus derbianus*	Lord Derby's scaly-tailed squirrel	Rodentia	present			LC	EN
Zinblawawè	*Anomalurus sp.*	Scaly-tailed squirrel	Rodentia	present			–	–
Zinka-ka	*Cercopithecus erythrogaster*	Red-bellied monkey	Primates	present		II	EN	CR
Zin-tchihé	*Procolobus verus*	Olive colobus	Primates	present		II	VU	EN

Taxonomy follows the IUCN Red List of Threatened Species. Domestic species are given in bold.
TMM = traditional medicine markets. BM = bushmeat markets. $IUCN_{RL}$ = IUCN Red List of Threatened Species. RLB = Red List of Benin.

multidimensional functional space (Legendre and Legendre, 2012). According to the mSD metric (Maire et al., 2015), which quantifies the quality of the functional space, we kept the first five axes of the PCoA accounting for about 70% of the total inertia. The *mFD* package was used in R (https://cran.r-project.org/web/packages/mFD/index.html) to compute the functional diversity metrics (Magneville et al., 2022).

3. Results

A total of 94 mammalian species were morphologically identified from the TMM stalls, while 25 species –all shared with TMM– were observed in BM (Table 1). Orders with the most number of species found in the TMM and BM combined were the Carnivora (33 spp.), Rodentia (26 spp.) and Cetartiodactyla (24 spp.) (Fig. 1 SI). One carnivoran (*Genetta* spp.) and one rodent (*Cricetomys* sp.) could not be identified to the species level because of acknowledged cryptic diversity.

DNA-typing targeted 42 species-level taxa (as assigned through morphological identification) collected both in TMM and BM (Table 2 SI). Overall, 113 out of 194 (58.2%) of the carcasses had their identification corrected or improved (i.e., reaching higher taxonomic accuracy; Table 2 SI). In total, 173 (89.2%) samples were identified to the species level, accounting for a final number of 43 DNA-based species distributed into Carnivora (12), Rodentia (9), Cetartiodactyla (9), Primates (4), Eulipotyphla (1), Glires (2), Hyracoidea (2), Tubulidentata (1), Pholidota (1), and Proboscidea (1). Six morpho-species could not be identified because of (i) the non-resolutive power of mtDNA (large-spotted genets: *Genetta pardina* or *G. "maculata"*; cats: *Felis silvest*ris or *F. catus*), (ii) among-gene conflicting identities (antelope: *Kobus* spp.), and (iii) lack of reference sequences in databanks (rodents: *Anomalurus* sp., *Funisciurus* sp., *Heliosciurus* sp.). The samples of dry heads from "leopard" and "wild dog" collected in TMM returned as domestic dogs (T2212 to T2214; Table 2 SI).

Of the 94 species-level taxa identified as being sold in the TMM and BM, 22 were subject to CITES regulations (Appendices I-II). In addition, 22 and 51 species had threatened conservation status according to, respectively, $IUCN_{RL}$ (NT to CR) and RLB (NT to EX, but 19 NE). A further three taxa were domesticated, whereas another five could not be identified to the species level (Table 1).

The species sold in the TMM originated from the three bioclimatic zones of Benin (Guinean, Sudano-Guinean and Sudanian zones), whereas those sold in the BM were Guinean or ubiquitous (whole country) species (Fig. 2 SI). TMM sold the greatest number of species

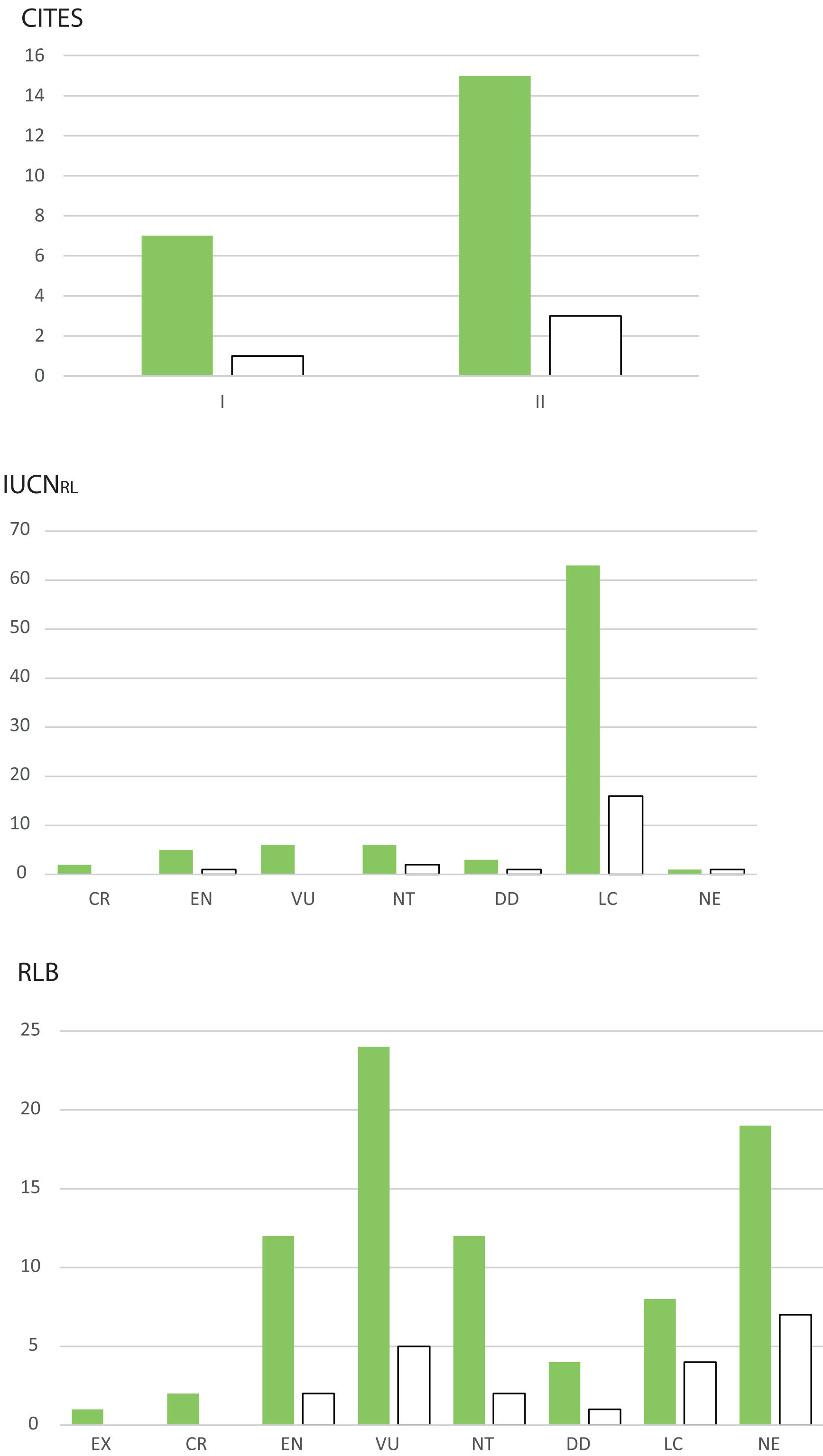

Fig. 3. The number of mammalian species sold in traditional medicine markets (green bars) and bushmeat markets (white bars) in southern Benin, according to their status under CITES, IUCN Red List of Threatened Species ($IUCN_{RL}$) and Red List of Benin (RLB). EX – Extinct; CR – Critically endangered; EN – Endangered; VU – Vulnerable; NT – Near Threatened; DD – Data Deficient; LC – Least Concern; NE – Not Evaluated.

of high conservation concern or regulated by international conventions (Fig. 3); 12 species were absent, possibly extinct or uncertain in Benin according to $IUCN_{RL}$. BM did not sell highly threatened or considered extinct species, and only one species was uncertain (Fig. 3 SI). BM and TMM sold species that were sourced from the four habitat categories, with the highest number of species overall coming from savanna followed by forest habitats (Fig. 4 SI). Species sold in BMM, however, tended to reside in forests.

Species sold in TMM had a large spectrum of diet specializations, including frugivorous and folivorous species (the most dominant: 57%), followed by invertivorous, carnivorous, omnivorous, granivorous, lignivorous, piscivorous, and nectarivorous species (Fig. 5 SI). BM sold mostly folivorous species (33%), and did not sell piscivorous and nectarivorous species. The diet categories regrouped into 52% herbivores, 47% carnivores and 1% scavenger in TMM, and 58% herbivores and 42% carnivores in BM (Fig. 5 SI). Ecological functions impacted by TMM included seed dispersion, prey regulation (together representing 73%), browsing, grazing and fertilization (Fig. 6 SI). The set of species found in BM was equally dominated by seed dispersers, prey regulators and browsers (totalizing 91%), whereas fertilizers were absent.

Regarding quantitative functional traits, TMM exhibited the largest median and variance (n-1) for mean body weight (4.0; 243594.6) and variance for generation length (13.4; median = 4.0 as in BM), whereas BM exhibited the largest median and variance for litter size per year (3.0; 83.9), although overall median values between the two types of markets were similar (Figs. 7–9 SI). TMM recorded the minimum litter size per year (0.25), and maximum generation length (25 yrs) and mean body weight (4250 kg) for a species. The species of folivores, carnivores and omnivores (diet specialization), as well as browsers and prey regulators (ecological function), reached much heavier maximum median weights in TMM, although median values were similar with BM (Fig. 10 SI).

The FD analyses first showed that the functional space occupied by the set of species found in BM was nested within the functional space of TMM (Fig. 4), which is expected given that all the species found in BM (N = 25) are also present in TMM (N = 94). By standardizing the FRic index between 0 and 1 (i.e. by dividing the two original FRic values by the maximal value found in TMM), we showed that the set of species found in BM occupied approximately 28% of the functional space of TMM (BM: FRic = 0.281; TMM: FRic=1; see Fig. 4). This roughly corresponded to the proportion of BM species found in TMM. However, when considering the FDis index, our results showed that the mean distance of species to the centroid of the functional space was similar between the two markets (BM: FDis = 0.654; TMM: FDis = 0.629).

4. Discussion

4.1. Taxonomic richness and conservation status of the mammalian species sold in wildlife markets from southern Benin

Bushmeat hunting and trade are significant factors of depletion of the mammalian fauna in tropical Africa (Fa et al., 2015), and wildlife markets from the Dahomey Gap are no exception (D'Cruze et al., 2020). Our integrative approach allowed identifying a total of 94 species-level mammalian taxa sold in the wildlife markets from southern Benin, which is slightly higher than previously reported (87 species; Djagoun et al., 2013). Such a number is about twice greater than what was ever found in large-scale bushmeat trade surveys conducted in the biodiversity-rich countries from western and central African forests (e.g., Avila Martin et al., 2020; Fa et al., 2014; Mbete et al., 2011). Our results are especially striking as Benin is situated in the Dahomey Gap, a supposedly diversity-poor savannah-forest mosaic zone relative to the two rain forest blocks that it separates (Booth, 1958). However, such a high score may be explained by the fact that we surveyed two different types of markets having different purposes, functioning and ranges of influence. BM (bushmeat market) by itself sold 25 species, which is in line with what was found in a recent bushmeat survey from the Dahomey Gap (Sonhaye-Ouyé et al., 2022).

TMM sold the greatest number of (i) mammalian species and orders (including bats, elephant and aardvark, which were not present in BM) and ii) species of high conservation concern or regulated by international conventions. Those notably included the western gorilla (*Gorilla gorilla*), the African savanna elephant (*Loxodonta africana*), the cheetah (*Acinonyx jubatus*), the lion (*Panthera leo*), the leopard (*Panthera pardus*), the African wild dog (*Lycaon pictus*), the hippopotamus (*Hippopotamus amphibious*), and the red-capped mangabey (*Cercocebus torquatus*) considered as likely extinct in Benin. Their presence in TMM implies transnational –in some cases, long-distance– trade with other countries and/or sourcing from populations at high risk of extinction in Benin, which will need to be urgently scrutinized.

Carnivorans have been reported as prevalent in medicinal and spiritual practices across tropical Africa (Doughty et al., 2015), which was extensively confirmed by our study. Carnivorans were dominant in TMM, with 27 species representing the seven families (Nandiniidae, Herpestidae, Viverridae, Felidae, Hyaenidae, Canidae, Mustelidae) that occur in the subregion. Small carnivorans constitute a valuable, regular-basis income for hunters in southern Benin (Djagoun and Gaubert, 2009). On the other hand, large carnivorans such as big cats and wild dogs, almost entirely extirpated from the country, may be persistently imported to feed the demand for their use in traditional medicine practices (see Williams et al., 2017), all the more since large benefits are expected from selling such rare species (Djagoun et al., 2013).

Overall, BM appeared as a subset of the taxonomic richness found in TMM (27% of the species), selling a local community of medium- to small-sized mammals dominated by antelopes and wild pigs, rodents and carnivores (72% of the total species richness). This can be explained by the fact that BM are predominantly supplied by hunters operating in and at the vicinity of LF (Sogbohossou and Kassa, 2016) with species from the Guinean (southern) forest zone or ubiquitous in southern Benin. The mammals sold in BM were generally of lower conservation concern, with the notable exception of the white-bellied pangolin, the wild cat (*Felis silvestris*), the mona monkey (*Cercopithecus mona*) and the patas monkey (*Erythrocebus patas*).

Several cases of uncertain species origin or identification illustrated the difficulty of identifying the species sold in West African wildlife markets. A few species sold in TMM were considered uncertain or not present in Benin, namely the southern reedbuck

(*Redunca arundinum*), the big-eared swamp rat (*Malacomys longipes*), and the Jackson's fat mouse (*Steatomys jacksoni*). Because the identification of the southern reedbuck was confirmed by DNA-typing, our results provide strong evidence for long-range wildlife trade from southern Africa (see IUCN SSC Antelope Specialist Group, 2016) to Benin, exemplifying again the wide footprint of TMM. On the other hand, the two species of rodents may prove difficult to identify from morphological grounds (Happold, 2013), so molecular identification –not available in these cases– will be needed to definitely confirm their taxonomic attribution. However, the species' ranges roam at the vicinity of southern Benin, and their –yet unreported– occurrence in the country remains conceivable (see Cassola, 2016; Gerrie and Kennerley, 2016). Despite our multiple-evidence approach, four taxa could not be genetically identified to the species level, including an antelope (*Kobus*), a scaly-tailed squirrel (*Anomalurus*), an African striped squirrel (*Funisciurus*) and a sun squirrel (*Heliosciurus*). Because cryptic diversity is likely affecting several groups of small to medium-sized mammals in tropical Africa and notably in the Dahomey Gap (e.g., Colyn et al., 2010; Gaubert et al., 2016; Oates et al., 2022), further investigations will have to be conducted to decipher whether these represent new taxa or yet unrepresented species in public databases.

Domestic species also constitute a part of the species spectrum sold in wildlife markets from the tropics (Karesh et al., 2005). In southern Benin, domestic cats and European rabbits were found both in TMM and BM, whereas domestic dogs were only sold –frequently– in TMM. DNA-typing proved useful in resolving the issue of the cranial artefacts sold as "leopard" or "wild dog", returning domestic dog as the disguised species (skull and skin) from which those artefacts were created. Similar cases of domestic species sold as wild species to increase profits have been reported in western Africa (Olayemi et al., 2011); however, these cases did not involve the same level of sophistication as those observed in this study. Here, the jaws of a domestic dog were maintained open with a wooden stick to make the head look "ferocious", and a piece of dog skin spotted with black markings was stuck around the skull so to imitate the leopard head. A similar strategy has also been observed to produce fake serval skins from dogs (PG and CD, pers. obs.). Artefactual wild dog heads seem to be created from a transformative protocol where the dog's head is placed in an unknown mixture that would result in inflating the tissues and remaining organs (e.g., eyes). In the neighbouring Togo, dogs may be killed as part of sacrificial rituals (Verdier, 1981) and can be found in TMM stalls (https://togo-tourisme.com/culture/marches/le-marche-aux-fetiches). In southern Benin, dogs seem to occupy a double function where they are both used in traditional medicine for specific purposes (as in Nigeria; Dongnaan Gurumyen et al., 2020) and as "cheap substitutes" to some rare species on the market such as the leopard and African wild dog.

4.2. Functional diversity of the mammalian community sold in wildlife markets from southern Benin

In the tropics, habitat loss and hunting activities are the main drivers of the loss of FD (Matuoka et al., 2020), jeopardizing equilibrium among ecological functions and thus the durability of ecosystem services (Brodie et al., 2021; Flynn et al., 2009). Hunting is predicted to exacerbate the degradation of ecological functions such as seed dispersal and forest regeneration quicker than the expected effects of climate change (Abernethy et al., 2013). As a matter of fact, a few case studies conducted in western and central Africa have shown the negative impact of hunting on the functional diversity of mammals (Tagg et al., 2020; Vanthomme et al., 2010). However, to our knowledge this is the first time that functional diversity is directly assessed through the prism of the African wildlife trade.

Our results suggest that wildlife markets in southern Benin have a broad impact on functional diversity and ecosystem services, jeopardizing at the same time regulatory, structural and production functions (Schmitz, 2009). The species sold at markets represented a total of nine diet specializations –the whole trophic space found in western African mammals (see Fa and Purvis, 1997)– and five major ecological functions. Frugivores (mostly bats, primates, antelopes and rodents), folivores (mostly antelopes and primates) and

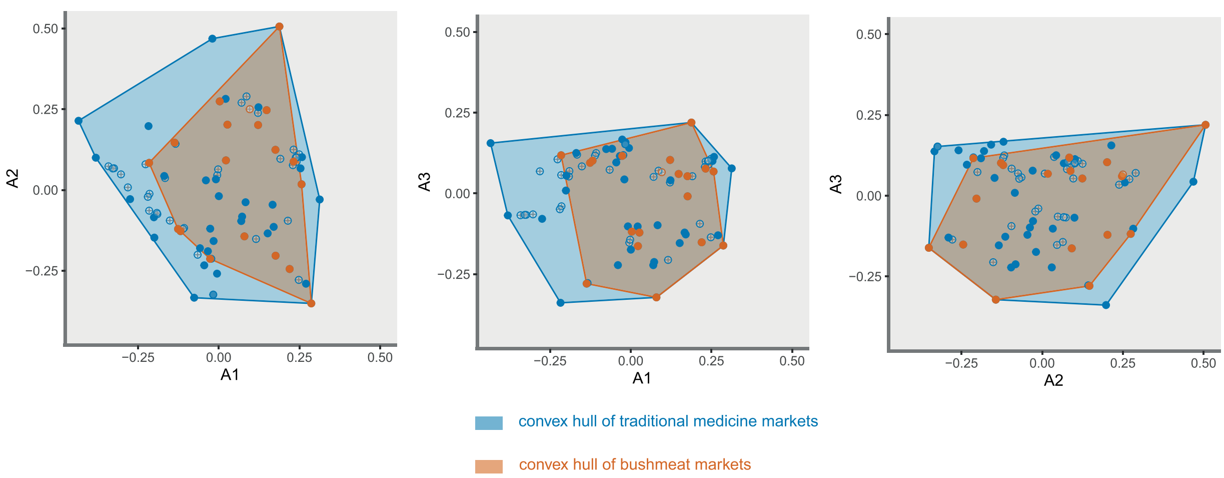

Fig. 4. Distribution of species in the functional trait space between traditional medicine markets and bushmeat markets as derived from a Principal Coordinate Analysis (PCoA). A1-A3: PCoA axes 1–3. Each circle corresponds to a species. In blue = traditional medicine markets. In red = bushmeat markets.

predators (carnivores and invertivores; mostly carnivorans) were the most represented. The consequences related to the over-hunting of medium to large frugivorous mammals on forest regeneration has been extensively studied in the tropics (Abernethy et al., 2013), including western Africa (Effiom et al., 2013). The depletion of frugivores has negative effects on seedling diversity, seed dispersal and, as a downstream consequence, forest carbon storage (Brodie et al., 2021; Kurten et al., 2015; Vanthomme et al., 2010). Frugivores may have an important impact on forest composition by acting on death and recruitment of the consumed trees, and enhancing nutrient cycling through fertilization (Chapman et al., 2013). They also act on the vegetation biomass, and their depletion might imply a cascading effect where stem densities increase and the recruitment of large trees reduces to result in homogeneous forest structure and lower carbon stocks (Poulsen et al., 2018). Invertivores play an important ecological function as they regulate pest abundance and may suppress arthropod outbreaks (Maas et al., 2016), thus limiting the propagation of disease vectors (Ghanem and Voigt, 2012). Mammalian carnivores have an important role in regulating ecosystems, acting as biocontrol agents against –for instance– the proliferating of rodents (Williams et al., 2018), which are both disease vectors and seed predators. Carnivores also have a cascading effect on the trophic chain and thus ecosystem equilibrium and productivity, and may enhance carbon storage by limiting the number of herbivore preys (Ripple et al., 2014).

Additional trophic groups, including omnivores (carnivorans and rodents), granivores (rodents), lignivores (mostly rodents), piscivores (otters) and nectarivores (bats), were also found in market stalls. Omnivores and granivores are considered ecosystem engineers positively acting on soil ecosystems but at the same time as seed predators likely influencing vegetation assemblages through targeted seed predation (Asquith et al., 1997; Mills et al., 2018). Lignivorous species act on nutrient cycling and ecosystem fertilization together with piscivores, the latter also participating to prey regulation and, as a top-down effect, shaping prey communities and aquatic habitats (Peterson and Schulte, 2016). Eventually, nectarivorous mammals, by pollinating flowers of many tropical and subtropical plant species, promote forest regeneration and support timber production (Ghanem and Voigt, 2012).

The five major ecological functions impacted by the wildlife trade in southern Benin included seed dispersion (mostly frugivores, folivores and omnivores), prey regulation (mostly carnivores and invertivores), browsing (mostly folivores), grazing (omnivores) and fertilization (nectarivores). Seed dispersers play an important role on tree species composition and downstream nutrient cycling, carbon storage capacity and browsing (Abernethy et al., 2013; Poulsen et al., 2018), all the more since several species were both grazers and seed dispersers (e.g., rodents, antelopes and elephant). The depletion of prey regulators is obviously linked to agricultural and health risks (pest pullulating, zoonotic spillover; Sinclair, 2003), but also involves cascading effects on the ecosystems such as density-compensation by grazers and seed predators, likely affecting patterns of forest regeneration (Effiom et al., 2013; Scabin and Peres, 2021). The interplay between browsing and grazing also plays a major functional role as involved in the dynamics of nutrient cycles and habitat structure (tree-grass equilibrium), ecosystem productivity and resilience (Milchunas and Lauenroth, 1993; Staver et al., 2021; Terborgh et al., 2016). Finally, fertilization via pollination by bats is key for fruit production and forest ecology (Ramirez-Francel et al., 2022).

In line with the taxonomic nestedness that we observed between the two markets, BM was a subset (about 28%) of TMM functional trait space. This indicates that the range of trait variation found in BM was lower than that observed in TMM. However, considering the FDis index, which is less affected by extreme values (Laliberté and Legendre, 2010) than the FRic index (Legras et al., 2018), we can conclude that the two markets displayed similar functional diversity. In other words, although BM contain species with less extreme trait values than TMM, BM is also representative of a large spectrum of functional traits. In BM, folivores and predators were the dominant groups, contrary to TMM where frugivores prevailed. Such discrepancy may be partly explained by the protection status of some frugivorous primates from the LF, such as the red-bellied monkey *Cercopithecus erythrogaster* and the white-thighed colobus *Colobus vellerosus* (Djègo-Djossou and Sinsin, 2009; but see Nobime et al., 2009). However, because BM are sourcing animals locally, the relative lack of frugivores may be better explained by local extinctions within such functional group through centuries of habitat fragmentation and hunting in southern Benin (Amadji and Roesch, 1990).

4.3. Conservation implications for mammalian species and ecosystems in southern Benin

Our study highlights the likely deleterious impact of wildlife trade in southern Benin on the taxonomic and functional diversity of mammals, ecosystem services and habitat resilience. Given their wide range of recruitment across taxonomic orders, bioclimatic zones and countries (Djagoun et al., 2013), their dense network (> 40 markets counted within the study area; SZ, pers. obs.) and the large demand for traditional medicine and religious practices (D'Cruze et al., 2020), TMM likely constitute the major threat to the conservation of mammals in the subregion. TMM heavily sourced across the full spectrum of (i) diet specializations and ecological functions and (ii) functional traits including body weight, generation length and litter size, available in western African mammalian communities. TMM notably sold the most endangered species with the greatest body weights and generation lengths, and smallest litter sizes, including the African savanna elephant, the hippopotamus, the buffalo (*Syncerus caffer*), the roan antelope (*Hippotragus equinus*), the lion, the western gorilla and the topi (*Damaliscus lunatus*). Because the depletion of large and medium-sized herbivores and keystone predators have serious downstream consequences on ecosystem, our results identify TMM as a main threat for ecosystem conservation in Benin. However, it remains challenging to accurately estimate the ecological impact of TMM as the market network is able to source from various geographic regions and habitats, sometimes in foreign countries. Moreover, the volumes of traded mammals remain uncertain as carcasses sold in TMM –skins, bones, skulls, appendages, organs– can stay for weeks, months and even years on the stalls (SZ, pers. obs.), contrary to BM where animals are generally sold within a few hours.

Because of their non-selective sourcing from an already depauperate taxonomic and functional spectrum of species, BM might also represent a significant threat to ecosystem functioning. Indeed, BM in southern Benin are locally supplied and as such, are a representation of the depleted mammalian fauna from the area, where the large- and most of the medium-sized mammals have been extirpated by agriculture and hunting. The wide functional diversity spectrum found in BM is the signature of non-selective hunting, and as a consequence is of concern for the ecological integrity of LF, which is the last large patch of semi-deciduous tropical forest preserved in southern Benin. Given that BM have restricted, identified sources, the system can be more easily characterized than TMM, notably regarding the volumes (numbers and biomass) of the trade. However, given the lack of available data, it is urgent to undertake long-term surveys of BM to quantify the threat they constitute for mammalian biodiversity and the sustainability of ecosystem services in and around LF.

5. Conclusion

Through our integrative approach crossing market interviews with direct observations, morphological-based identification and DNA-typing, we provide an unprecedented list of 94 species-level mammalian taxa sold in wildlife markets from southern Benin. Such an exhaustive taxonomic list should serve as a basis for future market surveys and re-assessment of conservation status across the Dahomey Gap region, where similar market networks targeting similar mammalian communities are at stake. Given its high level of taxonomic resolution, DNA-typing should be routinely applied in future wildlife trade surveys for species identification (Dipita et al., 2022; Gaubert et al., 2015; Gossé et al., 2022), geographic tracing of sourced habitats (e.g., Wasser et al., 2004) and unveiling of cryptic mammalian diversity.

Our study had the merit to highlight for the first time the potentially deleterious impact of the wildlife trade on the FD of mammalian communities in western Africa. Together with taxonomic diversity, FD is a marker of evolutionary heritage and ecosystem productivity (Ahumada et al., 2011; Ernst et al., 2006; Oliveira et al., 2016) that needs to be considered when tackling the sustainability of the wildlife trade. On the basis of the taxonomic and functional database that we provide, it will be important to further quantify FD in African mammals using continuous traits, given the existing knowledge gaps and the promise of such traits to better apprehend FD (Kohli and Rowe, 2019). Such dedication will ultimately help investigate the appropriate scales to which FD metrics may reflect changes in ecosystem functioning in western Africa (see Hatfield et al., 2018). This is particularly important to set up management strategies able to maintain ecosystem integrity, biodiversity and livelihoods in the subregion, anticipate the resilience of such ecosystems to global change, and provide public authorities with scientific evidence of the impact of the wildlife trade on ecosystem services.

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Ethical statement

This study was approved by the Ethics Committee of the University of Abomey Calavi, Benin, under clearance n°4613–2020/UAC/SG/SA. Data were collected under the research permit n°586/DGEFC/DCPRN/SCPRN/SA delivered by the Public Forest Services. The objectives of the study were explained to the administrative and local authorities, as well as to each participant before proceeding to questionnaires and investigations on carcasses. The surveys in wildlife markets received written consent from markets' stakeholders. Questionnaires were delivered individually in the wildlife markets after obtaining verbal consent.

Declaration of Competing Interest

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

Data Availability

All the data are available as appendices and in online repositories (Genbank).

Acknowledgments

We are grateful to the traditional medicine markets' local authorities who provided us with their written consent, and all the participants for generously giving their time to complete this survey. We thank two anonymous reviewers for their invaluable contributions on an early draft of the article.

Author contributions

CD and PG contributed to the study conception and design. Material preparation and data collection were performed by SZ and JD. Analyses were run by SZ, PG and FL. The first draft of the manuscript was written by CD, SZ and PG. All authors commented on previous versions of the manuscript. All authors read and approved the final version of manuscript.

Appendix 1. . PCR amplification and sequencing procedures together with post-processing validation of the nucleotide sequences used in the study

PCR mixture was carried out in 20 µl final volume with ~10–50 ng template DNA, 0.1 mg/mL BSA, 0.2 × 4 mM dNTPs, 0.5 × 2 µM primers, 1 X Flexi Go Taq Buffer, 1.5 mM MgCl2 and 0.5 U GoTaq® Flexi DNA polymerase (Promega, Charbonnières-les-Bains, France). Cycling conditions included a first step of denaturation (94 °C, 2 min), followed by 35 cycles of denaturation (92 °C, 30 s), annealing (30 s; 50 °C for cyt b and COX1 and 52 °C for 12 S and 16 S) and extension (72 °C, 30 s), and a final extension step (72 °C, 15 min). Amplicons were purified and sequenced in both direction on a 3730xl DNA Analyzer 96-capillary sequencer (Applied Biosystems, Foster City, CA) at Macrogen, Amsterdam, Netherlands (http://dna.macrogen.com/eng) and Genoscreen, Lille, France (https://www.genoscreen.fr/fr/). All the sequences produced in this study were deposited in Genbank under accession numbers OR167403 – OR167556 (cyt b), OR178526 – OR178609 (COX1), OR183805 – OR183961 (12 S) and OR183962 – OR184116 (16 S).

Sequences of cyt b and COX1 were edited and aligned manually using BioEdit 7.2.5. (Hall, 1999). We aligned the 12 S and 16 S fragments using MUSCLE (Edgar, 2004) at https://www.ebi.ac.uk/Tools/msa/muscle/ with default settings. In order to detect the presence of pseudogenes in cyt b and COX1 (coding genes), nucleotide sequence alignments were translated into amino-acids using MEGA 10.0.5 (Kumar et al., 2018), checking for putative stop codons and indels. We also checked atypical branch lengths and phylogenetic branching in the gene trees (see Material and Methods), a method applicable to genes without reading frames such as the 12 S and 16 S ribosomal subunits (Triant and DeWoody, 2007).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02630.

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