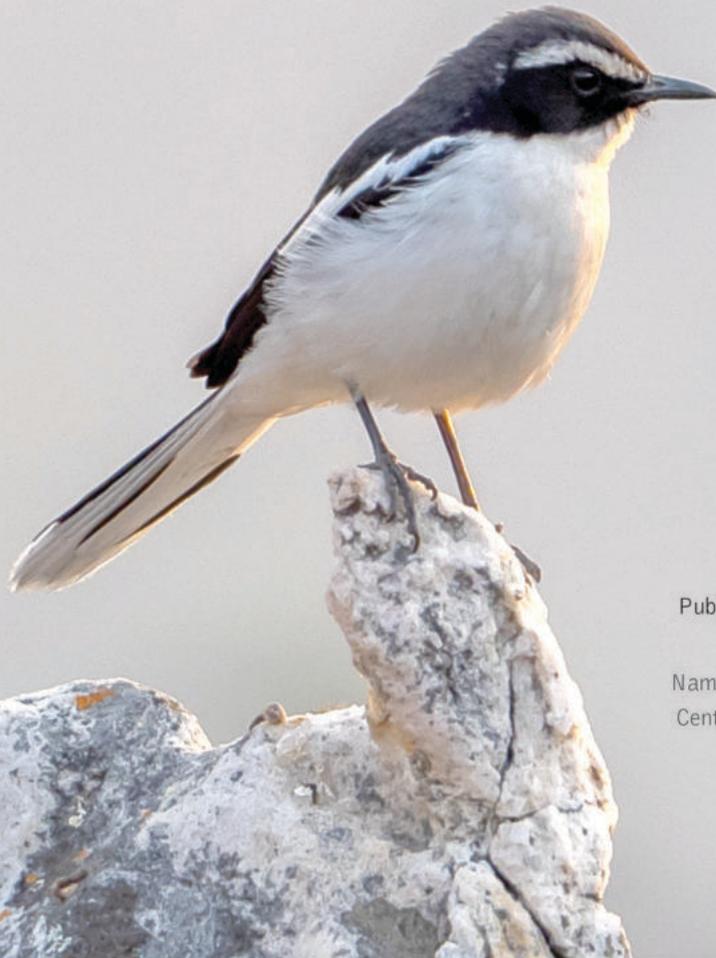


Monograph on
**Endemism in the
Highlands and Escarpments
of Angola and Namibia**



Angola Cave-Chat *Xenocopsychus ansorgei*
Photo: M Mills

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Green gem of the Northern Escarpment: biodiversity and endemism of the Serra do Pingano Forest Ecosystem

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ABSTRACT

The highlands and escarpments of Angola extend into the country's northern province, Uíge. The mountain ranges and scattered inselbergs there are characterised by small-scale geomorphological diversity that in turn supports a rich biodiversity, and together make up the Serra do Pingano Forest Ecosystem (SPFE). Drawing on previous studies, this paper briefly describes various taxonomic groups (fungi, Tracheophyta, Bryophytes, Odonata, butterflies, moths, amphibians, reptiles, birds and mammals) of the SPFE in terms of their diversity and endemism rates. The initial results presented show the need to fill the existing data gaps and point to the importance of a conservation status for the SPFE.

Keywords: Angola, biodiversity, endemism, escarpments, highlands, Serra do Pingano Forest Ecosystem

INTRODUCTION

At its very northern edge, the Angolan escarpment opens up into an elevated plane known as the Highland of Mucaba. Its western flanks rise abruptly from the surrounding lowlands of 500–700 masl to maximum elevations of 1,300 masl, gently sloping towards the northeast. The most striking and unique geomorphological feature in this remote part of the Northern Escarpment in Angola are several chains of parallel-running, densely forested mountain ranges or cordilleras – the Serra Canacanjungo, Serra Masselele, Serra do Pingano, Serra Uíge and Serra Vamba – and a number of scattered calcareous inselbergs that together form the Serra do Pingano Forest Ecosystem (SPFE; compare Ernst *et al.* 2020). Geologically, the area is almost entirely composed of siliciclastic sedimentary rocks (largely) and minor carbonates, such as arenite and limestone of the Schisto-Grosso Group (de Carvalho 1974, Schermerhorn 1981), which matches the Mpioka Subgroup of the West Congolian Group in the Democratic Republic of the Congo (DRC; Gärtner 2014).

The mountain ranges run in a northwest–southeast direction, forcing clouds from the Atlantic Ocean to ascend and discharge their moisture (Figure 1a). As a result, a highly branched network of watercourses dissects the area. While the northeastern part of Uíge Province and of the highlands drain northwards into

the Congo watershed, the serras are located in the Cuanza River's basin area. Its most important drainage line, the Loge River, meandering between the Serra Uíge and Serra do Pingano runs northwestwards and then westwards discharging into the Atlantic Ocean. The area's hydrological features support the persistence of sizable rainforest fragments (Figure 1b) that are unique to Angola (Lautenschläger & Neinhuis 2014, Lautenschläger *et al.* 2020a). During the rainy season (October to May), in particular, the steep slopes of the serras feature impressive waterfalls that carry large volumes of water which, over the course of time, have formed deep V-shaped valleys that today exhibit extraordinary microhabitats. The small-scale geomorphological diversity – comprising rainforest fragments on steep slopes and wet savannas at lower elevations and on high plateaus, as well as peat swamps on sandy soils (Figure 1c), limestone formations with extensive cave systems and isolated inselbergs (Figure 1d) – mirrors the exceptional biodiversity of the area making the SPFE very likely to be a bio- and geodiversity hotspot.

DATA COMPILATION

Limited accessibility, particularly in the aftermath of the struggle for independence and the civil war which ended in 2002, largely prevented any scientific exploration in the region. Consequently, there is a

limited number of museum specimens from Uíge Province. This situation has very recently changed, and systematic and intensified scientific assessments that aim at filling crucial knowledge gaps are now

underway. In northern Angola, a working group led by Technische Universität Dresden and consisting of colleagues from the Senckenberg Natural History Collections (Dresden and Görlitz), the University of



Figure 1: Landscapes and threats in the Angolan northwestern escarpment: a) Serra Uíge and Serra do Pingano in clouds; b) rainforest in Serra Uíge; c) swamp near Mucaba; d) inselbergs; e–g) slash-and-burn farming is one of the major threats; and h) logging of globally traded tree species (e.g., *Entandrophragma* sp.) and subsequent transport to Luanda. Photos by authors.

Hamburg and Purdue University has been working in cooperation with the regional university Kimpa Vita since 2012. During this period, numerous joint field trips were undertaken and material collected. The systematic assessments conducted by this association over the course of the past ten years plus have provided first basic data in support of the hypothesis that SPFE plays a pivotal role in shaping the biogeography of the entire western Central African realm. These findings have prompted the Angolan Ministry of Culture, Tourism and Environment to foster and promote the conceptualisation of a national protected area, which would make the SPFE the first and only protected rainforest area in Angola (Lautenschläger *et al.* 2020b).

The taxonomic sections that follow summarise the preliminary results and data generated by recent efforts and provide a first glimpse on the taxonomic composition, biogeographic patterns and endemism of the SPFE.

RESULTS

Fungi

As is true for most of Central, West and southern Africa, the fungi of Angola are poorly documented. Only 67 species, and two slime moulds, catalogued by Welwitsch and Currey (1868) represent the knowledge base of this group for the country. Of the species reported by Welwitsch and Currey (1868), 38 were described as new. Out of these, 21 that are considered valid species have never been collected outside Angola and may represent endemic species. Because fungi form symbioses with most known species of plants and animals, as well as acting as primary decomposers, they are essential components of ecosystem health and sustainability. Current estimates indicate that the species richness of fungi is approximately 6–30 times higher than that of plants (Hawksworth 2001, Blackwell 2011, Hawksworth & Lücking 2017). It is therefore highly likely that the actual diversity of fungi in northern Angola far exceeds current records. Between 2017 and 2019, 222 specimens of fleshy fruiting fungi were collected opportunistically in northern Angola, 202 of which have been identified to genus and/or species level. Only two of these were previously recorded in Angola (*Phallus tunicatus* Schldl. and *Cyathus stercoreus* (Schwein.) De Toni as *Cyathus striatus* Willd.). Newly recorded genera of fleshy fungi include *Arthroxyllaria*, *Bolbitius*, *Chaetocalathus*, *Clavulinopsis*, *Clitocybula*, *Crepidotus*, *Crinipellis*, *Cystolepiota*, *Datronia*, *Favolaschia*, *Galerella*, *Gerronema*, *Gleoporus*, *Hemimycena*, *Hygrocybe*, *Leocoagaricus*, *Penicilliopsis* (Figure 2e), *Pluteus*, *Podoscypha*, *Pseudofavolus*, *Pterula*, *Pterulicium*, *Ramaria*, *Russula*, *Scytinopogon*, *Simocybe*, *Tetrapyrgos* (Figure 2f), *Trogia*, *Xanthoagaricus*, *Xeromphalina* and *Xylodon*. The 202 specimens

identified represent 98 different species. About half of these are potentially new species.

Limited data on fungal distribution for most of Africa impede inferences regarding endemism of recorded species. Nonetheless, of the 202 specimens identified, 52 are probably new to science. Many of these are specialists on organic matter and debris and may represent endemics that are tightly associated with the unique flora of northern Angola. Such taxa face a high risk of coextinction with their severely threatened plant symbionts and/or the associated substrates on which they grow, as well as through direct competitive displacement by global invasives, such as *Coprinellus disseminatus* and *Schizophyllum commune* which are well adapted to anthropogenically disturbed areas and were both recently collected from the Serra Uíge, Mucaba and Serra do Pingano.

Trachaeophyta

To date, 1,063 species of Spermatophyta and Pteridophyta – about 15% of the total plant species listed for Angola (Figueiredo & Smith 2008) – have been identified in the northern Angolan provinces of Uíge and Cuanza-Norte (JACQ Consortium 2004). In recently published studies alone (Lautenschläger *et al.* 2020a, Lautenschläger *et al.* 2022), 46 species found in this northern area were added to the Angolan flora. While many species occur in many parts of Africa, the main distribution areas of those with a limited range are in the adjacent Congo Basin (Angola, DRC, Gabon and the Republic of Congo). Nevertheless, several species show a particular distribution pattern. Six species are endemic to Angola, including two species new to science: *Impatiens pinganoensis* (Figure 2a) which is only known from the Serra do Pingano in close proximity to a waterfall, at the spray zone of a creek (Abrahamczyk *et al.* 2016); and *Aloe uigensis* which was recently described from the limestone rocks east of the Serra do Pingano (Smith & Lautenschläger 2021). *Impatiens pinganoensis* was categorised as Critically Endangered by the authors of the description since it has a very limited distribution and has only been found on the cliffs of two waterfalls which have a very special microclimate; this habitat is endangered by deforestation and a proposed construction project (Abrahamczyk *et al.* 2016). Of the other Angolan endemics *Pandanus bilobatus* occurs in the rivers of the mountain ranges; *Sopubia graminicola* in the surrounding savannas; while *Crotalaria lundensis* and *Uvaria mendesii* are found further away from the escarpment but still at an elevation of 1,100 masl.

The limestone inselbergs exhibit an extraordinary flora, with species that had previously been found only in East Africa (*Begonia johnstonii*, *Rothea wildii*), species distributed southwards (*Obetia carruthersiana*) and species protected by the

Convention on International Trade in Endangered Species (CITES) regulations (*Encephalartos* aff. *laurentianus* (Figure 2b), *Polystachya adansonii*). In addition, randomly distributed swamps host species distributed to the east (*Polygala gomesiana*), and many orchid species. Other taxa were reported as potentially new species. Overall, with these initial results and the assumption that the Northern Escarpment around the mountain ranges of the Serra do Pingano *sensu lato* probably served as a refugium

for species of the tropical forests during the dry periods of glacial cycles and subsequent allopatric speciation in the wet interglacial periods (Couvreur *et al.* 2021), more plant endemics are to be expected in the area.

Bryophytes

In recent years, since 2013, our working group has started a more intensive investigation of the bryophyte flora of Uíge Province, specifically of the mountain



Figure 2: A selection of species of the Angolan northwestern escarpment: a) *Impatiens pinganoensis*; b) *Encephalartos* aff. *laurentianus*; c) *Weissia jamaicensis*; d) foliicolous liverwort *Cololejeunea furcilibulata*; e) *Penicillipsis* sp.; f) *Tetrapyrgos* sp.; g) large fairy hairstreak (*Hypolycaena antifaunus*); h) group of male 'forest grass yellows' (*Terias senegalensis*). Photos by authors, except 2a and 2e (Barbara Ditsch).

ranges Serra do Pingano and Serra Uíge. This work yielded 105 bryophyte species new to the flora of Angola and additional new records for Uíge Province (Müller 2015, Müller *et al.* 2018, 2019).

Several species are characteristic for mountain rainforests and their localities in Uíge Province represent the main, or exclusive, occurrences in Angola. In addition to pantropical and palaeotropical species, the flora of the area consists of a considerable number of African endemics, e.g., the liverworts *Archilejeunea elobulata*, *Caudalejeunea dusenii*, *Caudalejeunea yangambiensis*, *Cylindrocolea abyssinica*, *Plagiochila pinniflora*, and the mosses *Fissidens usambaricus*, *Fissidens darntyi* and *Leptotrichella nitidula*.

Among the recorded species, there are many bryophytes rarely reported in sub-Saharan Africa or worldwide. Examples of species newly recorded for Angola with limited distribution and therefore of special conservation value include *Physcomitrium bukobense* (hitherto only known from Tanzania), *Pogonatum congolense* (hitherto only known from Cameroon, DRC and Gabon), *Cylindrocolea gittinsii* (hitherto only known from Cameroon, Kenya and Uganda), *Frullania letestui* (a rare West African species, hitherto only known from Cameroon, Central African Republic, DRC and Gabon) and *Isopterygium mbangae* (a species with special substrate requirements, only growing on stems of tree ferns, hitherto only known from Cameroon, DRC, Gabon, Sudan, Tanzania and Uganda). *Weissia jamaicensis*, a species hitherto unknown from Africa and previously thought to be restricted to the New World, was found at several localities in Uíge Province (Figure 2c). It not only represents a new record for the African bryoflora, but also for the palaeotropical flora in general (Müller *et al.* 2018). The species prefers rock formations and was found, for example, in crevices and on bands of calcareous rocks of the Xisto-Calcário Formation. As outlined in Müller *et al.* (2018), it appears to be a ‘true’ historic bryofloral element rather than a recent introduction to sub-Saharan Africa and therefore provides crucial additional evidence for the intercontinental phytogeographical relationships between Africa and the Americas.

The foliicolous liverwort flora of Angola had previously been completely uninvestigated, but during the recent investigation, 24 foliicolous liverwort taxa were encountered, all of which, with the exception of *Radula flaccida*, were new for Angola. Examples of rare species among this ecological group are *Cololejeunea diaphana* (previously known in Africa only from Bioko Island, Malawi and Uganda), *Cololejeunea apiculata* (a rare Afromontane species, previously known only from Mt Cameroon, the Uluguru Mountains in Tanzania, Bwindi

Impenetrable Forest in Uganda and from Ethiopia), *Cololejeunea furcilibulata* (previously known in sub-Saharan Africa from Madagascar, Nigeria, Seychelles and Tanzania; Figure 2d), *Colura hattoriana* (previously known from Bioko Island, the Comoro Islands and Malawi) and *Colura mosenii* (previously reported, in Africa, only from Nigeria and, outside Africa, only from Java and the Caroline Islands).

As the southernmost extension of the Guineo-Congolian biogeographic region, the forest ecosystems of Uíge therefore also play a pivotal role in conserving and safeguarding an exceptional and unique bryophyte diversity.

Odonata

Angola is one of the richest countries for Odonata (dragonflies and damselflies) in Africa (Clausnitzer *et al.* 2012), with currently more than 288 recorded species and an estimation of well over 300 species based on the vast still largely unsurveyed areas (Kipping *et al.* 2019, Kipping *et al.* 2023). The expansive habitats in northern and eastern Angola, especially, have never been surveyed at all and the potentially species-rich highland catchments of the Congo, Cuanza, Cubango (Okavango) and Zambezi rivers are almost unknown.

Angola is also particularly rich in endemic Odonata species, with most of them being highland specialists found on the central plateau mainly between elevations of 1,300 m and 1,800 m and in open habitats. Angola’s endemic Odonata probably originated quite recently and proximally from the forests to the north and open habitats to the east. Such a local radiation of an insect order that has otherwise diversified in the highlands to the east, and forests to the north, fits the overall affinities of Angola’s endemic Odonata both geographically and ecologically (Kipping *et al.* 2023).

For the Serra do Pingano and its surroundings in the northern province of Uíge more than half of all known dragonfly species for Angola have been recorded in just two brief surveys, in 2012 and 2013 (Kipping *et al.* 2017). A total of 150 species have been recorded from the Serra do Pingano and its surroundings, including nine of Angola’s endemic species, of which *Eleuthemis eogaster* (Figure 3b) has yet to be found elsewhere (so far it is known only from several large streams and rivers near Uíge (western scarp) bordered by forest).

Here, where the Lower Guinean forests open southwards to the savanna areas, the fauna of the Guineo-Congolian Region meets the fauna of the Zambezian Region resulting in an extremely species-rich dragonfly fauna with a high number of endemics. The steep topography of the Serra do Pingano adds a mosaic of streams and rivers with lush tropical gallery forests and permanent and seasonal swamps,



Figure 3: A selection of animal species of the Angolan northwestern escarpment: a) *Kimpavita longleg* (*Notogomphus kimpavita*); b) *sunrise firebelly* (*Eleuthemis eogaster*); c) *African horned toad* (*Sclerophrys cf. superciliaris*); d) *ornate African water snake* (*Grayia ornata*); e) *black-necked weaver* (*Ploceus nigricollis*); f) *female black-casqued wattled hornbill* (*Ceratogymna atrata*); g) *white-bellied pangolin* (*Phataginus tricuspis*); and h) *Angolan roussette* (*Myonycteris angolensis*). Photos by authors, except 3e (Lucas Langer) and 3g (Anne Göhre).

most of them nutrient poor on sandy soils. It is this combination of different habitats and a fauna of different origins that has resulted in the very distinct and rich fauna with many endemic species in Angola's north.

More surveys are urgently needed to complement species lists and ranges in order to understand evolutionary traits in this area. We expect more than 200 species of Odonata in the wider area around Uíge Province in northern Angola. Kipping *et al.* (2019) conclude: "... new species are most likely to be found among genera prone to narrow (highland) ranges, i.e., with known Angolan endemics like *Platycypha* and *Pseudagrion*, but also *Agriocnemis*, *Elatoneura*, *Notogomphus* (Figure 3a) and *Paragomphus*. Also possible, however, is the discovery of endemics in genera that are well represented across the country and continent, and that have highland endemics elsewhere but not in Angola, such as *Africallagma*, *Neodythemis* and *Orthetrum*. However, given the biogeographic diversity of Angola's fauna and endemics, we could expect greater surprises."

Butterflies (Papilionoidea)

There are about 4,500 species of Afrotropical butterfly species (Williams 2023), 769 of which are known from Angola (Mendes *et al.* 2019). These authors also mention 32 species as being endemic to Angola.

During eight short assessment surveys to northern Angola between 2012 and 2015, as well as in 2019, a total of 905 Papilionoidea specimens have been collected, 788 of which originate from Uíge's escarpment area. So far, 207 butterfly species have been identified. Additionally, 31 species groups were still under investigation at the time of writing this paper. The 207 identified species represent 26.9% of all Papilionoidea species known from Angola to date. This is a remarkable amount considering the limited number of surveys in an area comprising less than 0.6% of Angola's territory, and indicates the high importance of the Uíge escarpment for butterfly diversity.

Many of the recorded species are rather common (e.g., *Neptis agouale*, *Terias senegalensis*, *Haydonia pythia*, *Leptosia nupta*), widespread throughout the country (e.g., *Azanus mirza*, *Sevenia benguelae*, *Acraea atolmis*, *Libythea labdaca*) or even the Afrotropical region in general (e.g., *Anthene larydas*, *Graphium leonidas*, *Byblia anvatara*, *Hypolimnas anhedon*). Many of the recorded species are known to be associated with degraded habitats (e.g., *Euphaedra medon*, *Ypthima doleta*, *Junonia stygia*, *Telchinia acerata*). The known degree of endemism of Angolan butterflies at species level seems to be surprisingly low considering the large extent of the country and the richness of highly diverse ecoregions. However, this is

probably due to limited sampling effort and a spatial/geographic bias that can only be resolved through intensified sampling across the area, including the escarpment. Moreover, unified and standardised monitoring schemes and updated taxonomies and phylogenies are urgently needed to elucidate actual diversity and endemism patterns in Angolan butterflies.

Moths

There are 28,866 species of night-flying moths known from the Afrotropical region and 1,312 from Angola (de Prins & de Prins 2011–2020). These counts, however, are rather preliminary, as several hundreds of new species are still being described each year, and surveys regularly add species to country lists.

Identification of African moths can be challenging, as summarising works for most subgroups are either largely out of date or simply not available. The available taxonomic information is scattered over numerous scientific publications spanning a period of about 150 years. Many groups still need revision, each awaiting a large proportion of new species descriptions. For the time being, the best overview on Afrotropical moths is given by de Prins and de Prins (2011–2020) in their comprehensive database, AfroMoths.

Monitoring moths in northern Angola has been focused on snout moths (Pyraloidea). There are more than 16,400 species of snout moths in the world, 2,770 of which are known from Africa south of the Sahara (Nuss *et al.* 2003–2023). In northern Angola, snout moths were attracted using UV-lights during 40 nights. Analysis of morphological and genetic data revealed 324 species of snout moths in the Serra Uíge and Serra do Pingano. This is equivalent to 11% of all known Afrotropical snout moths. Taxonomic revisions and analyses of data from various African countries are still needed to better understand the diversity of snout moths in Angola, and to uncover possible endemics.

A case study on agricultural pest species found in fruits of *Solanum aethiopicum* (Kikongo: *mbolongwa*) at a market in Negage (Uíge Province) in 2013 (Mally *et al.* 2015) revealed the scale of yet uncovered diversity in snout moths, and probably of other moth groups in Africa. This African-wide taxonomic revision resulted in the description of seven new species, three of which had been repeatedly imported into Europe. Altogether, there are 23 species of snout moths originally described from Angola (Nuss *et al.* 2003–2023), but research is necessary to uncover their natural distributions and possible Angolan endemics.

Although local species composition shows superficial resemblance to that of the larger Congo Basin and the West African realm, identifying actual

patterns of endemism and diversity requires a thorough taxonomic revision of several taxa. Particularly the so-called widespread taxa may turn out to be cryptic species complexes and a more detailed analysis will likely yield range-restricted lineages that can be considered true Angolan and/or escarpment endemics.

In addition to intensified research into insect groups that have already been addressed, systematic surveys of additional ecologically important and species-rich insect orders that have not been investigated so far (e.g., Coleoptera and Hymenoptera) are urgently needed. These will provide basic data required for addressing important issues, such as ecosystem functionality (e.g., nutrient fluxes) and ecosystem services (e.g., pollination).

Amphibians and reptiles

The history of herpetological explorations, including an updated atlas of Angolan herpetofauna has recently been summarised by Marques *et al.* (2018) and the amphibian fauna, in particular, was reviewed by Baptista *et al.* (2019). Since then, several new species of reptiles and amphibians have been described or await formal description, and new country records have been added to the lists (Bauer *et al.* 2023, Becker *et al.* 2023). Northern Angola, including the provinces of Cabinda, Lunda-Norte, Uíge and to a lesser extent Malanje and Cuanza-Norte, is unique with respect to its herpetofaunal diversity and composition because it harbours the last remaining tracts of already largely fragmented rainforest. Sizable and important patches can only be found in Cabinda and Uíge; these, particularly the SPFE, have been the sites of recent herpetological explorations.

A first comprehensive amphibian and reptile species list for this exceptional ecosystem was provided by Ernst *et al.* (2020). The herpetofauna is comparatively rich and unique for the country, consisting of species that are otherwise only known from the Central African forest systems of Cameroon and/or Gabon and have not been recorded from any other locality in Angola (e.g., *Trichobatrachus robustus*, compare Ernst *et al.* 2014; *Xenopus andrei*, compare Ernst *et al.* 2015; and *Sclerophrys superciliaris* (Figure 3c), *Cardioglossa gracilis*, *Chiromantis rufescens*, *Hyperolius (Alexeroon) hypsiphonus*, *Holaspis guentheri*, compare Ernst *et al.* 2020, 2021).

Although the number of true highland endemics appears to be limited (Becker *et al.* 2023), several phylogenetic lineages are very distinct and show signs of recent (Pliocene or even younger) species differentiation (Ernst *et al.* 2021, Jaynes *et al.* 2022), highlighting the evolutionary potential of the SPFE. Recent evidence from amphibian and reptile surveys

in the region also supports an assumed late Quaternary connection with Central African forest systems and the potential role as a late Pleistocene forest refuge.

If deforestation and habitat degradation continue at the alarming rates witnessed, however, this exceptional African rainforest ecosystem including much of its herpetofaunal diversity will be lost forever. For example, a closed rainforest site connecting the Serra Uíge with the Serra do Pingano that was visited in 2016, and in which several amphibian species were recorded for the first time in Angola, had been cleared for agricultural use two years later (Figure 1f). Slash-and-burn farming is very prominent in the region and particularly harmful to the steep and still-forested slopes of the cordilleras, as chimney effects can lead to rapid and uncontrolled spread of fires that then destroy huge areas of formerly intact forest (Figure 1e). Direct consumption of amphibians (e.g., *Amietia angolensis*) has been reported by local inhabitants, but amphibians are not frequently seen on otherwise extensive bushmeat markets, nor are they important elements in local diets as is the case in West Africa.

Research including a strong focus on amphibian and reptile diversity of the Serra do Pingano *sensu lato*, including the reassessment of cryptic species complexes (Jaynes *et al.* 2022, Chaney *et al.* subm.; cf. Figure 3d) and the description of new species (Lobón-Rovira *et al.* 2021) is ongoing and provides additional support for the importance of the region both on a national and Pan-African scale. Yet, as in other parts of Africa, this is a race against time.

Birds

So far, 940 bird taxa have been confirmed to occur in Angola, 29 of which are endemic (Dean *et al.* 2019, Mills & Melo 2023). Taking bird records retrieved from the Global Biodiversity Information Facility (GBIF.org 2022) into account, the mountain ranges around Quitexe and Uíge are home to 318 species, including some endemics. This emphasises the importance of this region for bird diversity in Angola.

Mostly, endemic birds are restricted to the Afro-montane grasslands and semi-evergreen scarp forests along the escarpment in Angola (Huntley 2019). The forested mountain ranges of Uíge Province form the northern part of the escarpment, but only one bird, Braun's bushshrike (*Laniarius braunii*), is strictly endemic to the region around Quitexe. Some more taxa show narrow distribution ranges, sometimes extending into the Congolian forests further north: Angolan white-throated greenbul (*Phyllastrephus albigularis* subsp. *viridiceps*) and Hartert's camaroptera (*Camaroptera harterti*) are both strict endemics; and Angola batis (*Batis minulla*), yellow-throated nicator (*Nicator vireo*) and pale-olive greenbul (*Phyllastrephus*

fulviventris) are all quasi-endemics (Dean *et al.* 2019, Vaz Pinto & Fernandes 2020).

The rate of (bird) endemism in Uíge is not as striking as along the escarpment further south. However, according to our own survey and analysis in 2019, at least 25 Afrotropical taxa occurring in the mountain ranges around Uíge show a peculiar distribution, with main distribution ranges in West and/or Central Africa, and an isolated population in Uíge and/or the Angolan escarpment (Mills & Dean 2007, Sinclair & Ryan 2010, Dean *et al.* 2019). Examples are the black-necked weaver (*Ploceus nigrifrons*) (Figure 3e) or the black-casqued wattled hornbill (*Ceratogymna atrata*) (Figure 3f). Furthermore, bird observations around Uíge and Quitexe in recent years has led to several new species records for Angola. For instance, white-collared oliveback (*Nesocharis ansorgei*) (Mills & Vaz Pinto 2015), forest swallow (*Petrochelidon fuliginosa*) (Mills & Tebb 2015) and Willcocks's honeyguide (*Indicator willcocksii*) (Mills & Boesman 2020) have recently been observed, all constituting isolated populations, disjunct from the main distribution ranges. Such findings highlight the unique setting of the Uíge mountain ranges, and their importance for endangered bird species. Braun's bushshrike for instance is a strict endemic to the region, but with only 3,500 to 7,000 remaining individuals, it is endangered (Mills *et al.* 2011).

Like tropical forests further north, the rainforest fragments around Uíge are increasingly exploited, leading to deforestation and degradation (Tegegne *et al.* 2016). This has far-reaching implications, because the species particularly threatened by forest degradation and subsequent population declines are often frugivores, like turacos, parrots, pigeons or hornbills (Whitney & Smith 1998, Menke *et al.* 2012). They avoid degraded areas where large fruiting trees have been removed by legal and illegal logging. However, frugivores are important forest tree seed dispersers and therefore crucial for forest regeneration (Chasar *et al.* 2014). Their absence in degraded areas implies that natural forest regeneration is slowed down, particularly if degradation is progressing. The mountain ranges of Uíge have the potential to remain a refuge for these iconic Afrotropical birds, but only if the rapid degradation is contained.

Mammals

The province of Uíge is a transition zone between the drier peripheral semi-evergreen Guineo-Congolian rainforest, the Zambezian dry evergreen forest and the transition woodland (White 1983) resulting in an extraordinary landscape of dense rainforest, caves, sandy swamps and savannas along the mountain ranges. This provides a diverse habitat template for very different mammal species. The proximity to the Congo Basin results in a high taxonomic

overlap between the Guineo-Congolian mammal communities and those found in Uíge Province. These include numerous rodents, such as the brush-tailed porcupine (*Atherurus africanus*), the forest giant squirrel (*Protoxerus stangeri*) and the fire-footed rope squirrel (*Funisciurus pyrropus*). Preliminary opportunistic surveys conducted during independent field campaigns in 2019 yielded a total of 27 mammal species in the province (Teutloff *et al.* 2021). Although not recorded during field campaigns, charismatic megafauna, such as the African forest elephant (*Loxodonta cyclotis*), are known to occur historically but have not been reported until recently. Most recent sightings date back to the years 2018 and 2019 where elephants were seen between the Serra do Pingano and Serra Uíge.

Several primate species, some of which are heavily hunted, like the red-tailed monkey (*Cercopithecus ascanius* ssp.), have been reported. Among them are species of high conservation concern, such as the rare southern talapoin (*Miopithecus talapoin*) which is endemic to northern Angola and the coastal watersheds south of DRC (Kingdon 2019). The southern talapoin is listed as Vulnerable on the International Union for Conservation of Nature (IUCN) Red List. It is a strictly riverine species that depends on dense evergreen vegetation restricted to the banks of the rivers that criss-cross the serras (Kingdon 2019, IUCN 2021). The nominate *Colobus angolensis angolensis*, endemic to northern Angola and the Congo Basin (Kingdon 2019), is very rare in the area and was only recorded from the Mucaba area.

Among the most heavily hunted, yet strictly protected mammal species, is the white-bellied pangolin (*Phataginus tricuspis*). Although still considered one of the more abundant species among the four African pangolin species, it is listed as Endangered (EN) by IUCN Red List in Ghana, where the white-bellied pangolin represented 82% of the observed pangolins traded by the stakeholders and annually 0.4–2.7 million pangolins are hunted in Central African forests alone (Boakye *et al.* 2016, Ingram *et al.* 2018). This matches our observations from Uíge Province.

In addition to the 27 reported species, several species known from the Guineo-Congolian region are expected to occur in Uíge Province. These include Ansorge's kusimanse (*Crossarchus ansorgei*) known only from deciduous rainforest and the Lunda rope squirrel (*Funisciurus bayonii*) living in mosaics of rainforest and moist woodlands in northeastern Angola and southwestern DRC (Kingdon 2019). Furthermore, the recently discovered Angolan dwarf galago (*Galagoides kumbirensis*), observed in the adjacent province Cuanza-Norte in 2013, lives in moist, tall forest and semi-arid baobab savanna-woodland very similar to the serras of the SPFE

(Svensson *et al.* 2017). Although it has not been observed so far, the possibility of its occurrence in the serras exists.

To date, many mammal groups have not been systematically studied in the region. These groups particularly include small mammals – rodents, as well as micro- and macrochiroptera that play important roles as seed dispersers and/or pollinators and therefore also significantly contribute to forest regeneration. Moreover, they are important pathogen reservoirs and disease vectors and, as such, significantly drive socioecological developments in the country and beyond. The species which are documented so far are Egyptian rousette (*Rousettus aegypticus*), collared fruit bat (*Myonycteris angolensis*), dwarf epauletted fruit bat (*Micropteropus pusillus*), hammer-headed fruit bat (*Hypsiphatidius monstrosus*) and horseshoe bats (*Rhinolophus* spp.). Due to heavy and completely uncontrolled hunting, in combination with habitat degradation and loss, Uíge's mammal diversity is at risk and faces serious decline; unique species, such as the white-bellied pangolin, the endemic southern talapoin and Angola colobus are likely to disappear in the near future (Kingdon 2019, Jansen *et al.* 2020). A better understanding of the actual diversity and population status of highly threatened taxa is urgently needed.

SYNTHESIS AND CONCLUSION

The Angolan escarpment has long been recognised as an important centre of biodiversity and geodiversity (compare Huntley *et al.* 2019 and references cited therein). However, despite an increasing research interest in this landscape in recent years, the vast majority of the extensive and heterogeneous ecosystem it supports remains largely unexplored. This is particularly true for the more remote outliers, such as the SPFE in the far north of the highlands and escarpments of Angola. Yet, our preliminary surveys and the data established through these efforts highlight the fact that these edge habitats are indeed unique and very special geo- and biodiversity gems in the chain of extraordinary habitats that make up the escarpment zone. Not only several species new to science were described, but in all species groups there were new records for Angola and thus an extension of the range of several species. At the same time, many species groups have not yet been studied at all, indicating that there are still large gaps in knowledge to be filled. In the case of fungi, for example, possibly half of the samples collected are new species. For all species groups, taxonomic revisions and analyses of data from various African countries are still needed to better understand the diversity and uncover possible endemic species.

Furthermore, urgent action is required to safeguard these treasure troves that are severely threatened by

human activities, such as logging, slash-and-burn farming and bushmeat trade (Figures 1e–h). Angola is at a crossroads of decisions and trade-offs around utilisation, conservation and preservation of its forests and, thus, substantial parts of the country's biodiversity. The SPFE deserves special mention in the wider context of exploring, understanding and protecting the biodiversity of the western escarpment. The establishment of a national protected area in the Serra do Pingano Forest Ecosystem is therefore a necessary and urgently needed first step towards protecting Angola's national biodiversity heritage.

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