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Red Listing African Goliath Beetles: Assessing Threats and Conservation Needs

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ABSTRACT

The loss of biodiversity is one of the most critical global environmental challenges, driven by deforestation, habitat fragmentation and overexploitation. This study focuses on the biodiversity crisis in Africa, with particular emphasis on the conservation status of the giant Goliath beetles (genus *Goliathus* Lamarck, Scarabaeidae: Cetoniinae). These beetles, renowned for their large size and striking colouration, are endemic to sub-Saharan Africa. They face significant threats from habitat loss and, potentially, from intensive harvesting for the entomological trade. The conservation status of Goliath beetles needs to be better understood. In this paper, we perform a Red List assessment based on our research carried out opportunistically for 30 years (1994–2024). We present critical data on four taxa of the genus *Goliathus*: *Goliathus goliatus* (Linnaeus), *Goliathus meleagris* Sjöstedt (currently classified as a well-differentiated subspecies of *G. goliatus*), *Goliathus regius* Klug and *Goliathus cacicus* Olivier. Two additional species, *Goliathus orientalis* Moser (endemic of Tanzania and Northern Mozambique) and *Goliathus albosignatus* Boheman (broadly distributed in Southern and Eastern Africa), were not assessed due to a lack of original field data. From data gathered opportunistically through incidental observations and field encounters, we analyse habitat preferences, the impact of deforestation and seasonal activity patterns. Our findings highlight the vulnerability of Goliath beetles to ongoing human-induced threats and underline the need for more targeted conservation efforts. However, using Salafsky's standard classification, there were different threats affecting the various species, and the needed conservation actions should, therefore, be species-specific. We applied the 2024 International Union for Conservation of Nature (IUCN) criteria to each species to inform future conservation strategies and support the survival of these remarkable beetles in the wild. Our assessment indicates that *G. cacicus* should be listed as Critically Endangered due to its catastrophic decline over recent decades, whilst *G. regius* qualifies as Endangered. Both species inhabit forest habitats in Western Africa. The other taxa assessed were found to be of lesser concern and evaluated as Near Threatened. This study contributes to our broader understanding of biodiversity loss in Africa, stressing the urgency of protecting critical insect populations. In particular, we present a salient example of how multiple overlapping threats endanger biodiversity across large parts of Africa, and in particular forest species in West Africa.

1 | Introduction

The loss of biodiversity represents one of the most critical challenges facing today's global environment today (Mora and Sale 2011; Hughes 2017). The decline in the variety and abundance of life forms is driven by multiple factors, including habitat loss (Brooks et al. 2002; Hanski 2011; Karger et al. 2021), pollution (McNeely 1992; Cristiano et al. 2021; Singh, Verma, and Prakash 2023) and overhunting (Abernethy et al. 2013; Peres et al. 2016; Ripple et al. 2016) identified as the most critical threats (Stork 1997; Singh 2002; Sánchez-Bayo and Wyckhuys 2019). These threats often interact synergistically, heightening the risk of biodiversity loss. For instance, habitat fragmentation can limit species dispersal, making them more vulnerable to overhunting (Peres et al. 2016). Additionally, conflicts and wars can lead to large-scale displacements of refugees, resulting in significant ecological impacts in new settlement areas (Behangana et al. 2024; Walde et al. 2024). The repercussions of biodiversity loss extend beyond the extinction of individual species, significantly affecting essential ecosystem services such as pollination, water purification, agriculture and climate regulation, all of which are vital for human well-being (Ostfeld and LoGiudice 2003; Worm et al. 2006; Tekalign et al. 2017). Addressing this complex issue necessitates a comprehensive understanding of its underlying causes, alongside a concerted effort to mitigate their impacts through effective conservation strategies and sustainable management practices. By integrating ecological knowledge with socio-economic considerations, we can devise targeted interventions that promote both biodiversity conservation and the resilience of ecosystems, ultimately benefiting human communities reliant on these vital services.

Biodiversity loss in the African continent, as in many other parts of the world, is driven by (i) deforestation and fragmentation of natural habitats (Green et al. 2013; Leisher et al. 2022) and (ii) overexploitation because of the extraction of species for consumption as well as the international trade (Van Velden et al. 2020; Fa, Funk, and Nasi 2023). The combined effects of these threats often lead to the degradation of ecosystems and a significant decline in many animal and plant species (for specific African examples, see Luiselli et al. 2022, 2024).

With 350,000 described species grouped into 24 superfamilies and 235 families, beetles (Coleoptera) constitute the most speciose order amongst all living organisms, including plants (Bouchard et al. 2017). These insects provide many ecosystem functions: for instance, dung beetles contribute remarkably to nutrient cycling, bioturbation, plant growth enhancement, secondary seed dispersal and parasite control, and even have a role in pollination and trophic regulation (Nichols et al. 2008; Slade, Mann, and Lewis 2011). Therefore, the conservation of beetles is very important to continue helping the ecosystem maintain stability (New 2007). Beetles, like many other life forms, are affected by the same anthropogenic threats (Tind Nielsen 2007). However, they are amongst the least studied taxa in terms of conservation status (Carpaneto, Mazziotta, and Valerio 2007; Homburg et al. 2019), resulting in fewer IUCN Red List assessments compared to vertebrates facing similar threats and declines. The IUCN Red List of Threatened Species is the most comprehensive resource detailing the global conservation status of plants and animals and has become a powerful tool for planning, management, monitoring and decision-making (Rodrigues et al. 2006; Bennun et al. 2018).

Despite their ecological importance and being one of the most numerous groups globally, many beetle species face significant threats to survival (New 2007). Therefore, there is an urgent need to explore the specific threats facing this group of insects, define their conservation status and conduct comprehensive Red List assessments to identify and protect species that may be experiencing unstudied declines (Luiselli 2023).

Amongst the most iconic African beetles are the giant African Goliath beetles (genus *Goliathus*; Scarabaeidae: Cetoniinae) (Figure 1). These beetles, currently comprising five species with three subspecies (De Palma et al. 2020), are endemic to sub-Saharan Africa (Mawdsley 2013). Renowned for their large size and striking colouration, Goliath beetles are amongst the largest and most conspicuously coloured coleopterans in the world. Their size, attractiveness and iconic status amongst beetles make them highly valuable in the entomological trade. Consequently, Goliath beetles are subject to intense harvesting by local collectors (Muafor and LeGall 2011). Additionally, because these beetles inhabit forested areas, their habitats are experiencing severe deforestation threats (Mallon et al. 2015; Luiselli 2024). The combined effects of habitat loss and, potentially, extensive harvesting make specific *Goliathus* populations particularly vulnerable to decline. Various studies have reported decreasing abundance in these beetles (Muafor and LeGall 2011; Dendi et al. 2021, 2023). Given this situation, Red List assessments of these beetles are urgently needed, using the appropriate IUCN (2024) criteria to quantify their extinction risks. Such assessments will provide objective data to guide conservation efforts, ensure the survival of these remarkable insects in the wild and regulate their removal from natural habitats.

The IUCN has yet to assess African Goliath beetles (genus *Goliathus*) for red listing. This article therefore aims to provide information that can support assessments of these species according to the IUCN (2024) criteria. These data are derived from ecological field research undertaken by the authors between 1994

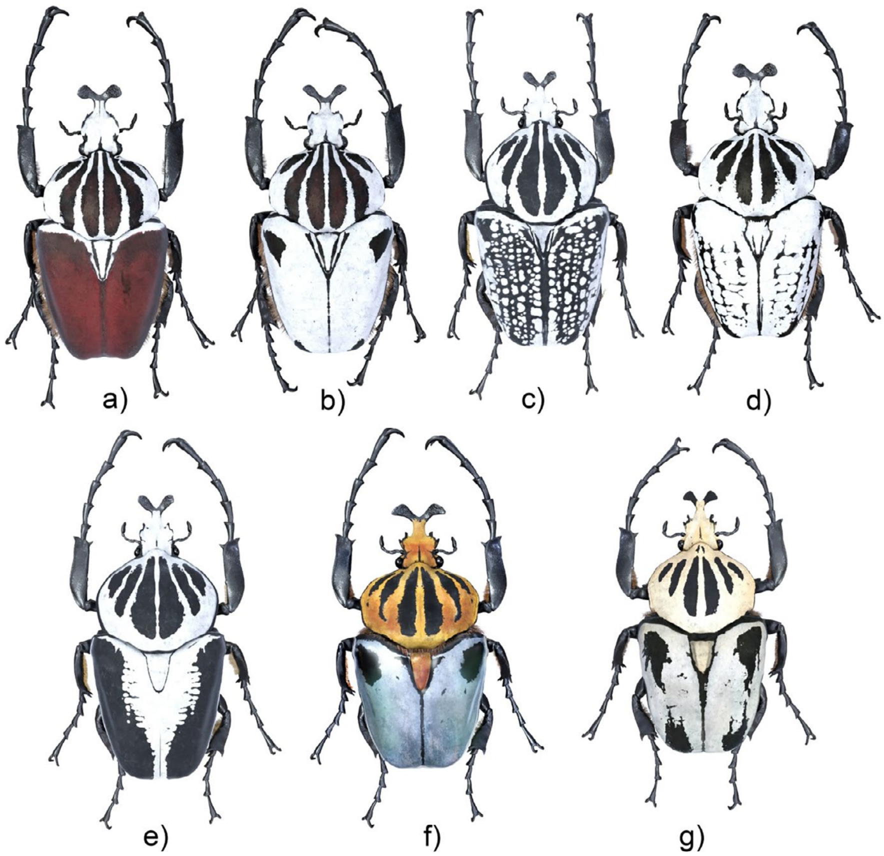

FIGURE 1 | Silhouettes of the males of some of the *Goliathus* species: (a and b) *Goliathus goliatus*, (c) *Goliathus g. meleagris*, (d) *Goliathus orientalis usambarensis*, (e) *Goliathus regius*, (f) *Goliathus cacicus* and (g) hybrid *Goliathus regius* × *Goliathus cacicus*. Artwork by Marko Steffensen.

and 2024 in Africa. Owing to logistic and funding limitations, our fieldwork covered only a subset of countries where *Goliathus* species are found (Liberia, Guinea, Cote d'Ivoire, Ghana, Burkina Faso, Benin, Nigeria, Cameroon, R.D. Congo, Uganda, South Sudan). Therefore, only four valid taxa in the genus could be assessed: (i) *Goliathus goliatus*, (ii) *Goliathus meleagris* (currently taxonomically ranked as a well-differentiated subspecies of *G. goliatus*, but here operationally treated as a separate species), (iii) *Goliathus regius* and (iv) *Goliathus cacicus*. Thus, we here refer to '*Goliathus goliatus*' as the nominal subspecies of that species (*G. goliatus goliatus*), which is broadly distributed in Central Africa, and to '*Goliathus meleagris*' as the valid subspecies of *G. goliatus*, which is broadly distributed in Southern Central Africa, according to the last revision of the group by De Palma et al. (2020).

Specifically, in this work we will (i) review what is known about the ecology and biogeography of the taxa of interest in the genus *Goliathus*; (ii) give new quantitative data collected in nature on the habitat use, phenology and general ecology of the various species; (iii) provide an assessment of the threats and population status of each species and (iv) define a Red List status for each species according to IUCN (2024) criteria.

2 | Data Availability – General Methodological Considerations

In this study, we used opportunistic records on the occurrence and activity of the four Goliath beetles studied. Table 1 shows the sample sizes of individuals examined for each beetle species, country and habitat variables investigated.

Within each country, we selected areas to study Goliath beetles based on one or more of the following criteria: (i) random searches in sites that were also used for other field studies (especially on reptiles) and therefore intensively monitored/surveyed; (ii) localities that were traditional harvest grounds for Goliath beetles by hunters and dealers (for instance, Banco Forest, Issia and Tai Forests in Cote d'Ivoire; Budongo Forest in Uganda, etc.); (iii) localities that were pointed to us by experienced persons during face-to-face interviews and (iv) localities indicated in labels of specimens encountered in local schools and small private collections.

We implemented a rigorous validation and verification process to ensure the accuracy and reliability of data collected in these study areas. For each selected site, data were cross-referenced with historical records, including those from past biodiversity assessments and species-specific surveys where available. Additionally, we used interviews with local hunters, dealers and field experts to verify reported Goliath beetle locations and assess harvesting patterns. Each specimen encountered was documented and compared against known morphological characteristics to confirm identification, focusing on distinguishing closely related species. Furthermore, specimens encountered in local collections were verified by cross-referencing label data with geographical and historical occurrence records to enhance reliability. This approach ensured our findings reflected

TABLE 1 | Synthesis of the sample sizes used to synthesise the ecology and conservation of the various Goliath beetle species.

Genus	Species	Sample size (original standardised data)	Description	Countries
Goliathus	*goliatus*	110	Tree size selection	Nigeria, Uganda
		216	Habitat selection	Nigeria, Uganda
		194	Monthly activity patterns	Nigeria, Uganda
		63	Daily activity patterns	Nigeria, Uganda
		248	Year-by-year decline	Nigeria
		Unquantified	Biogeography; other aspects	Benin, Nigeria, Cameroon, D.R. Congo, Uganda, South Sudan
Goliathus	*meleagris*	101	Habitat selection	D.R. Congo
		232	Monthly activity patterns	D.R. Congo
		24	Daily activity patterns	D.R. Congo
		Unquantified	Biogeography; other aspects	D.R. Congo
Goliathus	*regius*	69	Habitat selection	Cote d'Ivoire
		69	Monthly activity patterns	Cote d'Ivoire
		Unquantified	Biogeography; other aspects	Liberia, Guinea, Cote d'Ivoire, Ghana, Togo
Goliathus	*cacicus*	61	Habitat selection	Cote d'Ivoire
		61	Monthly activity patterns	Cote d'Ivoire
		Unquantified	Biogeography; other aspects	Liberia, Guinea, Cote d'Ivoire, Ghana

accurate, site-specific information and minimised sampling and species misidentification errors.

Goliath beetles were studied using a suite of field methods. Initial attempts using traps baited with ripe fruit proved inefficient, yielding only a few captures. To improve our success, we shifted our focus to conducting random surveys across potential *Goliathus* habitats, concentrating on trees with visible sap, as these beetles are known to feed on sap during the daytime (Muafor and LeGall 2011). We frequently observed beetles flying high in the treetops during morning surveys. However, capturing them was challenging due to their fast and elevated flight patterns. To address this, we recorded the GPS coordinates of these sighting locations and returned to the same areas at night. Night-time provided better opportunities to observe the beetles, which rest on branches after dusk. To capture the insects, we used torches and long bamboo sticks. A torch was placed on the ground, gently shaking the tree branches. The disturbed beetles, attracted by the light, would drop towards the torch, allowing us to collect and measure them before releasing them back into their natural habitat. During our surveys, we also discovered dead Goliath beetles or their remains, which we collected as vouchers. Most of these findings were male beetles, likely preyed upon by birds of prey. Another potential cause of death could have been the fierce and aggressive combat between males competing for females, as many specimens had scratches on the elytra and broken legs, particularly the anterior pair, suggesting injuries sustained during these battles.

Whenever possible, secondary school science laboratories, both in urban and rural areas, were visited to identify specimens possibly collected as educational demonstrations for students, as well as the entomological scientific collections of various universities (e.g., Makerere University in Kampala, Uganda; CNRST and Ouagadougou University in Burkina Faso, Lomé University in Togo, Juba University in South Sudan, etc.). When *Goliathus* specimens were found, their tags were consulted, or their locality of origin and collection period were investigated as best as possible.

We also interviewed experienced persons from communities situated around forest areas (hunters, farmers, snail and mushroom gatherers, collectors of timber and non-timber products) using a standardised questionnaire to inquiry about the presence of *Goliathus* beetles in their places (the questionnaire and the detailed methodological description are given in Dendi et al. 2023). Interviews with local informants focused on investigating changes in the abundance of *Goliathus* populations in each area and within a given time interval (usually over the last 20 years) (see Dendi et al. 2023 for more details). Interviews were conducted mainly in traditional harvesting localities of these beetles in Liberia, Ivory Coast, Nigeria, Cameroon, D.R. Congo and Uganda. In each site, people of different ages (21–85 years) were interviewed to stratify the answers by age group. This methodology allows to reconstruct (increasing or decreasing) abundance trends for a target species. Where a species is rarefying, it will be described as present/abundant more frequently by older interviewees whilst it will be considered mostly absent or very rare by younger interviewees. This approach has been successfully applied previously, both with Goliath beetles (Dendi et al. 2023) and with other animal species (Luiselli et al. 2021). In all cases, interviewees were informed of the scope of the research; no minors (< 21 years) were interviewed. No group interviews were undertaken. Therefore, stable or decreasing population abundance trends for the various species were assessed (i) based on the outcome of interviews stratified by respondent's age (see above) and (ii) according to field observations carried out in some sites that have been repeatedly sampled over the last 20 years (more details in the various species' accounts).

After each interview, using a snow-ball-procedure, we tried to locate any *Goliathus* specimens available in local villages, asking the owners for their locality of origin and collection period.

When a beetle (dead or alive) was observed, we measured the diameter at the breast height of all trees with a radius of 20 m surrounding the sighting spot; these measurements were then averaged.

The following categories were used to classify tree diameters:

Category 0: A few (1–2) isolated trees present but non-arboreal vegetation dominant; Category 1: < 20 cm; Category 2: 20.1–40 cm; Category 3: 40.1–70 cm and Category 4: > 70 cm.

To analyse differences in the frequency of observed individuals amongst habitats, months or locality, we used contingency tables and carried out χ^2 tests. We employed Spearman's rank correlation coefficients to examine correlations between the number of observed individuals and monthly rainfall (measured as the number of rainy days per month) (Sokal and Rohlf 2013).

Habitat niche breadth (B_s) was determined using Simpson's diversity index (He and Hu 2005). When comparing two species, higher B_s values indicate that a species is a more habitat generalist. Habitat niche overlap (O_{jk}) was calculated using Pianka's (1974) symmetric equation. This metric ranges from 0 (indicating no overlap in habitat use between two species) to 1 (indicating complete overlap).

For the classification of threats, we used the 'World Conservation Union-Conservation Measures Partnership (IUCN-CMP) classification of direct threats to biodiversity (version 1.1)', and for the classification of actions to reverse the threats, we used the 'World Conservation Union-Conservation Measures Partnership (IUCN-CMP) classification of conservation actions (version 1.1)', as reported in Salafsky et al. (2008).

Alpha was set at 5%, all tests were two-tailed.

3 | Species Accounts

3.1 | *Goliathus goliatus* Linnaeus

3.1.1 | Data Availability

We observed *G. goliatus* from 1996 to 2024, especially in south-eastern Nigeria, with additional data collected in Cameroon, Benin, South Sudan and Uganda. Since we could not dedicate equal effort to each month or habitat type, the quantitative data we present may be partially biased. However, given the long time spent in the field in the potential areas of the presence of the species, we are confident that the potential biases would not profoundly affect the collected data.

3.1.2 | Suggested Red List Category and Criteria

NEAR THREATENED (NT).

3.1.3 | Justification

Goliathus goliatus exhibits a vast distribution range and remains locally common across its expansive range in Central Africa (De Palma et al. 2020). This species inhabits many of the vast Congo Basin tropical forests (e.g., in Gabon, Northern Republic of Congo and Northern Democratic Republic of Congo), currently under negligible anthropogenic pressure. However, there are clear signs of decline in several countries studied, such as Benin, Nigeria, Cameroon and Uganda. Such decline can be attributed to significant habitat loss due to deforestation and, in selected localities, potentially also to high collection rates for the international entomological trade by local communities. These factors suggest that the species is approaching the criteria required by the IUCN to be classified as 'Threatened'.

3.1.4 | Geographic Range and Taxonomic Considerations

This *Goliathus* species has the most extensive distribution range in sub-Saharan Africa (Croizat 1994). It spans the Congolian rainforest block continuously from Cross River State in South-Eastern Nigeria to Kenya's Kakamega Forest and Nandi Hills, and from Southern Chad to the Central Democratic Republic of Congo (De Palma et al. 2020). Countries within its range include Benin, Nigeria, Cameroon, Equatorial Guinea, Central African Republic, Gabon, Congo, the Democratic Republic of Congo, South Sudan, Uganda, Rwanda and Kenya.

G. goliatus appears particularly abundant in Cameroon where it is known from many localities in the South-Western Province, including Korup National Park, Konye, Kobe, Manfe, Buea, Ibemi and the surroundings of Douala and Yaoundé. In the Democratic Republic of Congo, the species has been heavily collected in the North Kivu and Ituri Provinces, with historical hunting grounds being Limbe, Ituri and Kasuo. For other countries, like the Central African Republic, the labelling of the vouchers available in collections are generic (e.g., 'Bangui') and not always reliable.

Despite its extensive range, the species' distribution appears fragmented around the borders of its East African range in Uganda, Kenya and Rwanda. In Uganda, we have observed it in Maramagambo Forest, Bwindi, Kibale, Budongo, Mabira-Najembe and Mukono Forests. However, its distribution may be wider than presently known, including in relatively well-preserved forested fragments in central Uganda.

In Kenya, based on the specimens stored at the National Museums of Kenya, Invertebrate Zoology reference collection, *G. goliatus* is present at Kakamega and Kaimosi Forests (specimens collected in March 1914, 1915, January 1954, December 1931, 1934 and February 1935) and in North Nandi Forest (collected in December 1978). The specimens originating from Kenya in the ongoing entomological trade often indicate the Nandi Hills as a main source.

Goliathus goliatus displays disjunct and isolated populations that are highly threatened in West Africa. In Benin, the species has been recorded in the Pobé Forest, near the Nigerian border. This forest is found more than 700 km from the nearest known presence site for *G. goliatus* (Cross River State, South-eastern Nigeria), thus the Pobé Forest population may represent a relictual and highly threatened population (Le Gall 2010).

There are also records suggesting that *G. goliatus* may have occurred or still occurs in Togo, as evidenced by four specimens (two males and two females) in the scientific collections of the Centre Nationale de la Recherche Scientifique (CNRST) in Ouagadougou, Burkina Faso, labelled as 'Togo' and captured in 2005 (Figure S1). In the same collection, we observed several other beetles captured in 2005 in Fazao Malfakassa, including Togo's endemic *Fornasinius klingbeili*. It is therefore, unlikely that the four *G. goliatus* specimens have been mislabelled. In addition, one of us (M.M.) received a male individual labelled 'Kloto (Togo, 01/1973)' from a reliable source.

Yet, intensive surveys in the last 15 years in Togo, including Fazao Malfakassa National Park, by Luiselli, Segniagbeto and colleagues, have not encountered any free-ranging individuals of *G. goliatus*, suggesting that its presence in the country is uncertain and that the insect might even be locally extinct. It is notable that forest patches within the Dahomey Gap (for instance Fazao Malfakassa) harbour other species with a distribution pattern like *G. goliatus*, such as Jameson's green mamba (*Dendroaspis jamesoni*). The discovery of this elapid snake in a secondary hilly forest in Fazao Malfakassa in recent years, a species with a general pan-African distribution pattern nearly identical to that of *G. goliatus*, emphasises the potential for relict populations of *G. goliatus* to exist in Togo, although further confirmation is needed (Figure S1; G.H. Segniagbeto, L. Luiselli et al., unpublished data).

3.1.5 | Current Population Trend

DECLINING.

Available data on *G. goliatus* population trends consistently suggest a general decline over the years, although information is limited across the species' vast range. In South-eastern Nigeria, Dendi et al. (2021) reported a decrease in the total number of individuals observed in the same forest area, from 113 (1996–2004) to 73 (2005–2013) and 62 (2014–2021), with a nearly constant field effort of 61–66 field days. Similarly, in a forest area in Cameroon, Muafor and LeGall (2011) noted that the *G. goliatus* population was 'highly declining due to habitat destruction and, potentially, exploitation of adults for insect trade'. In Benin, our recent surveys (unpublished) revealed that the species is very rare, whereas it was common albeit localised to a single area in the early 2000s (Le Gall 2010). In Uganda's Mukono Forest, experienced local community members interviewed in 2023 by us suggested that *G. goliatus* is noticeably scarcer now than 15–20 years ago, mainly due to habitat loss and, potentially, overharvesting. Recent interview surveys in Kakamega Forest (Kenya) revealed that, upon showing images of the species to local people, they unambiguously responded that the beetles are becoming increasingly rarer, suggesting an ongoing decline in this part of the insect's range.

3.1.6 | Habitat and Ecology

This species is linked to primary and secondary rainforests, particularly in hilly and mountainous areas (Table 2). It is more abundant in montane forests, as observed in Western Cameroon (Muafor et al. 2012) and South-eastern Nigeria (Cross River State). In this latter area, we observed *G. goliatus* primarily in hilly-montane rainforest (500–1600 m a.s.l.) with tree species such as *Musanga cecropioides*, *Irvingia gabonensis, Berlinia africana*, *Coula edulis, Hannoa klaineana* and *Klainedoxa gabonensis*. However, it was more frequently found on *Vernonia* spp. and *Prunus africana*. These same plant species were associated with this beetle species in central Uganda (Mukono, Mabira-Najembe and Budongo Forests; our unpublished data), suggesting a relatively stable microhabitat preference across its wide range.

Whilst *G. goliatus* is more frequently associated with extensive forests, it can also be found in forest fragments surrounded by plantations, or in gallery forests. For instance, in the Mabira-Najembe Forest (Uganda) this species is also frequently seen along forest edges (our unpublished observations).

Our opportunistic records on 216 adult *G. goliatus* from Nigeria and Uganda revealed that 76.4% occurred in mature/primary forest patches, 23.6% in secondary forests, but none in plantations/deforested habitats, showing a statistically significant preference for mature forests ($\chi^2 = 60.2$, $df = 2$, $p < 0.0001$). For 110 of the 216 opportunistic observations, microhabitat data based on average tree size in the observation site were collected. Observations indicated a positive correlation between the frequency of sightings and the increasing average size of the trees ($r = 0.935$, $n = 5$, $p < 0.05$), confirming that *G. goliatus* prefers sites with larger mature trees (Figure 2).

The observed adult sex ratio seems uneven, with males more numerous than females or at least more easily visible due to their more frequent flying and active movement.

Adults are present year-round, with peak activity from November–March and especially from December to February (over 80% of observed individuals in Nigeria; our unpublished observations). In Uganda, the species can also be frequently observed from April–June, with a primary peak in February and a secondary peak in May (our unpublished observations). In Kenya, based on the labels of collected specimens housed in the National Museums of

TABLE 2 | Summary of the main characteristics of forest habitats of some *Goliathus* populations that have been monitored in detail during the present study.

Species	Locality	Country	Habitat description	Apparent population status
G. goliatus	Cross River National Park and its surroundings	Nigeria	Closed canopy hilly/montane forest, dominated by *Albizia zygia, Alstonia boonei, Coelocaryon preussii, Elaeis guineensis, Funtumia africana, Piptadeniastrum africanum, Pycnanthus angolensis, Terminalia ivorensis, Vitex grandifolia*	Fairly abundant but in clear decline (Dendi et al. 2021). Collected specimens are illegally exported to Cameroon for the international market, and especially the white morphs are searched for (and declining)
G. goliatus	Korup National Park	Cameroon	Closed canopy lowland semi-deciduous forest dominated by large, gregarious Caesalpiniaceae species and *Albizia zygia, Alstonia boonei, Coelocaryon preussii, Elaeis guineensis, Pycnanthus angolensis, Terminalia ivorensis, Vitex grandifolia* (Chuyong, Newbery, and Songwe 2000)	Widespread but apparently not-abundant
G. goliatus	Mamfé	Cameroon	Closed-canopy evergreen ecosystem with two unique types of vegetation: Mid-Altitude Forest vegetation and Lowland Rain Forest vegetation	Abundant
G. regius	Kakum National Park	Ghana	The dominant tree species in the Moist evergreen lowland forest with *Triplochiton scleroxylon, Celtis* spp., *Cynometra* spp. as dominant species. Mostly secondary and mature secondary vegetation	Fairly abundant
G. regius	Bobiri Forest	Ghana	Relatively sunny forest, with the dominant tree species being various *Celtis* species and *Triplochiton scleroxylon*	Fairly abundant
G. cacicus	Banco Forest	Cote d'Ivoire	Shady psammohygrophilous forest with *Turraeanthus africanus* and *Heisteria parvifolia, Lophira alata, Mitragyna ledermannii, Guarea cedrata, Petersianthus macrocarpus, Khaya ivorensis, Tieghemella heckelli, Entandrophragma utile, Dacryodes klaineana, Turraeanthus africanus, Milicia excelsa, Tectona grandis, Entandrophragma angolense*	Extremely rare/possibly extirpated
G. regius and *G. cacicus*	Southern Comoé National Park	Cote d'Ivoire	Open forests and gallery forests, characterised by a cover of between 70% and 90%, consisting of trees up to 15 m in height, including *Isoberlinia doka, Daniellia oliveri, Pterocarpus erinaceus, Uapaca togoensis, Parkia biglobosa, Vitellaria paradoxa*	*G. regius* is fairly abundant, especially in open forests; *G. cacicus* is rare and localised to gallery forest habitat
G. regius and *G. cacicus*	Taï National Park	Cote d'Ivoire	Dense humid pelohergephilous forest with *Diospyros* spp. and *Mapania* spp. as dominant species, and with *Eremospatha hookeri, Tetracera potatoria for vines; Chytranthus setosus, Diopsyros gabunensis, Diospyros chevalieri, Drypetes aylmeri, Soyauxia floribunda, Cephaelis yapoensis, Tarrietia utilis* as trees and shrubs	*G. regius* is fairly abundant, especially in the altered forest of the Northern part of the protected area; *G. cacicus* is rare and localised only to the Southern part of the protected area

(Continues)

TABLE 2 | (Continued)

Species	Locality	Country	Habitat description	Apparent population status
G. regius and *G. cacicus*	Man region	Cote d'Ivoire	Hilly areas with vegetation consisting of dense semi-deciduous humid forest with secondary vegetation resulting from agricultural activities	*G. regius* is widespread and abundant; *G. cacicus* is extremely rare and localised to very few humid forest patches
G. regius and *G. cacicus*	Danané/Nimba	Cote d'Ivoire	Forest patches are in the low-lying and wettest areas of the region. They are evergreen forests with tree heights of up to 30–35 m and forming a multi-layered stand, large vines and shrubs in the undergrowth. Tree species would include *Cola gigantea, Funtumia elastica, Triplochiton scleroxylon, Piptadeniastrum africana, Trilepisium madagascariense, Turraeanthus africanus, Parkia bicolor, Tectaria fernandaensis, Lonchitis currori, Synsepalum cerasifera, Syzygium guinéense, Santiria trimera, Homalium smythei, Syzygium standtiiqui*	*G. regius* is widespread and abundant; *G. cacicus* has a scattered local distribution but it is more abundant here than in any other surveyed region

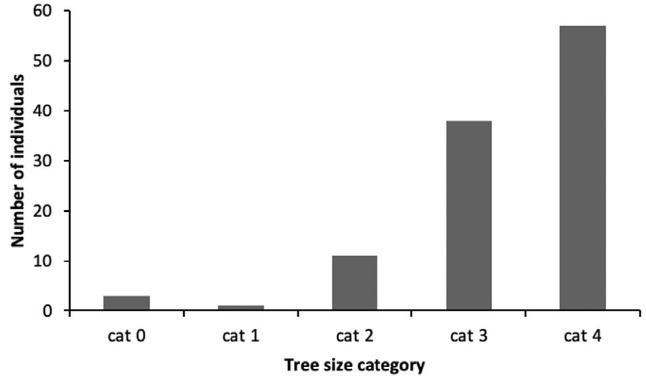

FIGURE 2 | Tree size selection by opportunistically observed *Goliathus goliatus* in Nigeria and Uganda (total $n = 110$). Symbols: Cat 0 = on a place where only one or two isolated trees are present whereas non-arboreal plants are dominant, cat 1 = majority of the plants was < 20 cm diameter; cat 2 = majority of the plants was 20.1–40 cm; cat 3 = majority of the plants was 40.1–70 cm and cat 4 = majority of the plants was > 70 cm. For the statistical details, see the text.

Kenya, *G. goliatus* is active from December to March, which is consistent with our data from Nigeria.

Overall, the number of individuals observed during our surveys was significantly negatively correlated with the number of rainy days per month (Spearman's $r_s = 0.614$, $p < 0.05$) (Figure 3a) confirming that *G. goliatus* adults are mostly active during the dry season.

Adults were observed at all times of the day, with a slight tendency to be more easily encountered in the evening and early night hours (Figure 4a).

Nothing is known about the species' larval ecology. However, some authors believe that the larvae of all *Goliathus* species may exhibit a predatory way of life (Vendl and Šípek 2016).

3.1.7 | Use and Trade

Hundreds to thousands of individuals of *G. goliatus* are known to be collected every year in the wild for the international entomological trade, primarily in South-western Cameroon and, to a lesser extent, in Kenya and Uganda. Large males and white morphs, found in South-Western Cameroon (De Palma et al. 2020), are highly valued by insect collectors, leading to their active harvesting by local communities. White morphs tend to decline more quickly than brown morphs because they are more attractive to collectors and less cryptic in their natural habitat (Dendi et al. 2021). Illegal trade of specimens, especially the white-coloured ones, from Nigeria's Cross River to Cameroon, where they are exported to the Western markets, is known (Luiselli et al., unpublished data).

3.1.8 | Conservation Actions

To the best of our knowledge, there are no direct conservation actions specifically aimed at protecting *G. goliatus*. However,

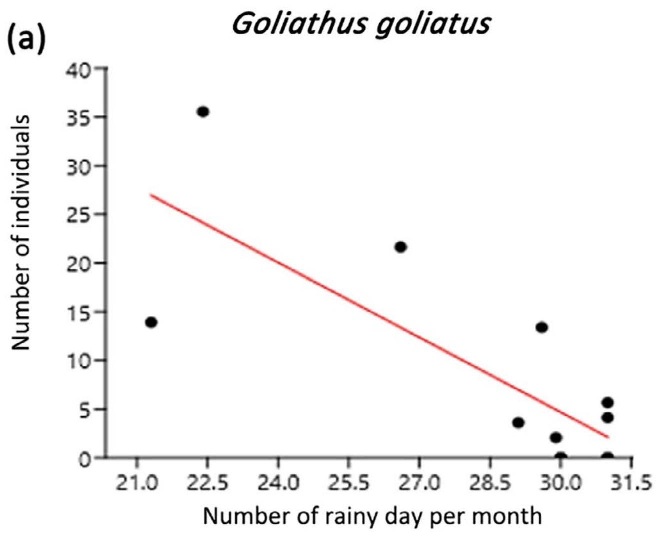

FIGURE 3 | Opposite correlation between the mean number of rainy days per month and the number of observed individuals in *Goliathus goliatus* and *Goliathus meleagris*. For the statistical details, see the text.

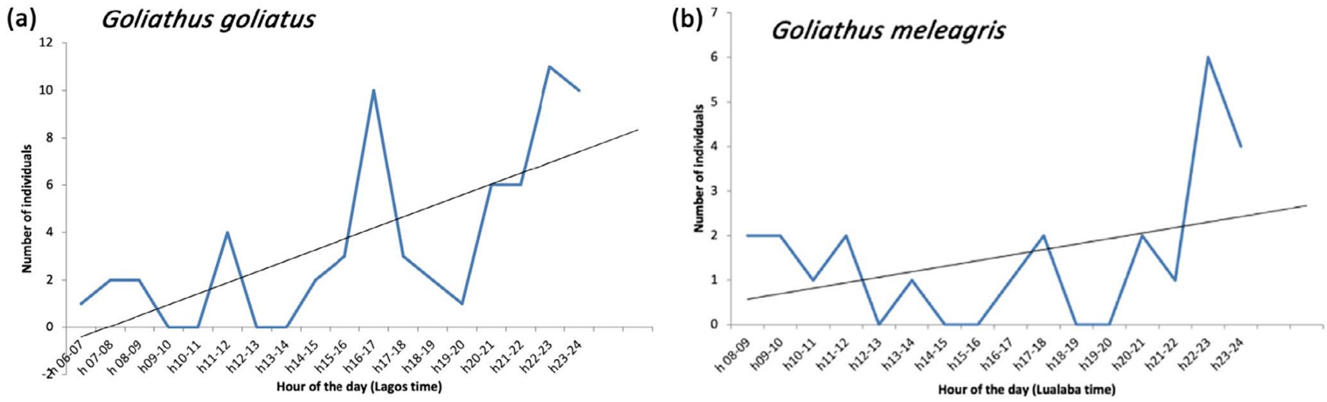

FIGURE 4 | Frequency of sightings of *Goliathus goliatus* and *Goliathus meleagris* in relation to the daily hours.

populations benefit from the general protection afforded to several protected forest areas (national parks, nature reserves or community forests) where it is found. Key protected areas include the Cross River National Park (Nigeria), Mount Cameroon, Korup, Parc de la Mefou, Nki National Parks and Dja Faunal Reserve (Cameroon), Bwindi Impenetrable Forest and Kibale National Parks (Uganda), Southern National Park (South Sudan), Nyungwe Forest and Virunga National Parks (Rwanda) and Kakamega National Reserve and Nandi Forest Reserve (Kenya). Vast and largely pristine, inaccessible or non-exploited forest habitats persist in Gabon, Northern Republic of Congo and Northern Democratic Republic of Congo, in which this insect is evidently not threatened.

3.2 | *Goliathus meleagris*

3.2.1 | Data Availability

We were able to dedicate equal effort each month (overall 10 days per month, spanned between 2015 and 2024) in the Lualaba region of the Democratic Republic of Congo, thus resulting in unbiased seasonality data. As for the other taxa, when possible, we collected data on habitat characteristics and daily activity patterns of the encountered individuals.

3.2.2 | Suggested Red List Category and Criteria

LEAST CONCERN (LC).

3.2.3 | Justification

Goliathus meleagris exhibits a relatively large range in Southern Democratic Republic of Congo, Northern Zambia and Eastern Angola (De Palma et al. 2020), where it is a habitat generalist and locally abundant, even occurring in areas around human settlements. Therefore, it is considered LC in this study. However, its life cycle may depend on the persistence of relatively humid woodland areas, which may face increasing threats due to deforestation, land conversion, mining and climate change. Therefore, a categorisation as NT might be needed if further studies reveal a decline in their populations.

3.2.4 | Geographic Range and Taxonomic Considerations

Goliathus meleagris is endemic to the plateaus of the former Katanga Province (Haut-Katanga and Lualaba) in the Democratic Republic of Congo and neighbouring areas of Angola and Zambia (De Palma et al. 2020). Historical and confirmed records of presence were Khoni (thousands of specimens collected in the 1980s/1999), Kundelungu National Park, Upemba, Sakundundu, Lumambashi, Kaponda, Kansense, Kamina-Kazadi, Kilangwa, Likasi, Muthsasha, Nkonda and in the whole area of Kolwezi.

The taxonomic status of *G. meleagris* has been clarified recently (De Palma et al. 2020). The *Goliathus* populations of Katanga have been previously attributed to *G. orientalis*, a distinct species from Tanzania (Figure 1). In the most recent revision of this genus, De Palma et al. (2020) ranked *meleagris* as a subspecies of *G. goliatus* because of the limited genetic separation between the two taxa, the different ecological characteristics, and the occurrence of morphologically intermediate forms, particularly in the Tanganyika region (Figure S2). Whilst these parameters justify subspecific ranking, the geographical and ecological separation of the two taxa has urged separate assessments and, therefore, their operational treatment as separate species.

3.2.5 | Current Population Trend

STABLE.

The species is widespread but localised within its range. It occupies wooded areas in or around human settlements and towns, and there is no evidence that the species is declining in the regions surveyed.

3.2.6 | Habitat and Ecology

This species occurs in the Central Zambezian Miombo ecoregion's deciduous woodlands and gallery forests (De Palma et al. 2020). The main limiting factor for its presence is humidity since *G. meleagris* does not occur in sites that are too dry or consist exclusively of herbaceous vegetation. Therefore, although *G. meleagris* is a species linked to areas of wooded savannah, it tends to select the wettest and highest canopy sites (De Palma et al. 2020).

Males seem much more numerous than females, or at least more easily visible since they fly more often and appear more active.

Although *G. meleagris* is a common species, no reported ecological studies exist. Our field observations suggest that adults are active year-round, but are most active between November and February, with a peak in January. We observed 232 free-ranging individuals, with a frequency of occurrence significantly uneven across months ($\chi^2 = 137.4$, df $= 11$, $p < 0.0001$) and positively correlated with the mean number of rainy days per month (Spearman's $r_s = 0.626$, $p < 0.05$; Figure 3b). Based on these observations, it is likely that *G. meleagris* exhibits an activity pattern opposite to that of *G. goliatus*, that is, *G. meleagris* is highly active during the rainy season, whilst *G. goliatus* is primarily active during drier months (Figure 3).

An excellent flyer, *G. meleagris* tends to exhibit fairly dense populations, with groups of individuals fluttering 5–15 m above the ground around individual trees where they congregate. Although there are no conclusive experimental data, our opportunistic observations indicate that *G. meleagris* reaches population densities greater than any other species of *Goliathus* around the trees on which it assembles.

This species is active throughout the day, with a slight tendency in our studied sample for more individuals to be observed during twilight and the early night hours (Figure 4b). Thus, the daily activity patterns of this species were almost identical to those of *G. goliatus* (see above). Interestingly, the height from the ground at which *G. meleagris* specimens were sighted increased significantly from early morning towards twilight (Spearman's $r_s = 0.847$, $p < 0.05$).

Nothing is known about the larval ecology.

3.2.7 | Use and Trade

Hundreds of specimens are collected yearly in the wild (particularly in Lualaba) for the international entomological trade. Insect collectors especially value large males, so these beetles are actively harvested by local communities. Local collectors exploit sites where cocoons of these beetles are present, because most of the specimens offered in the Western markets are of excellent quality, without the imperfections and breakages more frequently observed in wild Goliath beetles belonging to other taxa. Alternatively, a less combative behaviour of the males may be envisioned.

3.2.8 | Conservation Actions

There are no direct conservation actions to protect this species, but *G. meleagris* populations are protected within the Upemba (11,730 km^2) and Kundelungu (7600 km^2) national parks.

3.3 | *Goliathus regius*

3.3.1 | Data Availability

We observed *G. regius* opportunistically from 2012 to 2024, especially in Côte d'Ivoire, and more sporadically in Togo, Ghana, Republic of Guinea and Liberia. Since we could not dedicate equal effort to each month or habitat type, the quantitative data we present may be partially biased. However, given the long time spent in the field in the potential areas of the presence of the species, we are confident that the potential biases would not profoundly affect the collected data. We also interviewed many local people to get information on this species; these data are synthesised in Dendi et al. (2023). Additionally, one of us (MDP) observed *G. regius* in Ghana from 2015 to 2019.

3.3.2 | Suggested Red List Category and Criteria

ENDANGERED (EN) according to the criteria A2, c, d.

3.3.3 | Justification

The population reduction was inferred/suspected to be more than 50% (A2) compared to 20 years ago. This is based on (1) surveys of study areas historically used as hunting grounds by collectors supplying the international entomological trade; (2) detailed in-person interviews with informed people from many communities in Côte d'Ivoire and Liberia (Dendi et al. 2023) and (3) the high deforestation rate in most of the range of the species, particularly in Ghana and Côte d'Ivoire (see Mallon et al. 2015; and database in University of Maryland and World Resources Institute, 'Global Primary Forest Loss'. Accessed through Global Forest Watch on 18/02/2024 from www.globalforestwatch.org). Additionally, site-specific data in Eastern Côte d'Ivoire suggest possible local extinctions after just a few years of monitoring (see below).

Notably, the replacement of lowland rainforests and agro-forestry habitats with extensive cocoa plantations in South-western Côte d'Ivoire has certainly negatively affected, and likely decimated or locally extirpated, populations of *G. regius*, by drastically reducing the connectivity between metapopulations and the number of viable population units. Moreover, if the deforestation rate continues at the current pace (average tree cover loss between 2001 and 2022 = 13%; Luiselli 2024), it can be inferred that even criterion E (≥ 20% extinction probability in 100 years) would be met. This process may not be reversible due to the ongoing infrastructural and industrial development of the West African countries where *G. regius* lives. This species is also exploited for the international entomological trade, and this threat may further affect its natural populations.

3.3.4 | Geographic Range and Taxonomic Considerations

This species is endemic of the Upper Guinean Forest Block (Mallon et al. 2015), from Sierra Leone to Western Togo (De Palma et al. 2020), including the Comoé-Lérabà National Park in Southern Burkina Faso. Old records for Benin and Nigeria (Lachaume 1983) were most likely inaccurate because (i) about 30 years of extensive field research in the rainforests of these countries did not provide any record; (ii) no positive interviews with any local hunter/farmer was obtained (Luiselli, Akani, Eniang et al., unpublished data) and (iii) *G. goliatus goliatus*, its ecologically equivalent, is instead present in the two countries mentioned above.

In Côte d'Ivoire, specimens with reliable label data were collected in Bingerville (1960s) and other localities around Abidjan (many specimens collected in the 1980s/90s); Tonkpi, Mount Tonkoui, Danané and Man (all up to current days); Foret de Mopri and other areas in Tiassale (many specimens collected in the 1980s/90s); Foret de Taï (up to current days); South-eastern Abongoua (1998); Bouaké (1960s and up to current days), Kpapekou (1960s), Sassandra (1980s/90s) and Issia (many specimens collected up to the 2000s). Currently, the species is more easily observed, and thus presumably abundant, in the Western part of the country, especially in the Taï Forest and in the regions 'Montagnes' and 'Haut Sassandra' and more specifically in the area situated within the villages/towns of Zoukougbeu, Logouale, Man, Biankouma, Mahapleu and Danané. In the Man area, for instance, we observed populations in Kagui (Gbangbegouine sub-prefecture). As for Ghana, historical hunting grounds were: Eastern Kade (last ascertained record in 1978), Begoro (2023), Kadjebi (2024), Kakum National Park (2022), Bia National Park (2011) and M. Agoumanatt (leg. H. Schultz-Garben 2013).

There are no recognised subspecies of *G. regius* (De Palma et al. 2020).

3.3.5 | Current Population Trend

DECLINING.

The species is widespread within its range, occupying wooded areas and spots with few trees in between plantations and abandoned lands near human settlements and towns. However, the apparent abundance of *G. regius* is not uniform across its range:

1. There are no data concerning its status in Sierra Leone (a heavily deforested country where this species is probably rare and confined to few localities).
2. The species is fairly widespread and locally abundant in Liberia (due to the extensive forest cover, especially in the Eastern part of the country). Still, its presence in the Republic of Guinea, Côte d'Ivoire and Ghana has become increasingly fragmented, with noticeable declines in large sections of the historic distribution area. *Goliathus regius* is still present in the Mount Nimba region of the Republic of Guinea, in several areas of Western Côte d'Ivoire (Taï Forest, Haut Sassandra, Montagnes district, Sangouiné and other regions in Danané, Mahapleu, Tonkpi, Man and Mount Nimba) (Figure 5), and in various but disjunct localities of Ghana (Bia National Park, Kakum National Park and several localities in the Ashanti and former Volta Region). In the Bobiri Forest Reserve (Ghana, nearby Kumasi, Ashanti region), our team captured two individuals of *G. regius* after 5 days of sampling. These individuals were found on *Albizia zygia*, likely feeding on nectar and fruits. The tree was in an intact area of the Bobiri Forest Reserve; *Albizia zygia* produces fruit between March and April, with fruit maturing from May to July. It sheds old leaves, grows new ones between August and September and has a minor fruiting season from November to December.
3. The species is now much rarer and potentially extirpated in the extensively deforested Southern, Central and Eastern Côte d'Ivoire regions. It is also extremely rare in Togo, where it occurs only in scattered sites of the hilly forests at the border with Ghana (Togo hills, up North to Fazao Malfakassa National Park).

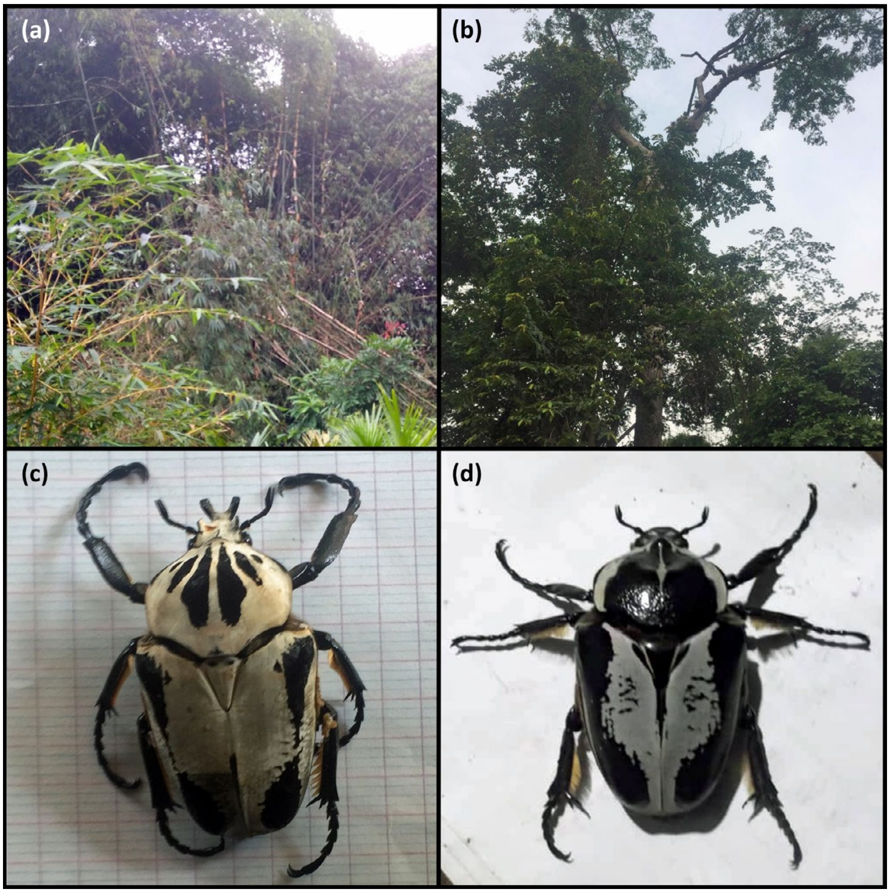

FIGURE 5 | Macrohabitat (a), microhabitat (b), an unusually coloured male (c) and a female (d) of *Goliathus regius* in Western Côte d'Ivoire. Place-name is not reported for conservation reasons.

Lachaume (1983) considered *G. regius* as common. However, there is clear evidence that the species is in decline and may have already been extirpated from many localities. For instance, in 2022 (6 days of field research) and 2023 (8 days of field research), we failed to observe individuals of this species in two sites nearby Grand Bassam (South-eastern Côte d'Ivoire) where we regularly observed the species in 2009 (2 days of field research), 2014 (2 days of field research) and 2016 (3 days of field research), suggesting a potential local extirpation. Moreover, many interviewees in Côte d'Ivoire and Liberia agreed that this species is much rarer nowadays than in the past decades, although it is still considered present in many sites (Dendi et al. 2023). The most worrying and severe threat is represented by the ever-growing cocoa cultivations in Côte d'Ivoire, which are destroying the forest habitat in a large part of its range (Sabas et al. 2020).

The extensive 'full sun' plantations of cocoa and coffee in South-western Côte d'Ivoire (the world's leading producer of cocoa) (Smith Dumont et al. 2014) certainly pose a serious threat to *G. regius*, since it has never been observed during our research in plantations above 4 ha surface, whilst it has been observed on several occasions at the edge of small subsistence non-cocoa plantations (jam, cassava, etc). The area cultivated for cocoa production in Côte d'Ivoire is approximately 3 million hectares. The development of this crop has led to significant degradation of the forest cover over the last decades (respectively 60.80%, 46.39%, 20.76% and 51.18% of the forest area in the Eastern, in the Centre-western, South-western and Western Côte d'Ivoire from 1985 to 2019; Sabas et al. 2020). Therefore, it can be extrapolated that at least 43% of *G. regius* habitat has been lost in the Ivorian territory only, and there is no indication that this trend will reverse in the decades to come.

3.3.6 | Habitat and Ecology

Nothing is known on the ecology of this species apart from that it is a typical inhabitant of the Upper Guinean rainforests (Croizat 1994). Our field studies showed that it is not explicitly linked to climax or mature forests but can be found along the whole succession of the West African forest (Table 2), including forest-plantation mosaics and the neighbouring human settlements (Figure 6). For instance, in the district 'Montagnes' (Western Côte d'Ivoire) it is easily encountered in the montane secondary forests but can also occur in patches with small tree clusters separating plantations and human settlements.

In Ghana, the species is also found in secondary hilly forests, such as the Bobiri Forest Reserve near Kumasi and heavily degraded hilly forests in the Jasikan District, Oti Region. One of us (M.D.P.) observed about 50 live specimens in the surroundings of Kadjebi (Jasikan District) during a field-observation study of about 80 cumulative days (July/August) between 2015 and 2019. Therefore, *G. regius* can be considered a habitat generalist within the West African forest block, although not present within large urban centres and extensive plantations/

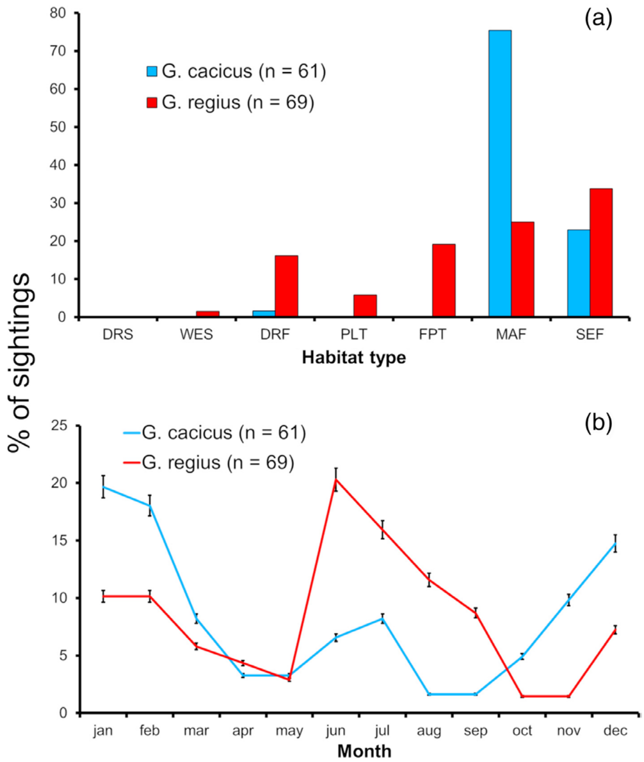

FIGURE 6 | Ecological comparisons between *Goliathus regius* and *Goliathus cacicus*: (a) number of records in different habitat types and (b) number of records in each month of the year. For statistical details, see the text. Symbols: DRS = herbaceous savannah-like vegetation; WES = clusters of trees within grasslands; PLT = plantations; DRF = dry forest; FPT = forest-plantation mosaics; MAF = mature rainforest (including gallery forest); SEF = secondary and very altered rainforest.

monocultures. The tree species used more frequently by *G. regius* in Côte d'Ivoire is *Prunus africana* (L. Luiselli et al., unpublished observations).

In a sample of 69 opportunistically encountered *G. regius* individuals, most records were from secondary/altered rainforest, but there was also a high frequency of observations in the mature rainforest (including gallery forests in this category), dry forest and forest-plantation mosaic, whilst open savannah-like grasslands did not provide observations (Figure 6a).

G. regius is active year-round, with a higher apparent peak from May to July (wet season) and a lower second peak from October to December (Figure 6b). However, the sample size was small ($n = 69$) and, therefore, it cannot be ruled out that the apparent monthly differences observed in the annual activity patterns of these beetles are partly biased. It is also possible that there are oscillations between years in the peaks of activity depending on factors such as rainfall. For example, during non-standardised research in 2024, many individuals were observed on September 3 (two males and one female, on the Guinean side of Mount Nimba), September 12 (7 males and 5 females in Logoualé), September 13 (one male in Sanguoiné), September 16 (two males and one female in Danané), September 25 (one male in Biankouma), October 4 (one male in Mahapleu) and October 10 (one male in Sanguoiné), that is in a period of the year in which the activity of *G. regius* would not seem to be very high.

Males vigorously combat for access to females, and this results in many individuals showing broken legs and scratches on the pronotum and elytra (Luiselli et al., unpublished observations).

Nothing is known about the larval ecology.

3.3.7 | Use and Trade

Several hundred specimens of *G. regius* were captured annually to supply the entomological trade in the 1980's, 1990's and early 2000's. The species is currently expensive in the Western markets, and insect collectors especially value large males. Many specimens are still collected in the wild, particularly in Ghana, Liberia and Côte d'Ivoire, although successful captive breeding in the last several years may compensate for reduced exports of wild specimens from historical collection sites, such as Côte d'Ivoire. These beetles are harvested by local collectors operating singly and without the concerted efforts that some communities make to collect *G. goliatus goliatus* in Cameroon (Muafor et al. 2012).

3.3.8 | Conservation Actions

There are no direct conservation actions to protect this species, but *G. regius* populations are protected within the Taï Forest and Comoé National Parks, Haut-Bandama, Mont Nimba, Cavally, Mabi-Yaya, Aghien, Bossématié and N'zo Natural Reserves in Côte d'Ivoire, Comoé-Lérabà National Park in Burkina Faso, Kakum, Nini Suhien, Digya, Bia National Parks and Bobiri Forest Reserve in Ghana.

3.4 | *Goliathus cacicus*

3.4.1 | Data Availability

We observed *G. cacicus* opportunistically from 2012 to 2024, especially in Côte d'Ivoire, Liberia and the Republic of Guinea. Since we could not dedicate equal effort in each month or each habitat type, the quantitative data we present may be biased. However, given the long time spent in the field in the potential areas of the presence of the species, we are confident that the potential biases would not profoundly affect the collected data. We also interviewed large numbers of local people to get information on this species; these data are synthesised in Dendi et al. (2023).

3.4.2 | Suggested Red List Category and Criteria

CRITICALLY ENDANGERED (CR) according to the criteria A2, a, c, d.

3.4.3 | Justification

The population reduction was inferred/suspected to be more than 80% (A2) compared to about 20 years ago. This is based on (1) surveys of study areas historically used as hunting grounds by collectors supplying the international entomological trade; (2)

detailed in-person interviews with informed people from many communities in Côte d'Ivoire and Liberia (Dendi et al. 2023) and (3) the high rate of deforestation in most of the range of the species, namely in Ghana and Côte d'Ivoire (see Mallon et al. 2015; and database in the University of Maryland and World Resources Institute. 'Global Primary Forest Loss'. Accessed through Global Forest Watch on 18/02/2024 from www.globalforestwatch.org).

Once widespread and locally abundant, the species is likely extirpated from many historical sites of presence and survives only in a small section of the original range, mainly in Eastern Liberia and Western Côte d'Ivoire. Few people reported that *G. cacicus* remains in the forests surrounding their villages (Dendi et al. 2023). One of us (M.D.P.) failed to observe live *G. cacicus* in Western or Eastern Ghana during a field-observation study of about 80 cumulative days (July/August) between 2015 and 2019.

The replacement of rainforests and agro-forestry habitats with extensive cocoa plantations in South-Western Côte d'Ivoire has decimated and likely extirpated several populations of *G. cacicus*, drastically reducing its connectivity between metapopulations and the number of viable population units. This decline is accentuated compared to *G. regius*, possibly because this species is a rainforest specialist. Moreover, if the deforestation rate continues at the current pace, it can be inferred that even criterion E ($\geq$ 50% extinction probability in 100 years) will be met. This process may not be reversible given the ongoing infrastructural and industrial development of the West African countries where *G. cacicus* lives. This species is also exploited for the international entomological trade, and this threat may further affect its natural populations.

3.4.4 | Geographic Range and Taxonomic Considerations

This species is endemic to the Upper Guinean Forest Block (Mallon et al. 2015), where it occurs in the following countries: Sierra Leone (Wiebes 1968), Liberia (Savage 1842), Côte d'Ivoire, Ghana (De Palma et al. 2020) and Republic of Guinea (Nimba area, our unpublished data). Its range was reported to include also Benin and Nigeria (Lachaume 1983). However, the reported presence of *G. cacicus* in the latter two countries is almost certainly wrong or, alternatively, the species has long been extirpated therein because (i) about 30 years of very extensive field research in the rainforests of these countries did not provide any specimens and (ii) no positive interviews with any local hunter/farmer was obtained (Luiselli, Akani, Eniang et al., unpublished data). Sjöstedt (1927) reported its easternmost locality of presence being Barombi (Nigeria, nowadays in South-western Cameroon), but this record is certainly wrong.

Recent data do not exist for Sierra Leone, a heavily deforested country. In Liberia, the species was already known to occur in the South-eastern regions in the 1840s (Savage's notes on its phenology were taken from Cape Palmas), and recent records are from the forest areas bordering Côte d'Ivoire (Dendi et al. 2023). Unspecified capture locations (years 2021–2023) in Eastern Liberia, at about 80 km from the coastal line, were also reported by Ting, Yu, and Alhassan (2023), but without any further details, it is impossible to trace the collection area.

In Côte d'Ivoire, reliable data from institutional and private collections indicate that the species was common in the Soubré Forest (Bas Sassandra; dozens of individuals received alive until 2008), Abidjan and Banco Forest (possibly thousands of specimens collected until the late 1990s), Akoupé (Lagunes district), Bouaké (Gbêkê), Attinguié (Lagunes, 24 km NW Abidjan), Issia (Haut-Sassandra, many specimens), Foret de Taï (up to current days) and Danané. The species was also frequently exported from Daloa (Haut-Sassandra), where it was undoubtedly syntopic with *G. regius* as testified by many hybrid specimens (*G. 'atlas'*) that were captured in the 1980s. Currently, the species is found in a few scattered sites in the Western part of the country (see below for more details and Figure 7).

As for Ghana, many historical specimens, collected mainly in the Ashanti Region, are deposited in the British Museum of Natural History (London). Additional records are from Bia National Park. One of us (M.M.) recently obtained *G. cacicus* from Ankasa Forest (Western Region). Several specimens were also collected during the 1970s in the Eastern Kade (Eastern Region), now a widely deforested area, according to the original labels from former German collections. The historical easternmost area of ascertained species' presence is Ghana's Volta region.

There are no recognised subspecies of *G. cacicus* (De Palma et al. 2020).

3.4.5 | Current Population Trend

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All information in our possession suggests that this species is in a strong decline and may even be extinct in many of its classic presence locations, especially along the coastal strip between Côte d'Ivoire and Ghana. It was considered abundant by Lachaume (1983), and indeed, in the 1970s and 1980s, many hundreds of individuals were exported yearly for the international entomological markets, especially from Côte d'Ivoire and Ghana. Some areas (Abidjan, Banco Forest, Issia, Sassandra and Taï Forest) were the collection hotspots for these beetles. The species was abundant in the above-mentioned specific sites until at least the early 1990s, and the native collectors were paid minimal amounts for each specimen collected (about \$1; Dendi et al. 2023). These massive exportations for the Western markets likely threatened these exploited populations' survival. Currently, *G. cacicus* appears to be extinct from the small fragments of scrub and altered forest that are still found in the urban fabric of the metropolitan area of Abidjan. For example, the species has not been observed since 2004 in a residual forest fragment of 1615 ha located in Riviera Bonoumin (Luiselli et al., unpublished data; Figure S3).

In addition, the habitat of *G. cacicus*, which is a rainforest specialist (see below), has been strongly affected by urbanisation (especially in Abidjan, where it was once common) and the development of the cocoa industry, as described above for *G. regius*. The decline of this species in areas with expanding cocoa plantations may also be due to the heavy utilisation of insecticides for the control of pests (Ohoueu et al. 2017).

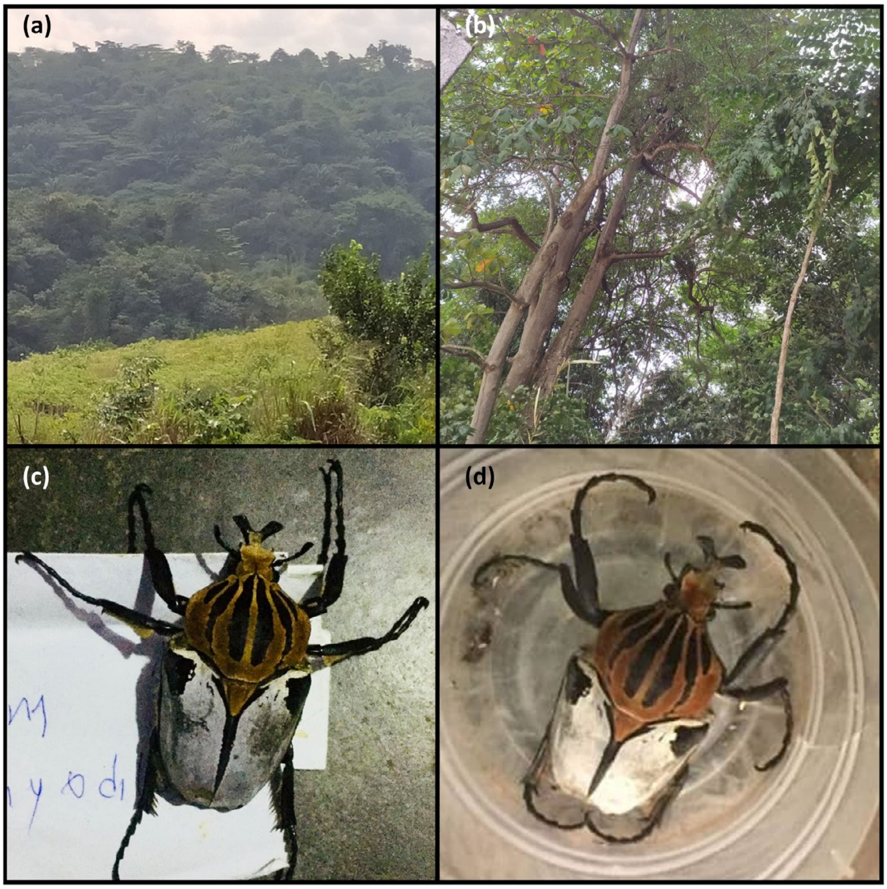

FIGURE 7 | Macrohabitat (a), microhabitat (b) and males (c, d) of *Goliathus cacicus* in Western Côte d'Ivoire. Place-name is not reported for conservation reasons.

Currently (2022–2024), *G. cacicus* is known to survive in some scattered populations:

1. In Liberia, it is found in the Zwedru and Nimba areas. The species is also present in the forested patches between Toetown and the border with Côte d'Ivoire up to the town of Toulepleu.
2. In Côte d'Ivoire, it is still found in Taï Forest (the southern part of the protected area) and in the neighbouring Forêt Classée de Rapide Grah (Haut Sassandra), in the forested hills nearby Danané and Toulepleu (Montagnes district), in the Mount Nimba Strict Nature Reserve and in the Southern Comoé. Smaller populations occur also elsewhere: in December 2023, four individuals were recorded from the Biankouma area (Tonkpi region), and in December 2022, an adult male was captured at Petit Yapo (Lagunes district).
3. In the Republic of Guinea, it occurs in the Nimba area.
4. In Ghana, this species is certainly present in Bia National Park (Claude Joly, personal communication) and potentially in some of the small fragmented forests present in the southwestern part of the country. For example, a male specimen was collected in Ankasa Forest (Western Region) in December 2023 (M.M., unpublished data).

Overall, Eastern Liberia and Western Côte d'Ivoire appear to be the most critical regions for conserving this Critically Endangered species. Although it is possible that *G. cacicus* still survives in other sites (especially in gallery forests), there is no doubt that its populations have suffered a catastrophic collapse in the previous 30 years. Overall, we estimate that at least 80% of its populations were extirpated in the last 30 years; for instance, there are no records over 10 years from Banco Forest and from the surroundings of Abidjan, where *G. cacicus* was once very abundant. Although it cannot be excluded that *G. cacicus* still survives in the Banco Forest, it is undoubtedly scarce nowadays.

In 2023–2024, the personnel of 'Parcs et Reserves de Côte d'Ivoire' surveyed (under the request of Col. Drissa Koné) the hunting grounds where *G. cacicus* have been historically harvested by local collectors, but no positive observations were obtained. Standardised interviews with local communities in Liberia and Côte d'Ivoire confirmed that *G. cacicus* is reported to still be present in just a few sites, but also suggest an apparent temporal decline in its abundance as elders but not young people typically know the species (Dendi et al. 2023). When this pattern is observed in interviews, a species' heavy decline can be considered practically confirmed (Luiselli et al. 2021).

Another indirect indication of the rarity of the species nowadays is the average high price for specimens offered for the international entomological trade and the scarcity of recently captured specimens at entomological fairs (M.M., unpublished observations). In contrast, the species was inexpensive until about 20 years ago.

3.4.6 | Habitat and Ecology

No study has been published on the ecology of this species and the few available natural history notes are due to Savage (1842). However, we collated field data during the period 2012–2024, that are summarised below.

G. cacicus is a forest specialist (Table 2), that inhabits mostly mature rainforest patches (including gallery forests, over 75% of our records, total $n = 61$, Figure 6a), both in lowlands and in hills and mountains (Figure 7), for instance, in the surroundings of Danané, Côte d'Ivoire. However, it is also found in secondary forests and fragments of relatively sunny rainforests, in the vicinity of settlements and small plantations and secondary forest/plantation mosaics and degraded forests (for instance, in the Forêt Classée de Rapide Grah). However, the frequency of observation of *G. cacicus* individuals in this environment is significantly lower than in mature forests (Figure 6a). For instance, in Tai Forest this species is present only in the southern and central portions of the protected area, whereas in the northern part, which is much more altered, only *G. regius* is found (Luiselli et al., unpublished data). It is not found in extensively deforested areas and areas with intensive plantations. As you proceed northwards, it seems more and more enfeoffed to gallery forests or mountain areas, whilst in the coastal area it also inhabits flooded forests.

Despite earlier observers (Savage 1842) reported that this species is linked to a single tree species (unknown at the time), we observed adults in different plant species, mainly *Vernonia* spp., *Prunus africana*, *Ficus* sp. This is consistent with data from Ting, Yu, and Alhassan (2023), who observed this species not only on the aforementioned trees but also in *Acacia mangium* (in Cote d'Ivoire), a species that was introduced from Australia in the 1970s as a plantation tree. It may be speculated that this tree species might have represented an 'ecological trap' for this beetle species, contributing to its rarefaction. However, this hypothesis is entirely tentative and should be verified by further studies.

Although the distribution range of *G. cacicus* largely overlaps with that of *G. regius*, up to the point that they can hybridise in the wild, the two species differ significantly in habitat choice ($\chi^2 = 41.53$, $df = 5$, $p < 0.0001$; Figure 6a). In quantitative terms and considering only the specimens whose precise observation point with geographical coordinates is known ($n = 61$ for *G. cacicus* and $n = 69$ for *G. regius*), the habitat niche breadth was significantly narrower in *G. cacicus* ($B_s = 1.61$) than in *G. regius* ($B_s = 4.11$). In general, *G. cacicus* seems to prefer wetter and shadier microhabitats, in points with a much more closed canopy, than *G. regius*, (e.g., compare Figure 5b with Figure 7b) (L. Luiselli et al., unpublished observations). However, there was considerable habitat niche overlap between the two species ($O_{jk} = 0.439$), showing that they can be relatively similar in terms of habitat preferences and can coexist with low interspecific competition. The occurrence of hybrid individuals, referred to as '*Goliathus atlas*', in the Southern part of Taï Forest (Côte d'Ivoire) and historically in the Volta region (Ghana) (De Palma et al. 2020), confirms that these two species are/were syntopic in various locations within their range (Figure 8). Ting, Yu, and Alhassan (2023) confirmed that hybridisation between *G. cacicus* and *G. regius* occurs in the wild (eastern Liberia). They reported interesting observations of interspecific mating and hybridisation patterns in captivity. During our surveys, we captured individuals of the two species within the same tree and on the same night in a secondary forest of the Mahapleu prefecture, department of Danané (Western Côte d'Ivoire) (Figure 8). The syntopy spots between the two species seem to correspond to sites with a very closed canopy, apparently more suitable for *G. cacicus* than *G. regius* (Figure 7a) (Luiselli et al., unpublished observations). Further studies are needed to verify the generality of this pattern.

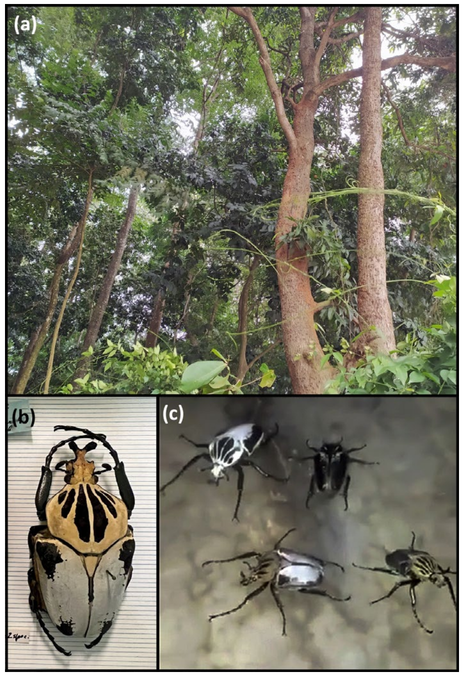

FIGURE 8 | Ecological coexistence of *Goliathus cacicus* and *G. regius* in Western Côte d'Ivoire: (a) microhabitat of syntopy, (b) adult hybrid male ('*G. atlas*') from the entomological collection of the Museum National d'Histoire Naturelle, Paris and (c) individuals of the two species captured by night on the same tree and on the same day. Placename of the locality of syntopy is not reported for conservation reasons.

Ting, Yu, and Alhassan (2023) stated that *G. cacicus* tends to inhabit coastal forests whereas *G. regius* is typically a species from areas situated in more internal regions. This speculation is unsubstantiated, given that many non-coastal localities have been known for a long time for *G. cacicus*, as well as several coastal sites for *G. regius*. Moreover, even Savage, in the 1840s, already reported that, in the Liberian territory of Cape Palmas, *G. cacicus* did not usually occur in the coastal forests but a few kilometres inside the country.

Adults of *G. cacicus* are active year-round, with an apparent peak of activity between November and January (early dry season). However, our sample is relatively small ($n = 61$), and therefore, it cannot be excluded that variations observed between various months merely reflect different levels of outdoor activity. Ting, Yu, and Alhassan (2023) also reported a phenology consistent with our data for a population from Eastern Liberia but did not present any quantitative data to support their suggestion. Specimens in institutional and private collections indicate that many specimens were collected between April and July.

The monthly frequency of observation of *G. cacicus* individuals differed significantly from that of *G. regius* ($\chi^2 = 24.6$, df = 11, $p < 0.05$), with the former being more active during the dry season whereas the latter during the wet season (Figure 6b).

Males are much more numerous than females, as also Savage (1842) noted in his letters about this species. Males vigorously combat for access to females, and this results in many individuals showing broken legs and breakage and scratches on the elytra (Luiselli et al., unpublished observations).

Nothing is known about the larval ecology.

3.4.7 | Use and Trade

Thousands of specimens of *G. cacicus* had been exported annually, especially from Côte d'Ivoire in the 1980s and 1990s, to supply the entomological trade. Currently, the number of exported specimens is relatively low and old material is more frequently offered in the entomological trade. Thus, *G. cacicus* has become expensive in the Western markets. There is no evidence that these beetles are still regularly and abundantly harvested by local collectors, except for new sites in eastern Liberia.

3.4.8 | Conservation Actions

There are no direct conservation actions to protect this species, but *G. cacicus* populations are protected in the Taï Forest and Comoé National Parks, Mount Nimba Strict Nature Reserve and Foret Classée de Rapide Grah in Côte d'Ivoire. *G. cacicus* will likely persist in the Ankasa and Bia Natural Parks of Western Ghana.

Ting, Yu, and Alhassan (2023) suggested that ex-situ captive breeding may be a good conservation strategy for *G. cacicus*. However, these authors did not provide any evidence that this strategy may be needed for the species' survival or that it could be efficiently and reasonably used to enhance genetic variability in the free-ranging populations. Therefore, ex-situ captive breeding should not be considered a conservation measure for *G. cacicus*. In contrast, habitat protection and awareness of local communities should remain the core activities to be applied.

4 | Discussion

4.1 | Continuing Pressures on Goliath Beetles

Overall, our study suggests that a number of threats are affecting the natural populations of the *Goliathus* beetles. Whereas *G. regius* and *G. cacicus* experience nearly identical threats, *G. goliatus* and *G. meleagris* are exposed to different threats (Table 3). *G. meleagris* is the only *Goliathus* taxon that may be seriously affected by climate change, and the significance of this potential threat should be studied in the future.

TABLE 3 | Synthesis of the 'World Conservation Union-Conservation Measures Partnership (IUCN-CMP) classification of direct threats to biodiversity (version 1.1)' applied to the various species of the genus *Goliathus*. For more details, see the text.

Threat code (1st level)	Threat code (2nd level)	Threat name	Species affected
1		**Residential and commercial development**	
	1.1.	Housing and urban areas	*G. cacicus*, *G. regius*
2		Agriculture and aquaculture	*G. cacicus*, *G. regius*
4		**Transportation and service corridors**	
	4.1	Roads and railroads	All species
5		**Biological resource use**	
	5.1	Hunting and collecting terrestrial animals	All species
	5.3	Logging and wood harvesting	All species
6		**Human intrusions and disturbance**	
	6.2	War, civil unrest and military exercises	*G. goliatus*, *G. meleagris*
	6.3	Work and other activities	
7		**Natural system modifications**	
	7.3	Other ecosystem modifications	
9		**Pollution**	
	9.3	Agricultural and forestry effluents	*G. cacicus*, *G. regius*
11		**Climate change and severe weather**	
	11.1	Habitat shifting and alteration	*G. goliatus*

The findings of this study also shed light on the pressing conservation challenges faced by Goliath beetles of the genus *Goliathus*. Our research highlights the significant threats posed by habitat loss and overexploitation to these iconic beetles, emphasising the need for comprehensive conservation strategies.

Deforestation and habitat fragmentation are critical factors driving global biodiversity loss. Our study confirms their substantial impact on Goliath beetle populations in sub-Saharan Africa. The degradation of tropical forests, primarily due to agricultural expansion and logging (mainly cocoa plantations in Côte d'Ivoire), has led to a decline in suitable habitats for Goliath beetles. The correlation between tree diameter categories and beetle occurrence underscores the importance of mature, undisturbed forests for the survival of these species. Specific tree species (*Prunus africana* for instance) should be particularly protected as the survival of *Goliathus* populations is often linked to just a few suitable trees inside a given forest patch. Indeed, Goliath beetles, particularly those with larger body sizes, likely depend on specific microhabitats provided by old-growth trees. The lack of such micro-habitats due to deforestation significantly reduces their populations.

The entomological trade threatens certain Goliath beetle populations, and it should be carefully evaluated in the future. Commercial trade of *G. goliatus goliatus* is known to provide significant income to rural communities in several villages in Western Cameroon. Their striking appearance and perceived rarity make them highly sought after by insect collectors, which may lead to unsustainable harvesting practices at selected sites. Our study indicates that intense harvesting, combined with habitat loss, exacerbates the vulnerability of these beetles. The reported decline in beetle abundance at various locations (Muafor and LeGall 2011; Dendi et al. 2021, 2023) is a clear signal of the detrimental effects of overexploitation. This said, only *G. goliatus goliatus* is currently actively exploited for the entomological trade, and only in a low percentage area of its broad distribution range.

Despite their ecological significance, beetles (Coleoptera) generally have been underrepresented in conservation assessments (Carpaneto, Mazziotta, and Valerio 2007; Homburg et al. 2019). Goliath beetles, as large and conspicuous insects, likely play crucial roles in their ecosystems, such as in decomposing organic matter. The decline of these beetles might have cascading effects on ecosystem functions. Our study calls for urgent Red List assessments for Goliath beetles, using the IUCN (2024) criteria, to quantify their extinction risks accurately. Such assessments are essential for prioritising conservation efforts and allocating resources effectively.

4.2 | Methodological Considerations

Our study employed opportunistic records to gather data on beetle occurrences, which has limitations regarding sampling consistency and coverage (Eschen et al. 2019; Jeliazkov et al. 2022). Future research should aim for systematic surveys across the entire range of Goliath beetles to obtain more comprehensive data. Additionally, our correlation analysis between beetle abundance and rainfall provides insights into the seasonal activity patterns of these beetles. However, long-term monitoring is necessary to better understand population dynamics and the impact of climatic variations. Although based mostly on opportunistic observations, our study demonstrates major strengths in long-term field research involving multiple countries. Despite possible limitations, our dataset is by far the largest available on the ecology and conservation of African Goliath beetles. It is possible that (i) different sampling efforts between seasons and locations or countries and (ii) differences in the observability of the various species (greater or lesser elusiveness) may have somewhat biased our results. However, the methods used in our research were comparable in all study sites involving random searches, night searches, face-to-face interviews and so on. It is, therefore, likely that biases were minor, similar to those present in most field studies on the ecology of tropical insects, due to logistical difficulties.

4.3 | Recommendations

Based on our findings, we propose several conservation measures to protect Goliath beetles (summarised in Table 4, using the standardised classification of conservation actions by Salafsky et al. 2008).

4.3.1 | Habitat Protection

Strengthening the protection of remaining tropical forests is crucial, particularly maintaining the main tree species known to host these beetles. Establishing and enforcing protected areas, particularly in regions identified as critical habitats for Goliath beetles, will help preserve their populations. To make this strategy successful, it is necessary to have a detailed knowledge of the local distribution of *Goliathus* to carry out accurate habitat management at the microhabitat level. Therefore, once an area has been identified where *Goliathus* specimens are present, it will be important to finance/logistically support selected people from local communities to thoroughly explore the relevant area and report the tree sites where the beetles congregate. Once the cataloguing of the sites has been completed, targeted actions can be organised to minimise human disturbance that may impact *Goliathus* populations.

4.3.2 | Regulation of Trade

Implementing and enforcing laws to control the collection and trade of Goliath beetles is felt to be essential. International cooperation and coordination are necessary to address the cross-border trade of these beetles. Certified forests, from which sustainable exploitation of Goliath beetles is carried out, should also be promoted, particularly in West Africa, with *G. cacicus* and *G. regius* as primary targets (Luiselli and Fa, in press). However, conservation agencies should pay attention to the needs of local communities exploiting *Goliathus* beetles for their subsistence, such as in some localities of Western Cameroon. Our observations indicate that several communities depend on trading Goliath beetles as their primary income source, especially in Western Cameroon. Therefore, enforcing stricter protection measures for Goliath beetles could adversely affect the livelihoods of certain local communities. Rather than outlawing trade, it would be essential to support these communities in adopting sustainable practices that safeguard their beetle

TABLE 4 | Synthesis of the 'World Conservation Union-Conservation Measures Partnership (IUCN-CMP) classification of conservation actions (version 1.1)' applied to the various species of the genus *Goliathus*. For more details, see the text.

Actions code (1st level)	Actions code (2nd level)	Action name	Species to be targeted
1		**Land/water protection**	
	1.1	Site/area protection	All species
	1.2	Resource and habitat protection	All species
2		**Land/water management**	
	2.1	Site/area management	All species
	2.3	Habitat and natural process restoration	*G. cacicus*
3		**Species management**	
	3.1	Species management	*G. cacicus, G. regius, G. goliatus*
4		**Education and awareness**	
	4.2	Training	*G. cacicus, G. regius, G. goliatus*
6		**Livelihood, economic and other incentives**	
	6.1	Linked enterprises and livelihood alternatives	All species
	6.3	Market forces	All species

populations. For example, educating local communities about the importance of primarily collecting male Goliath beetles (whilst sparing female specimens) may represent a key strategy. This practice would significantly reduce the harvesting impact on the natural populations of *Goliathus*, ensuring the long-term viability of both the species and the communities that rely on them for economic stability (Luiselli and Fa, in press). By promoting sustainability and fostering community engagement, we can achieve a balance that benefits both the environment and the local economy (Fa and Luiselli 2024).

4.3.3 | Public Awareness and Education

Raising awareness amongst local communities and stakeholders about the ecological importance of Goliath beetles and the threats they face can foster community-based conservation efforts. Educational programs can promote sustainable practices and reduce the pressure on beetle populations (Fa and Luiselli 2024). Public awareness and education play a crucial role in conserving Goliath beetles, for example by highlighting their ecological significance and challenges. Engaging local communities and stakeholders can cultivate a sense of ownership and responsibility towards these remarkable insects (Luiselli and Fa, in press). Implementing targeted educational programs can enhance understanding of Goliath beetles' roles in their ecosystems, such as nutrient recycling. Furthermore, these initiatives can promote sustainable harvesting practices, encouraging community members to limit their trade to male beetles encountered in forests, thereby reducing pressure on populations. Workshops, informational campaigns and school programs can provide practical knowledge on biodiversity conservation, fostering community-based efforts to protect *Goliathus* and their habitat. Collaborating with local leaders and organisations will amplify these messages, ensuring they resonate within the community. By empowering local stakeholders through education, a conservation ethic may be inspired that supports the Goliath beetles' survival and the economic needs of the communities that depend on them. Ultimately, informed communities are more likely to engage in and sustain conservation practices, creating a positive feedback loop that benefits biodiversity and livelihoods.

4.3.4 | Research and Monitoring

Continued research on the ecology, population dynamics, and threats to Goliath beetles is necessary. Long-term monitoring programs can track population trends and the effectiveness of conservation interventions. Protecting remaining tropical forests is essential, particularly conserving key tree species that host Goliath beetles. Establishing and enforcing protected areas in regions identified as critical habitats for these beetles will help preserve their populations. Success in this strategy relies on a detailed understanding of *Goliathus* beetles' local distribution, enabling precise habitat management at the microhabitat level. Once areas with *Goliathus* populations are identified, it would be vital to provide financial and logistical support to selected community members to explore these zones thoroughly, for example, by cataloguing trees where beetles congregate. Following this cataloguing, targeted measures can be implemented to minimise human disturbances affecting *Goliathus* populations. Capacity building for 'wise' persons from local communities could be effective acting with small actions of 'citizen management' (local control of trade; small actions to protect forest patches; share education and skills and informative pictures in sensitive areas realised by children and so on; see Battisti and Cerfolli 2021).

4.4 | Conclusions

The habitats of Goliath beetles, already vulnerable to biodiversity loss, face intensified threats from climate change, undermining ecosystem stability and posing far-reaching consequences for global biodiversity. Goliath beetles encounter significant risks from habitat loss and, potentially, overexploitation, underscoring the urgent need for targeted conservation efforts. Our study provides essential data for assessing their status, emphasising the importance of habitat protection, trade regulation and increased public awareness. Implementing these measures is crucial for the survival of these iconic insects and for preserving the ecological integrity of their habitats. Additionally, we recommend Red Listing for other Goliath beetle species affected by deforestation, particularly *Fornasinius higginsi* and *Fornasinius klingbeili*, both endemic to West Africa (Ajong et al. 2024).

As iconic insects, Goliath beetles act as sentinel species, reflecting the broader impacts of habitat degradation and climate change on ecosystems. Their vulnerability to environmental disruptions signals the health of their habitats, making them vital indicators of the cascading effects on biodiversity. Monitoring their populations provides insights into the resilience of ecosystems facing deforestation, climate shifts and growing ecological threats to species stability.

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Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.