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Systematic review of sustainability assessment approaches for wildlife exploitation: Uncovering limitations in tackling the bushmeat crisis

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ABSTRACT

Wildlife exploitation constitutes an important socio-economical and nutritional resource to many communities worldwide. Yet, wildlife exploitation -whether legal or illegal- may be conducted at an unsustainable rate, notably with the globalization of the socio-economical context in the tropics. Our systematic review provides an update on the approaches employed to evaluate wildlife exploitation sustainability in fisheries, recreational hunting and bushmeat harvesting, while critically assessing their relevance to the ongoing bushmeat crisis in Africa. From an initial pool of 2803 documents retrieved from Web of Science using Boolean search, 125 peer-reviewed articles covering 66 countries across five continents were selected for analysis. A total of 15 index- and model-based approaches were used to study wildlife exploitation, with fisheries being the most investigated, driving the overall predominance of model-based approaches. GLM analysis showed that wildlife exploitation assessment outcomes were significantly influenced by species' reproductive strategy (positive effect for r-strategists) and type of exploitation (negative effect for fisheries). Bushmeat exploitation has been studied –mostly in South America– through a mixture of index- and model-based approaches, with a series of important methodological limitations related to species-specific traits, spatio-temporal dynamics of hunting areas, model parameter assessment and hunting offtake calculations. In tropical Africa, research has primarily focused on two genera of mammals (duikers and guenons), not reflecting the wide spectrum of species targeted. We conclude that a multifaceted approach integrating societal involvement, long-term monitoring for data collection, and the full adoption of advanced wildlife survey technologies is needed, in conjunction with long-term policies prioritizing the bushmeat issue.

1. Introduction

Wildlife exploitation for subsistence is an ancestral activity that has been practiced by human populations in virtually every region of the planet (Camera et al., 2023; Surya et al., 2023). Wildlife exploitation remains an important nutritional resource, economical income and cultural activity to many communities worldwide (Dutta, 2023; Khatun et al., 2023; Nadia et al., 2023). Because of high economical stakes, the delimitation between legal and illegal wildlife trade is often permeable, the mitigation of illegality depending on the capacity and will of states regarding law enforcement (Jiao et al., 2021; Sosnowski and Petrossian, 2020). Global incomes from illegal wildlife exploitation have been estimated to US$7–23 billion per year (Coad et al., 2019), with c. 100 million organisms traded annually representing around 6000 species making it the 4th largest transnational organized crime after human and drug trafficking, and counterfeiting (Harfoot et al., 2018; United Nations Office on Drugs and Crime (UNODC), 2021). Because wildlife trafficking is among the most lucrative illegal trades, the high and persistent demand drives intensive and often uncontrolled wildlife extraction, which in turn increases the risk of overharvesting and leads to unsustainable wildlife exploitation (Brook et al., 2019; Motlagh et al., 2021). In return, this can create a vicious cycle of poverty, environmental degradation

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0006-3207/© 2025 Elsevier Ltd. All rights reserved, including those for text and data mining, AI training, and similar technologies.

and sanitary risks, as communities are depleted from the very resources they depend on and ecosystem services are disturbed in the long term (Vasiliev, 2021).

Bushmeat, or wild meat, refers to wild terrestrial vertebrates including mammals, birds, reptiles, and amphibians, hunted for human consumption across tropical Africa, Asia, and Latin America (Annapragada et al., 2021; Camera et al., 2023; Fa and Brown, 2009; Wahab et al., 2020). This term extends beyond consumption, covering the entire supply chain from harvesting to trade (Nasi et al., 2008). In Africa, over 500 species are estimated to be affected by the bushmeat trade (BES Press Office, 2020), which represents over 5 million tonnes of game consumed yearly (Nasi et al., 2011). The annual bushmeat harvest in the Congo Basin alone is estimated at approximately 4.6 million tonnes, compared to 1.3 million tonnes in the Amazon Basin (Nasi et al., 2011). Although the bushmeat trade may represent up to 2 % of the Gross Domestic Product GDP (Desiere et al., 2018; World Bank, 2015), exact figures are difficult to ascertain because of the trade's informal nature. Bushmeat accounts for up to 50–80 % of protein intake in certain rural communities and is often intertwined with cultural traditions that can hinder conservation efforts (Fa et al., 2003; Friant et al., 2015). Despite its economic benefits and contribution to food security (Chausson et al., 2019; Ingram et al., 2021), the uncontrolled depletion of wildlife populations jeopardizes the mid-to-long-term sustainability of the bushmeat trade (Rija et al., 2020). Indeed, overhunting often outpaces the reproductive rates of the hunted species, especially in tropical rainforests (Harrison et al., 2016). The trade is also associated with sanitary risks (Zanvo et al., 2021), including zoonotic disease transmission from wildlife to humans (van Vliet et al., 2017) in link with ecosystem service disruption (Ripple et al., 2016).

Measuring the impact of wildlife exploitation on wild populations has been motivated by the concern of maintaining sustainable exploitations on which humans could rely. Because of the complex, intricate factors influencing the sustainability of wildlife exploitation (Chaves et al., 2019; Surya et al., 2023), a panel of various assessment approaches, which divide into two main categories, have been developed. The first resides in the static (indice-based) approach (Bodmer et al., 2020), which evaluates sustainability at a given time (T) by monitoring or comparing over time harvest levels or population densities of exploited species, either at a single site or across multiple locations (Borgerson et al., 2023; Riddell et al., 2022). A widely used static method for assessing wildlife exploitation sustainability is the hunting yield variation index, which tracks the number of animals caught or the biomass hunted per unit of effort over time (Moreno-Zarate et al., 2023). A prolonged decrease in hunting yields and the need to hunt over longer distances may signal the gradual depletion of local wildlife populations, pointing to unsustainable practices (Camera et al., 2023).

However, the static approach, often based on single indicators and lacking long-term monitoring of the harvested species, has been shown to generally yield poor indication of sustainability (Trump et al., 2022). The second main category of sustainability assessment is the so-called dynamic approach (Fa et al., 1995), which relies on the predictive modeling of sustainability based on a spectrum of variables including natural history data and population demography proxies of the wildlife species, patterns and dynamics of exploitation, human demography, market prices and other economical factors (e.g., maximum sustainable income) (Jurado-Molina et al., 2021; Levi et al., 2011; Ling and Milner-Gulland, 2006; Shaffer et al., 2018; Van Vliet et al., 2010). These approaches are considered dynamic because parameters used in their algorithms can be modified at a later time (T+ n) to reassess sustainability. Such an approach is considered more realistic as taking into account the socio-ecological context of the studied systems. The production model by Robinson and Redford (1991) is one of the most frequently applied methods for evaluating the sustainability of bushmeat hunting. It quantitatively estimates the maximum sustainable yield (MSY), i.e. the greatest number of individuals that can be harvested from a population each year without depletion. To assess sustainability, the current annual offtake (the number of animals harvested) is compared to the MSY. If the offtake surpasses the MSY, it indicates unsustainable hunting, as the population is being overexploited. Conversely, if the offtake remains below the MSY, it suggests that harvesting is more likely to be sustainable, with less risk of population decline.

Beyond the different nature of these approaches, sustainability outcomes (yes or no) remain heavily conditioned by the biological traits of the surveyed species (e.g., *Rmax*; Thibault and Blaney, 2003; Shaffer et al., 2017), the status of populations in the targeted areas (e.g., population density; (Shaffer et al., 2018), hunting pressure intensity and the spatio-temporal scale delimiting the study system (Levi et al., 2009; van Vliet et al., 2015a). Thus, sustainability assessments tend to remain highly context-sensitive, reflecting the difficulty to establish a clear quantitative delimitation between sustainable and unsustainable wildlife exploitation regimes (Hughes et al., 2023; Robinson and Bodmer, 1999).

Attempts at determining the impact of hunting and identifying sustainability thresholds have been conducted across tropical Africa, including the Democratic Republic of Congo (Hart, 2000; Wilkie et al., 1998), the Central African Republic (Thibault and Blaney, 2003), Gabon (van Vliet and Nasi, 2008), Cameroon (Muchaal and Ngandjui, 1999; Vermeulen et al., 2009), Equatorial Guinea (Fa et al., 1995; Kumpel et al., 2010), Ghana (Cowlishaw et al., 2005) and Ivory Coast (Refisch and Koné, 2005). Although the bushmeat trade has generally been considered highly unsustainable (e.g., van Vliet et al., 2015a), notably for common species with *K* strategies, the deficiency of protocols fitted to capture the issue of trade sustainability remains blatant (Fa et al., 1995; Kumpel et al., 2010). In fact, many case studies have concluded to uncertain sustainability outcomes, basing their assessments on a variety of static indices (Brook et al., 2019; Kumpel et al., 2010; Van Vliet et al., 2015b) that do not appropriately capture changes in hunting yield and population density (Baker et al., 2004; Hill et al., 2003). For instance, a review of case studies on duikers from central Africa (*Cephalophus* spp.) showed a great variability of the methodologies applied to the assessment of maximum sustainable harvests and annual hunting offtakes, jeopardizing general conclusiveness on the sustainable hunting of the species (van Vliet and Nasi, 2008).

Several reviews have examined the sustainability approaches used to assess wildlife exploitation, employing either systematic (Milner-Gulland and Akçakaya, 2001; van Vliet et al., 2015a) or critical (Colloca et al., 2017; Gallo-Cajiao et al., 2020) methodologies to describe these approaches, their underlying assumptions, data requirements, strengths, and limitations. They also evaluated the applicability of these approaches to specific forms of wildlife exploitation, such as bushmeat harvesting (game hunting and selling in the tropics), recreational hunting (killing of animals primarily for enjoyment purposes in northern countries), or fisheries (marine and riverine; Gallo-Cajiao et al., 2020; Teh et al., 2017; Weinbaum et al., 2013). Unlike previous reviews, which were either purely systematic or critical, we integrate both approaches in a hybrid framework where the systematic review serves as a base for a critical review focused on a specific issue (bushmeat trade in Africa). Additionally, our review is unique as it compares sustainability approaches across the three major types of wildlife exploitation, including bushmeat, recreational hunting, and fisheries. An earlier review covered these three categories (Sutherland, 2001), but did not undertake a comparative analysis. Most previous reviews were geographically restricted (continental to local scales; Cuthbert, 2010; Doughty et al., 2015; Duporge et al., 2020) or are now outdated (Robinson and Redford, 1994), while two recent reviews (Brotherton et al., 2020; Di Minin et al., 2021) focused exclusively on fisheries and recreational hunting. Here, we present a comprehensive and up-to-date review of sustainability approaches for assessing wildlife exploitation, encompassing bushmeat, recreational hunting, and fisheries in order to identify current limitations and propose future refinement of sustainability assessment approaches within the specific context of the African bushmeat trade. Our specific objectives are to (i) update global trends in wildlife exploitation sustainability assessment approaches, (ii) re-assess the determinism of sustainability assessment outcomes depending on these approaches, (iii) identify the main potential caveats when those approaches are applied to the issue of the bushmeat exploitation in tropical area, and (iv) propose avenues for improving sustainability assessment in tropical context.

2. Methods

2.1. Literature search

The systematic review was conducted following the Guidelines and Standards for Evidence Synthesis in Environmental Management (Collaboration for Environmental Evidence 2022), in line with the methodology used in recent reviews on similar topics (e.g., (Duporge et al., 2018; Groom et al., 2023). Using the Web of Science (WoS) database (Fig. 1), we applied Boolean searches including the following word combinations, to screen title, abstract and topic from the peer-reviewed literature: hunting AND sustainab* AND (Index* OR indice*); bushmeat AND sustainab* AND (Index* OR indice*); hunting AND sustainab*; fish* AND sustainab* AND (Index* OR indice*); hunting AND sustainab* AND (Model); bushmeat AND sustainab* AND (Model). Such Boolean searches were also able to capture articles using the term "wild meat". The same searches were also conducted in French, as approximately half of the African countries are French-speaking. In addition, some publications in other languages (Spanish, Portuguese)

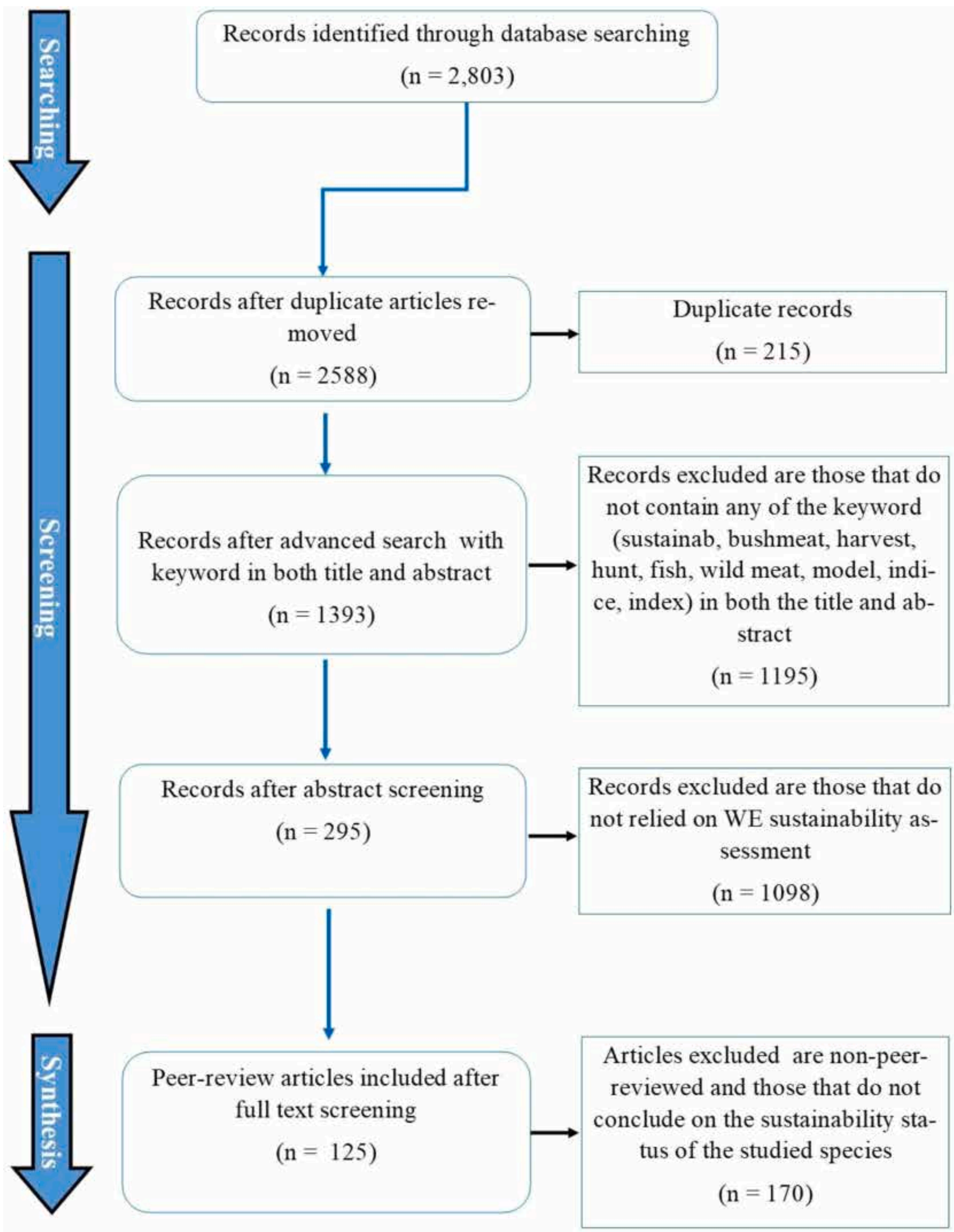

Fig. 1. Flowchart of literature search, screening and inclusion followed as part of this critical review.

which have their abstracts translated into French or English were also recovered.

The bibliographical search was conducted between October 2023 and December 2024, resulting in a publication range from 1992 to 2024. All the publications were stored and curated in Zotero v. 6.0.37 (Zotero, 2006). Overall, the search returned 2803 published material including peer-reviewed articles, book chapters, technical reports, proceedings, these and other scientific documents. After removing duplicates, an advanced search was carried out in Zotero to select the publications that included the words "bushmeat", "wild meat", "fish", "harvest", "hunt*", "indice", "index" "model" and "sustainab*", in both title and abstract. This resulted in a filtered list of 1393 publications. Relevance of each of these publications with sustainability assessment was verified by visual inspection of abstract, resulting in the selection of 295 publications. After comprehensive text screening, 125 peer-reviewed articles were ultimately selected, comprising 43 focused on bushmeat harvesting, 28 on recreational hunting and 54 on fisheries (see Appendix S1 Table S1). By restricting our review to peer-reviewed literature, we ensured scientific validation of the data compiled and may have excluded some relevant grey literature. The final set of articles answers to the following criteria: (i) focus on the exploitation of one or several taxa in natural areas; (ii) use of at least one sustainability approach in their methodology; and (iii) provision of a conclusion on the sustainability status ("sustainable" or "unsustainable") of the taxa under study. Publications on extinct species and archeological studies were not taken into account. One co-author (PG) independently reviewed the first 10 articles (8.0 % of the total) of the list for cross-check validation.

The following information were extracted from the 125 articles (see Appendix S2): (1) Bibliographical metrics, including authors, title, publication year, journal; (2) Study site context, including continent, country; (3) Study design, including type and category of sustainability assessment approaches, type of exploitation; (4) Biological parameters, including taxa under study, reproductive strategy (r-strategy vs K-strategy - based on species' biological parameters in www.iucnredlist.org and Kingdon, 2015); and (5) Outcomes of the sustainability assessment (sustainable / unsustainable). When a study covered several countries / species / sustainability approaches, it was counted as separate observations.

2.2. Data analysis

All the graphical visualization and statistical analyses were carried out in RStudio V. 4.4.2 (Posit team, 2024). Descriptive quantifications were conducted to highlight frequencies of use among the different sustainability approaches (stacked barplot), publication trends (bar plots) and the taxonomic spectrum of bushmeat studies (Sankey diagram), using the R packages *ggplot2* (Wickham, 2016) and *networkD3* (Allaire et al., 2017). Spatial mapping of the studies conducted in Africa was produced with QGIS (QGIS Development Team, 2024). In order to evaluate the determinism of the reported sustainability outcomes across study systems and approaches, we developed a generalized linear model (GLM) to determine whether the outcomes of sustainability studies depended on the type of sustainability approaches (indices, models), reproductive strategy of the target taxon (*r, K*), and the type of exploitation (bushmeat harvesting, recreational hunting and fisheries). We used a logistic link function to model a binary response variable (sustainable / unsustainable) with the *pscl* package (Jackman, 2024). The interactions between the explanatory variables was also tested. We compared the candidate models using Akaike Information Criterion (AICc) and selected the model with the lowest value (see Appendix S3 Table S2). The significance of dependency among factors of categorical explanatory variables were investigated using Wald's Z statistic. The χ^2 test was used to assess the goodness of fit of the GLM to the data and the pseudo-coefficient determinant R^2 (Nagelkerke, 1991) was calculated to evaluate the model's explanatory power. Using sandwich packages (Zeileis and Lumley, 2004) we also calculated the 95 % confidence interval (CI) using the parameter estimates and their robust standard errors.

3. Results and discussion

3.1. Global trends in sustainability assessment approaches applied to wildlife exploitation

We present the first systematic review of global wildlife exploitation sustainability assessments, analyzing 125 studies (Appendix S4. Fig. S1). The majority of the articles were published in *Conservation Biology* (n = 15, c. 12 %) and *Biological Conservation* (n = 9, c. 7 %), two journals being recognized as key sources in global biodiversity conservation research (Fazey et al., 2005). Among the 125 studies, 22.4 % (n = 28) focused on recreational hunting, 34.4 % (n = 43) on bushmeat harvesting, and 43.2 % (n = 54) on fisheries. Fisheries remain the most extensively studied due to their industrial-scale exploitation and pioneering role in wildlife exploitation sustainability research. This field introduced key concepts such as optimal fishing mortality, culminating in the maximum sustainable yield (Beverton and Holt, 2012; Schaefer, 1991). Since the early 1950s, governments have invested heavily in routine data collection and analysis of fisheries' catch and age composition (Pauly et al., 2002). In contrast, sustainability assessments of recreational hunting emerged more recently, primarily in northern countries, focusing on conservation management plans to ensure the long-term availability of exploited species (Camera et al., 2023; Diaz-Fernandez et al., 2012; Taylor et al., 2005), though not necessarily driven by conservation concerns. Interest in bushmeat sustainability arose in response to the "bushmeat crisis," a term highlighting concerns over unsustainable wildlife extraction in tropical forests, though criticized for oversimplifying local hunting practices and their socio-economic context (Nasi et al., 2008). Consequently, sustainability recently became a key focus in wildlife management and conservation discourse in the tropics (Groom et al., 2023; Ingram et al., 2021).

Geographically, wildlife exploitation studies covered 66 countries across five continents. Regarding fisheries exploitation, which occurs globally, research has primarily focused on the Indian Ocean and adjacent seas. This region encompasses nine large marine ecosystems (Pauly et al., 2002; Sherman et al., 2002) and holds vast natural resources (Llewellyn et al., 2016; Moustahfid et al., 2018), highlighting the critical interests for scientific studies on resource management and sustainable exploitation. Investigations on recreational hunting were most prevalent in North America and Europe (43 % both). In the global North, game animals may provide significant recreational benefits, contributing to local and national economies (Barnes et al., 1999; Gren et al., 2018; Hofer, 2002). Although the bushmeat crisis has been coined from the African continent, bushmeat research activities were most represented in southern America (56 %), confirming previous trends (Weinbaum et al., 2013). This likely reflects differences in research infrastructure, long-term ecological monitoring programs, and international funding priorities in the Neotropics, as well as the underrepresentation of African studies in peer-reviewed journals despite extensive local research. Strengthening research capacity, improving publication support, and fostering international collaborations in African countries could help bridge this gap and ensure a more balanced global understanding of bushmeat sustainability.

Wildlife exploitation sustainability has been assessed through a total of 15 approaches (Fig. 2). These different approaches all rely on fundamental data regarding harvest rates and population density, as well as key life cycle parameters of wild animal populations (Ahamed et al., 2023; Bodmer et al., 2020) (Appendix S5. Table S3). These approaches include model-based methods such as bioeconomic (Bioeco), biodemographic (Biode), biometric (Biome), harvest rate (HR), potential biological removal (PBR), production (Pro), stock recruitment (SR), and surplus production (SP). Additionally, index-based approaches were recorded, including age structure comparison (ASC), change in hunting

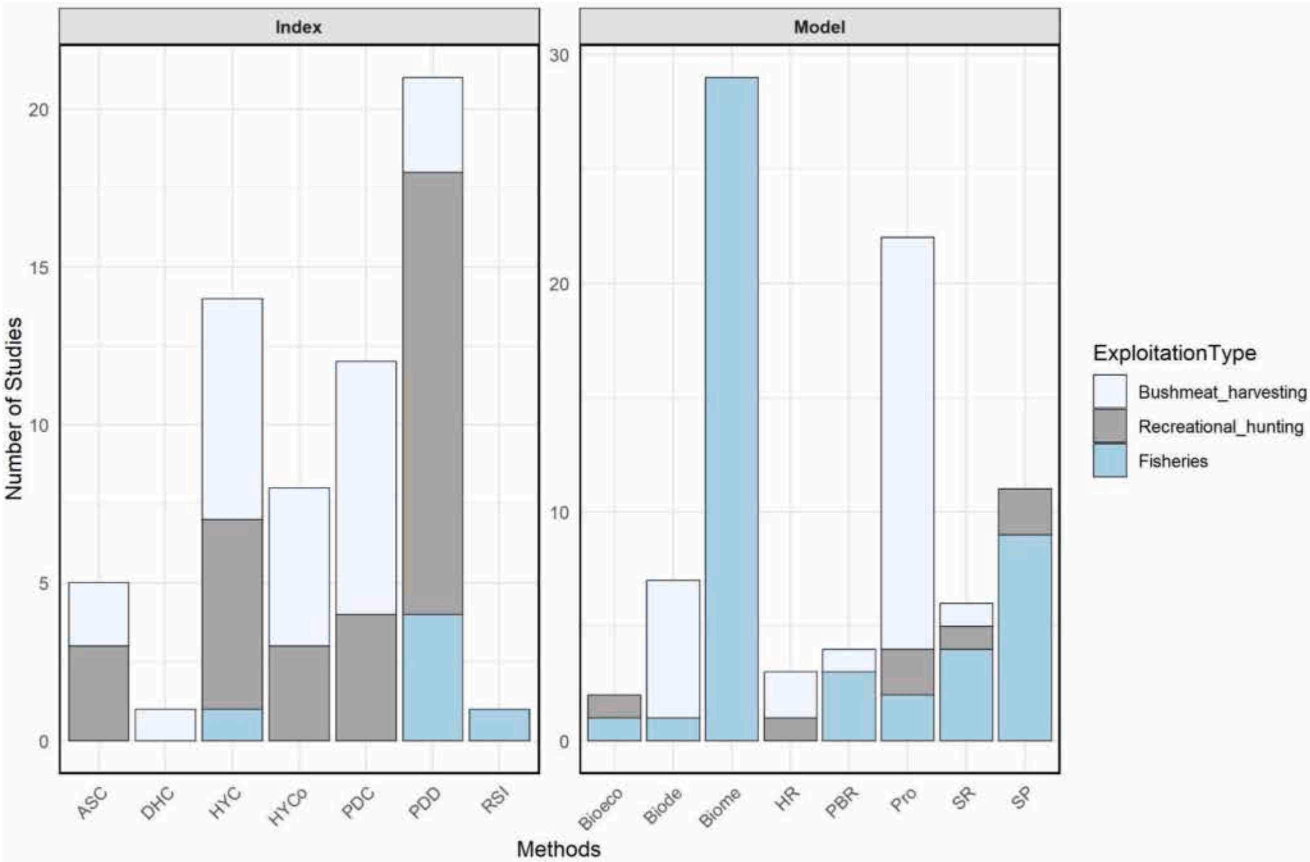

Fig. 2. Trends in index- and model-based approaches for assessing sustainability across different types of wildlife exploitation. Methods of assessment: ASC = age structure comparison, DHC = change in hunting distance, HYC = hunting yield change, HYCo = hunting yield comparison, PDC = population density change, PDD = population density decline, RSI = relative sustainability index; Bioeco = bioeconomic, Biode = biodemographic, Biome = biometric, HR = harvest rate, PBR = potential biological removal, Pro = production, SR = stock recruitment, SP = surplus production.

distance (DHC), hunting yield change (HYC), hunting yield comparison (HYCo), population density change (PDC), population density decline (PDD), and relative sustainability index (RSI).

Globally, wildlife exploitation sustainability was assessed through more models ($n = 80$) than indices ($n = 45$) (Fig. 2). This global trend was mostly driven by fisheries, where 88 % of the studies relied on model-based approaches. Although complex, model-based approaches are effective descriptors of wildlife exploitation sustainability as they integrate species-specific biological traits and spatio-temporal dynamics data (Bashar et al., 2021; Eleodoro Perez-Pena et al., 2021). Among these, the biometric model is the most widely applied in fisheries research (c. 59 %), utilizing length-weight relationships (LWRs) to convert length distributions into weight estimates for biomass assessment (Gerritsen and McGrath, 2007; Nadia et al., 2023).

In contrast, studies on recreational hunting exploitation mostly relied on index-based approaches (75 %). Recreational hunting is a legal and regulated activity promoted as a means to support human well-being, ecosystem restoration, and potentially, biodiversity conservation (Di Minin et al., 2016; Heffelfinger et al., 2013). As a result, assessing the sustainability of recreational hunting is less complex compared to other forms of exploitation, as many influencing factors are under controlled conditions. Our review found that 46 % of the studies on recreational hunting relied on the population density decline (PDD) index. The impact of recreational hunting on the abundance of targeted species is typically assessed by analyzing population trends over time, using protocols such as long-term camera surveys, transect surveys, radio-collared individual tracking, mark-recapture techniques, and official records (Di Minin et al., 2021).

Studies on bushmeat exploitation were more balanced in terms of approach, with model-based approaches being slightly more prevalent (60 %). In tropical regions, particularly in Africa, the lack of key biological and population-level parameters necessary for implementing model-based approaches (Weinbaum et al., 2013) has led researchers to favor index-based methods such as HYC (Wahab et al., 2020) and PDC (Khadiejah et al., 2019). An alternative solution has been the use of the production model proposed by Robinson and Redford (1991), which were applied in approximately 64 % of the model-based studies. This model is relatively simple to implement as it applies Cole's formula (1954) to calculate the maximum finite rate of population growth (λ). This approach requires minimal demographic data from local contexts and involves relatively straightforward calculations (Robinson and Redford, 1994).

3.2. Determinants of sustainability assessment outcomes based on intrinsic factors

A previous review identified various interacting parameters, such as methods, continent of study, species body mass, taxonomic group, and the socioeconomic status of study sites, as key predictors of the sustainability outcomes of wildlife exploitation assessment (Weinbaum et al., 2013). Our critical review builds upon this by using new parameters, including the reproductive strategies of studied species (r-strategists vs K-strategists; Appendix S6 - Table S4) and comparing sustainability outcomes across three categories of exploitation: fisheries, bushmeat, and recreational hunting. Results from a Generalized Linear Model (GLM) based on binomial distribution demonstrated a statistically significant influence of the reproductive strategies and domains of wildlife exploitation on sustainability outcomes ($p < 0.05$; Table 1).

Table 1
Parameter estimates of the GLM with binomial distribution for the factors predicting outcomes of wildlife exploitation sustainability assessment.

Variables	Estimate	Std. Error	z value	df	Pr	95 % Confidence Interval		
					(>|z|)	Lower Bound	Odds Ratio	Upper Bound
Reproductive strategies								
r	0.680	0.257	2.648	1	0.008	1.204	1.975	3.310
K	0*			0			1	
Approaches								
Model	−0.387	0.215	−1.799	1	0.071	0.443	0.6781	1.033
Index	0*			0			1	
Type of exploitation								
Fishery	−1.384	0.326	−4.242	1	<0.001	0.129	0.250	0.468
Hunting	−0.067	0.308	−0.219	1	0.826	0.510	0.934	1.720
Bushmeat	0*			0			1	

* Set as reference modality

Specifically, assessments conducted on species with r-strategies were more likely to conclude on sustainable exploitation compared to those on K-strategists. This first result aligns with the hypothesis that species traits influence population productivity and resilience under harvest pressure (Cardillo et al., 2005).

In this context, our findings complement those of Weinbaum et al. (2013), who observed that harvests targeting rodents -which are predominantly r-strategists- are more likely to be deemed sustainable compared to vertebrates with primarily K-strategies such as carnivorans and primates. Indeed, K-strategists taxa are more vulnerable to overharvest (Bodmer et al., 1994; Price and Gittleman, 2007). According to MacArthur and Wilson (2001), K-strategists reproduce at slower rates, producing fewer offspring with substantial parental investment, which increases individual survival rates. Conversely, r-strategists reproduce rapidly, generating numerous offspring with minimal parental care. Due to their higher reproductive capacity, r-strategists are generally more resilient to high hunting pressures, making the impact of exploitation less severe compared to K-strategists. Our findings also reinforce the importance of integrating species life-history parameters into sustainability frameworks when evaluating the impact of bushmeat hunting. Neglecting these differences can lead to misleading conclusions, especially when applying uniform assessment criteria across diverse taxa. Thus, tailoring sustainability assessments to account for species-specific ecological and demographic profiles is critical for accurately predicting long-term viability under harvesting regimes, particularly in regions like the tropics where both r- and K-strategists coexist and are targeted by hunters.

As a potential consequence, K-strategists have received greater attention in sustainability studies worldwide to prevent their extinction. Our review showed that among the 280 wildlife species analyzed (including 162 mammals, 31 birds, 12 reptiles, and 75 marine species), K-strategists represented 58 % (n = 164 species), while r-strategists accounted for 42 % (n = 117) (see Appendix S6 - Table S4). In terms of research frequency, K-strategists were studied c. twice (n = 333) as often as r-strategists. Looking at the total number of individual assessments, there were 353 studies on mammals, 42 on birds, 14 on reptiles, and 79 on marine species, confirming that mammals -which are mostly K-strategists (Wu et al., 2021)- were the most frequently studied taxonomic group, in line with Weinbaum et al. (2013). The most extensively researched orders included Artiodactyla (n = 136), Primates (n = 87), Rodentia (n = 48) and Carnivora (n = 42). Specifically, species such as *Pecari tajacu* (n = 19), *Mazama americana* (n = 17), *Tapirus terrestris* (n = 13), and *Tayassu pecari* (n = 13) from South America, as well as *Atherurus africanus* (n = 10) and *Cephalophus monticola* (n = 11) from tropical Africa were most studied. These species are abundantly represented in the hunting catches from their respective regions (Eleodoro Perez-Pena et al., 2021; Esbach et al., 2024; Hallett et al., 2019; Kumpel et al., 2010).

The impact of wildlife exploitation domains on sustainability outcomes (likely related to the effect of the variable "continent" in Weinbaum et al., 2013) showed no significant difference between recreational hunting and bushmeat exploitation ($p > 0.05$; Table 1). In both cases, studies reported more sustainable outcomes (55 % and 53 %, respectively). Recreational hunting is a legally regulated practice often advocated for its potential benefits in supporting human well-being, promoting ecosystem restoration, and contributing to biodiversity conservation (Di Minin et al., 2016; Heffelfinger et al., 2013). As a result, its management focuses on ensuring the sustainability of hunting activities, both to preserve biodiversity and to maintain the associated benefits. Most of the sustainability assessments relied on index-based approaches (78 %). However, these methods are known to be limited in identifying the genuine threshold at which hunting becomes unsustainable (Chaves et al., 2019; Crookes et al., 2005; Peres et al., 2016).

Traditionally, subsistence hunting in tropical regions has relied on methods such as snares, spears, firearms, and sometimes dogs (Afriyie et al., 2021; Carpaneto and Fusari, 2000; Santos et al., 2022), as opposed to the mass harvesting techniques employed in marine fisheries. This has led to considering bushmeat harvesting as relatively sustainable in some tropical areas (Cowlishaw et al., 2005; Eleodoro Perez-Pena et al., 2021). Nevertheless, bushmeat hunting in many tropical regions is considered unsustainable due to the sheer volume of species harvested annually (BES Press Office, 2020; Nasi et al., 2011; Shaffer et al., 2018). Indeed, when comparing the two main tropical moist-forest regions, the Amazon and Congo basins, estimates suggest that over 5 million tons of bushmeat are consumed each year (Fa et al., 2003; Nasi et al., 2011). Model projections indicate that even if bushmeat harvests could be maintained at sustainable levels in the Congo Basin, many countries in the region would still experience significant declines in wild protein supply (Lee et al., 2020). Given this context, it is surprising that most studies on bushmeat exploitation reported predominantly sustainable outcomes. This discrepancy is likely linked to methodological biases in bushmeat sustainability assessments (van Vliet and Nasi, 2019).

In contrast, our model indicated a 75 % lower likelihood of sustainable exploitation in fisheries compared to bushmeat (Table 1). This second result is in line with previous knowledge expressed in the literature, where industrial-scale fisheries have seldom been genuinely sustainable (Gascuel and Menard, 1997; Marino-Briceno et al., 2022; Mendonca et al., 2010). Instead, fishing practices have led to sequential depletions, often obscured by advancements in technology, geographic expansion, and the exploitation of previously disregarded species lower in the food chain (Pauly, 2008). With global fish catches declining since the late 1980s, current trends suggest an impending supply shortfall (Pauly, 2008).

3.3. Main limitations when applying sustainability assessments to bushmeat exploitation

Wildlife exploitation in the tropics remains a vital source of protein, nutrition, traditional medicine, and income, with c. 100 million organisms traded annually representing around 6000 species (Alves et al., 2013; Coad et al., 2019; Harfoot et al., 2018; Milner-Gulland and Bennett, 2003; Nasi et al., 2011; van Vliet et al., 2017). Given the critical role of bushmeat hunting in poverty alleviation, assessing its sustainability with appropriate approaches is essential (Bennett and Rao, 2002; Lee et al., 2020; Nasi et al., 2008).

Our systematic review showed that various methods have been employed to evaluate the sustainability of subsistence hunting in the tropics (see Appendix S5. Table S3). Some studies have focused on changes in hunting offtake over time (Wahab et al., 2020) or trends in wildlife abundance (Bodmer et al., 2020). Others compare wildlife abundance (Khadiejah et al., 2019), hunting offtake (Hallett et al., 2019), and age structures (Hurtado-Gonzales and Bodmer, 2004) between hunted and non-hunted sites. However, these methods often fail to pinpoint the effective threshold at which hunting becomes unsustainable, for various reasons. Interpreting offtake data in the bushmeat context presents challenges, as it reflects the outcomes of multiple processes (Crookes et al., 2005). It is crucial to consider the duration for which an area has been subjected to hunting; in newly hunted areas, reductions in hunting yields may be expected until a balance is achieved (Robinson and Redford, 1994). Another complexity arises from changes in species composition among the captured animals. In tropical forests, hunters often prioritize larger species for subsistence and profit (Peres et al., 2016). Consequently, when larger species are overexploited, hunting efforts may shift toward smaller species, which tend to be more abundant. This shift can create an illusion of increased hunting yields if measured by the number of individuals captured per unit effort, for instance in assessment based on ASC, HYC and HYCo indices, thereby obscuring an unsustainable hunting scenario (Chaves et al., 2019). Moreover, results can be significantly influenced by the area assessed and sampling effort, leading to ambiguities regarding the obtained information (Weinbaum et al., 2013).

Another approach for assessing sustainability involves monitoring changes in population density and structure (PDD, PDC, and ASC). However, a lower density of animals in a hunting area does not necessarily imply unsustainable hunting (Bodmer and Robinson, 2004); it may merely reflect geographical variations. Additionally, even when animal densities fall below expected carrying capacities, one cannot definitively conclude that hunting is unsustainable, as hunting pressure inherently reduces faunal density. Therefore, understanding the impact of reduced abundance on local birth and mortality rates is crucial (Robinson and Redford, 1994). Moreover, identifying comparable hunted and non-hunted populations can be challenging in the bushmeat context. Survey design should ensure that hunting pressure is the primary factor affecting the evaluated populations in the study area, while controlling for the influence of other variables such as microhabitats, fragment size, and resource availability as much as possible (Chaves et al., 2019). In conclusion, while indice-based approaches can provide insights into bushmeat densities and harvesting rates, interpretations on whether hunting is sustainable or not remain often indirect and inconclusive if not taking into account species-specific traits and the spatio-temporal dynamics of hunting areas.

Model-based approaches have also been used to assess bushmeat hunting sustainability. Among the most commonly applied models in recent studies are the production (Robinson and Redford, 1991) and the biodemographic models (Levi et al., 2009). Both estimate the maximum sustainable harvest (MSH) based on population density and productivity. However, estimating MSH is generally fraught with two main sources of uncertainty (van Vliet and Nasi, 2008). The first source is the variability in the values and methods used to assess model parameters. Key model parameters include population density (D), mortality rate (F), and the maximum population growth rate (Rmax). Rmax is typically calculated using either the Cole (1954) formula or Caughley and Krebs (1983) equation. Previous studies have shown that Rmax derived using Caughley & Krebs' equation can be up to four times higher than values obtained with Cole's formula within the same species, introducing significant uncertainty into sustainability assessments (van Vliet and Nasi, 2008). Population density (D) estimates also vary considerably depending on the method used. For instance, comparisons of population density derived from visual counts versus camera counts for the same species at the same site often yield different results (Jumail et al., 2021). Similarly, estimates of MSH differ when density is assessed using call counts versus day count methods for duikers. These discrepancies arise from biases inherent to each method, such as poor visibility in dense vegetation, the elusive behavior of animals, or the physical similarity of different species (Fragoso et al., 2016; Nakashima et al., 2021). The mortality factor (F) is another source of variability. For Neotropical species, F is typically estimated at 0.6 for animals with a lifespan of five years, 0.4 for those living 5–10 years, and 0.2 for species with a longevity exceeding 10 years. However, researchers often disagree on the appropriate longevity scale, as observed in the case of duikers (Ngandjui and Blanc, 2000; Noss, 2000). These inconsistencies across methods and parameters highlight the challenges in reliably estimating sustainable harvest levels for bushmeat hunting. Currently, there is limited data on key demographic parameters, such as reproduction, dispersal, home range size, mortality, longevity, and seasonal variations, for tropical mammals (van Vliet and Nasi, 2019). Most available information comes from studies on captive animals, and dates back to the 1980s–1990s or earlier. This lack of robust, context-specific data on life-history traits poses a significant obstacle to developing effective and sustainable management practices for bushmeat species. Despite this, decisions regarding sustainable yields often rely on outdated or inaccurate estimates of maximum sustainable harvests (van Vliet and Nasi, 2008). Without substantial investment in gathering life-history data across different ecological and socio-economic contexts, quota-setting efforts are likely to fail.

The second source of uncertainty originates from inconsistencies in calculation methods of the hunting offtake. To evaluate hunting sustainability, the observed annual offtake is compared to the estimated maximum sustainable harvest (MSH). If the observed offtake surpasses MSH, hunting is deemed unsustainable, potentially exposing exploited populations to extinction risks (Robinson and Redford, 1991). However, the methods used to derive harvest profiles vary significantly based on (i) the geographic scale of the study (local or regional), (ii) the sampling techniques employed, and (iii) the approaches used to extrapolate the data. Some studies have been conducted at a regional scale, focusing on the number and composition of carcasses sold in urban markets (Fa et al., 1995, 2000; Juste et al., 1995). However, harvest rates derived from market data typically underestimate the true offtake because only a fraction of the hunted animals is sold in markets. For instance, Colell et al. (1994) found that 20 % of antelope catches in villages in southern Bioko, Equatorial Guinea, were retained for household consumption. Additionally, cultural taboos in certain areas influence market availability, as seen in northeastern Gabon, where species like *C. sylvicultor* and *C. leucogaster* are rarely sold in markets (Van Vliet, 2008), further underestimating offtake for these species. Other studies have relied on data gathered at the village or household level through direct participation in hunting activities, or via regular (daily, weekly, or monthly) interviews and monitoring of kills brought back from the forest (Brook et al., 2019; Wahab et al., 2020). In some cases, these studies focused on specific hunting methods, such as snares or nets, and compared the MSH only to the offtake associated with that particular method. The data were then extrapolated to estimate total village-level hunting offtake per unit area per year. However, when surveys were limited to only a few months, the average monthly offtake was often extrapolated to estimate annual figures, without accounting for seasonal variability in hunting effort. Such simplifications can lead to significant inaccuracies in bushmeat sustainability assessments.

3.4. *Avenues for improving bushmeat harvesting sustainability assessments in tropical Africa*

Our review indicates that bushmeat sustainability surveys are underrepresented in tropical Africa and have focused on three main classes of vertebrates, including Mammalia, Reptilia, and Aves (Fig. 3). Among these, mammals represented 88.2 % of the studies, with species from the genus *Cephalophus* (duikers; 13 species) and *Cercopithecus* (10 species) being the most predominant. Such specific focus on small forest duikers is to be related to their significant contribution to the hunting offtake throughout tropical Africa (van Vliet and Nasi, 2008). Duikers are among the most heavily hunted species in Central Africa, both in terms of numbers and biomass (Kumpel et al., 2010; Muchaal and Ngandjui, 1999; Vermeulen et al., 2009). As for primates, they represent a key model for studying human evolution, behavior, and health (Phillips et al., 2014), and for maintaining various ecological functions and services at the community level (Brodie, 2016; Peres et al., 2016). Additionally, wild primates are subject to both legal and illegal trade across multiple countries worldwide (Badihi et al., 2024; Gamalo et al., 2024; Prescott, 2023).

Having said that, we also observed that certain emblematic species of the bushmeat trade (e.g., *Phataginus tricuspis*) and other duikers frequently targeted by hunters (e.g., *Philantomba* spp.) remain understudied in Africa (Fig. 3). *Phataginus tricuspis* is highly elusive and nocturnal, making it particularly challenging to assess its population size and distribution in the wild using traditional survey methods (Adeniji et al., 2023; Zanvo et al., 2023, 2020). The genus *Philantomba* lacks essential data on age at last reproduction, mortality rate, population density and the seasonality of both mortality and dispersal in wild populations (Houngbegnon et al., 2019; van Vliet and Nasi, 2019), which are crucial for assessing the sustainability of hunting. Rodents represent another understudied taxon, despite being the primary source of animal protein for rural populations and contributing significantly to their dietary intake (Assogbadjo et al., 2005; Missoup et al., 2021). The main limiting factor is the lack of comprehensive knowledge about their ecology and population densities (Assogbadjo et al., 2005). Thanks to their high reproductive rates, many rodent species are supposed to have managed to withstand recurrent hunting without facing extinction (El Bizri et al., 2017). However, assessing the abundance of bushmeat species populations should be considered the first and most essential parameter to acquire in order to improve the sustainability surveys in Africa.

In Africa, the bushmeat trade is estimated to impact over 500 species (BES Press Office, 2020), with more than 5 million tonnes consumed annually (Nasi et al., 2011), posing a significant threat to biodiversity. Bushmeat provides 50–80 % of protein intake in some rural communities and is deeply embedded in cultural traditions while mostly carried out illegally, often complicating conservation efforts (Fa et al., 2003; Friant et al., 2015). Despite its importance, research on wildlife exploitation sustainability in Africa remains underrepresented, accounting for only 28 % of total bushmeat studies ($n = 43$). Until now, only 10 African countries have been subject to investigations (totalling 12 surveys; see Appendix S7. Fig. S2), underscoring the lack of required data availability on bushmeat species in tropical Africa (Groom et al., 2023). Indeed, as highlighted above, conducting wildlife exploitation sustainability surveys requires extensive data and long-term monitoring of wildlife population density together with critical biological parameters for target species. Indeed, basic indice-based methods typically necessitate data on population density, age-structure, and harvest intensity, at the ecosystem scale (Borgerson et al., 2023; Camera et al., 2023; Moreno-Zarate et al., 2023). Besides, more complex, model-based methods require not only these parameters but also vital life-history

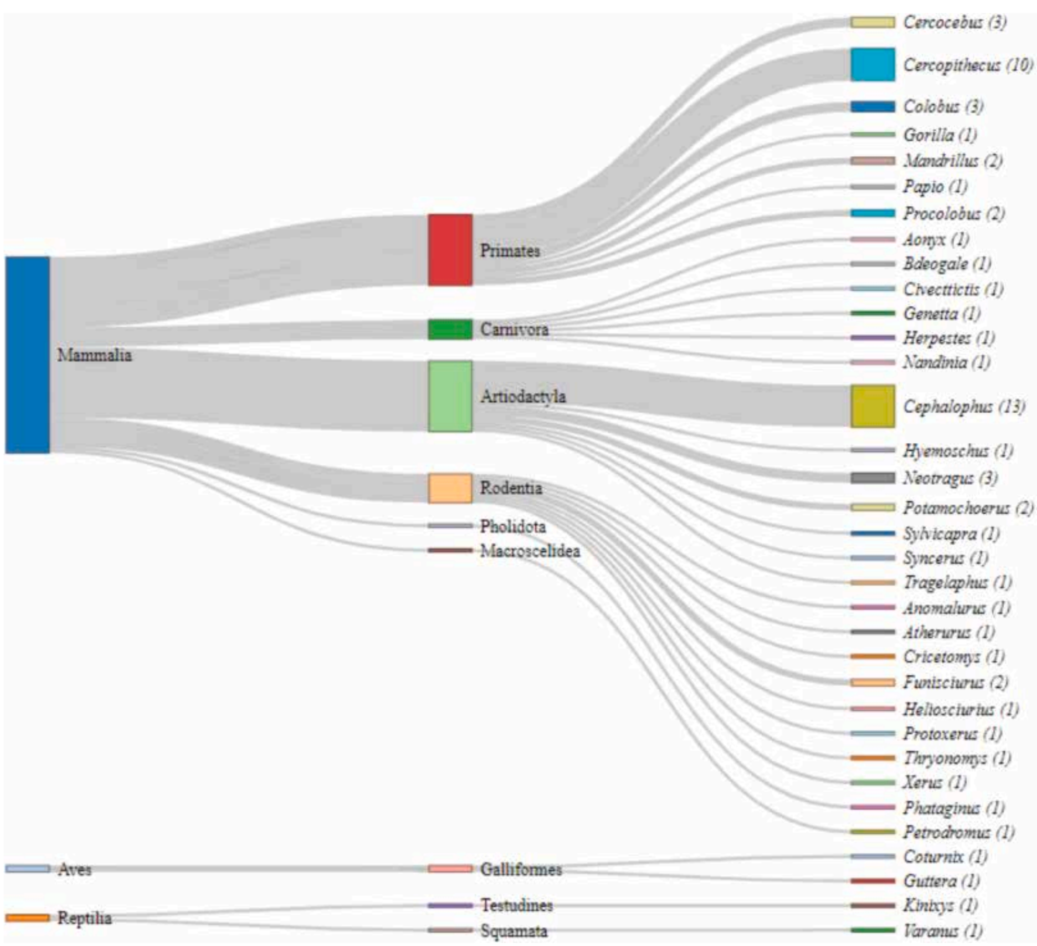

Fig. 3. Sankey diagram of the taxa (genus-level) studied in bushmeat sustainability assessments across tropical Africa. Number of studies between parentheses.

metrics, such as the maximum intrinsic population growth rate for species, which can be challenging to estimate from wild species (Jurado-Molina et al., 2021; Manlik et al., 2022). This challenge is even more pronounced in developing African countries, where biodiversity management infrastructures are inadequately maintained. We argue that firstly, the political prioritization of bushmeat exploitation (including the sector's legalization), combined with the durable support toward dedicated infrastructures, could facilitate the long-term collection of bushmeat data in Africa. Additionally, it may enhance state oversight of hunting and trade activities by enabling informed management measures and the estimation of realistic harvest volumes measures (Groom et al., 2023). Secondly, researchers and protected area managers should work within a collaborative framework to collect the required data on bushmeat species. In this context, participatory surveys, such as involving hunters in monitoring pregnant females, is an economically efficient approach that could provide valuable insights into reproductive patterns (El Bizri et al., 2021).

Advancements in methodologies and technologies also present opportunities to bridge the knowledge gap on African bushmeat species, notably by enhancing our understanding of demographic parameters for forest mammals. These include modern camera traps (Khwaja et al., 2019; Nakashima et al., 2021), non-invasive DNA sampling (Bell et al., 2024; Sun et al., 2024), injectable sensors, electronic tags and passive integrated transponder tags (Ousterhout and Burkhart, 2017), microchip implants and vaginal implant transmitters (Newbolt et al., 2017), advanced acoustic monitoring systems (Crossin et al., 2017), together with state-of-the-art telemetry systems using ultra-light GPS devices (Alippi et al., 2017) and satellite/drone surveys (Duporge et al., 2025; Wu et al., 2023). With the provision of substantial financial support, leveraging these innovations could enable better collection of information on the demographic and life-history traits of tropical mammals and in return, improve the bushmeat harvesting sustainability assessments.

It is also important to note that hunting can negatively impact the genetic diversity of exploited wildlife (Allendorf et al., 2008; Chen et al., 2023), yielding to inbred populations and limiting dispersal. In turn, loss of genetic diversity and inbreeding caused by population declines and fragmentation can directly reduce population fitness (Ceballos et al., 2017; Harris et al., 2002). Because threats to wildlife populations act synergistically, and genetic factors are central to the challenges they face, genetic information can play a critical role in informing the sustainability of bushmeat hunting. The genomics revolution has expanded the field of population genomics, enabling high-throughput sequencing to be applied to a wide array of organisms, including rare or elusive species (Luikart et al., 2019; Rajora, 2019; Supple and Shapiro, 2018). Consequently, genomic approaches are vital to integrate into bushmeat exploitation surveys, for gaining fundamental insights into population demography and health (Coltman, 2008; Wolfe et al., 2000).

We conclude that effective bushmeat exploitation surveys require a multifaceted approach integrating societal involvement, strategic planning for data collection, and the full adoption of advanced wildlife survey technologies. For tropical Africa, where the stakes are particularly high, long-term policies prioritizing the bushmeat issue are essential to ensure sustainable management and conservation efforts. Despite the recognition of these avenues, the overall conclusion of our systematic review is that the sustainability of the bushmeat trade in tropical Africa remains to be determined.

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CRediT authorship contribution statement

Gilles Renaud Mahugnon Adounkè: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Emilie Lecompte:** Writing – review & editing, Project administration, Funding acquisition. **Akomian Fortuné Azihou:** Writing – review & editing. **Mireille Scholastique Toyi:** Writing – review & editing. **Brice Augustin Sinsin:** Writing – review & editing. **Bernard Hugueny:** Writing – review & editing. **Philippe Gaubert:** Conceptualization, Data curation, Funding acquisition, Project administration, Supervision, Validation, Writing – original draft. **Chabi Adéyèmi Marc Sylvestre Djagoun:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – original draft.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve the readability of the English language. After using this tool, the authors reviewed and edited the content as needed and took full responsibility for the content of the published article.

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Declaration of competing interest

The authors declare that they have no competing interest.

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Data availability

All data used in this study are available as an appendix

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