Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

Angola Cave-Chat *Xenocopsychus ansorgei*
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Diversity and endemism of geoxylic plants on the Angolan Planalto

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ABSTRACT

The Angolan Planalto and adjacent areas are characterised by flammable grassy ecosystems. Within these old-growth grasslands, geoxyles are a dominant component and play a key role in the functioning, diversity and beauty of these ecosystems. Geoxyles are a plant life form characterised by having low aboveground biomass and massive belowground wooden structures from which they can draw stored reserves and resprout quickly after disturbances such as fire. The Angolan Planalto has a high number of geoxyle taxa of which many are endemic to the area. We give an overview of the number of geoxyle taxa in these highlands based on a compilation of all available data, discuss reasons for this remarkable diversity, and point out research and conservation priorities for this important life form that is threatened by upcoming land-use changes.

Keywords: Angola, Angolan Planalto, diversity, endemism, geoxyles, highlands, suffrutices

INTRODUCTION

Geoxylic suffrutices, also known as geoxyles, are woody plants with an eccentric growth form, earning them the name ‘underground trees’ because most of their woody biomass is underground (White 1976, Maurin *et al.* 2014, Pausas *et al.* 2018, Zigelski *et al.* 2019a). Figure 1 illustrates some endemic geoxylic plants of the Angolan Planalto. The underground biomass encompasses roots, woody rhizomes or xylopodia and serves as an underground storage organ and bud bank, which is essential for resprouting after disturbance (Pausas *et al.* 2018, Ott *et al.* 2019). By locating critical organs underground and restricting their aboveground biomass to short-lived flowering and fruiting shoots, species with this growth form are well adapted to rainfall seasonality and fire, herbivory and frost (Maurin *et al.* 2014, Finckh *et al.* 2016, Wigley *et al.* 2019).

Geoxyles grow in frost- and fire-prone tropical grasslands and savannas dominated by C4 grasses. They can cover the ground densely (Meller *et al.* 2022a) and reach ages of thousands of years (Alves *et al.* 2013, B van Wyk pers. comm.). Coexistence with grasses is possible because geoxyles begin to resprout and flower in the dry season, well before the grasses do; this asynchronicity in assimilation periods and generative propagation reduces competition between geoxyles and grasses (Zigelski *et al.* 2019a). Although geoxyles tend to be overlooked in grasslands due to their lower stature, they contribute to biodiversity, functionality, carbon stocks and the resilience of their habitats (Fidelis *et al.* 2014, Zaloumis & Bond 2016, Gomes *et al.* 2021).

Starting in the late Miocene around 10 mya, tropical forests in south-central Africa gave way to open vegetation types as the CO_2 levels dropped and the climate became drier and more seasonal (Zachos *et al.* 2001, Trauth *et al.* 2009, Bonnefille 2011, Herbert *et al.* 2016). In this context, the geoxylic growth form evolved convergently in response to seasonality in a multitude of plant families, particularly from savanna and tropical forest lineages (Meller *et al.* 2022b). Many geoxyles evolved from tree and shrub species (White 1976, Maurin *et al.* 2014), and many of them have remarkably similar morphological traits to closely related tree species, except for the growth height (Meerts 2017, Gomes *et al.* 2019).

Geoxyles occur in tropical regions that are affected by fire, herbivory and/or frost, and these types of periodical aboveground disturbances and biomass removal are regarded as a prerequisite for their occurrence (Fidelis *et al.* 2014). Globally, the Cerrado (Brazil) and south-central Africa represent hotspots of diversity and endemism for geoxyles (White 1983, Maurin *et al.* 2014, Pennington & Hughes 2014). In Angola, the Zambezian phytochorion, i.e., centre of endemism (White 1983; Figure 2A), with its mosaic of miombo woodlands and open vegetation types, and particularly the Angolan Montane Forest–Grasslands mosaic (Olson *et al.* 2001) provides ideal conditions for geoxyles: sufficient and seasonal precipitation combined with frequent abiotic disturbances like fire and frost which promote areas of low tree cover. Parts of South Africa, Zambia, Democratic Republic of the Congo, Zimbabwe, Mozambique and Malawi are also rich in geoxyles, whereas most parts of Namibia and Botswana are too

Figure 1: *Endemic geoxylic plants of the Angolan Planalto. A)* Leptactina prostrata *(Rubiaceae); B)* Thunbergia retefolia *(Acanthaceae); C)* Adenodolichos mendesii *(Fabaceae); D)* Protea ongotium *(Proteaceae); E)* Dolichos dongaluta *(Fabaceae); F)* Protea ongotium *excavated (lignotuber); G)* Clutia benguellensis *(Phyllanthaceae); H)* Eriosema albo-griseum *(Fabaceae); I) resprouting geoxyles (light green:* Brachystegia russelliae*, dark green:* Cryptosepalum *sp. nov. aff.* maraviense*) on the Bié high plain, end of dry season.*

arid. Several highland areas in Africa harbour endemic geoxyles, e.g., the Nyika Plateau in Malawi (Willis *et al.* 2001), and the Highveld (Davy 1922) and Cape Floral Region of South Africa (Grobler & Cowling 2021).

According to the catalogue of Angolan plants (Figueiredo & Smith 2008), our own compilations (Zigelski *et al.* 2019a, Meller *et al.* 2022b) and research for this paper, Angola is home to at least 133 different geoxyle species in the strict sense (i.e., species with close tree relatives), of which 42 are endemic (31.6%). When defining geoxyles in a broader sense, i.e., the majority of woody biomass is underground and species descriptions include phrases like "from a woody rootstock", "with a woody tuber" or "suffruticose", there are 229 different taxa in Angola, 83 of which are endemic (36.2%). The high number of endemic species and the floristic singularity of the Zambezian phytochorion (Clayton & Cope 1980, White 1983) is thus prominently shaped by Angolan geoxyles. Strikingly, the geoxyle communities of the Angolan Planalto, being part of the highlands and escarpments of Angola and Namibia (HEAN), are predominantly composed of different species and endemics than those of the Kalahari sands in the eastern, less elevated parts of Angola. In this paper, we focus on Angola's endemic geoxyle species that are restricted to the Ancient Plateau (Angolan Planalto) and the Marginal Mountain Chain (see Mendelsohn & Huntley 2023) of the HEAN. By collating available data on those species and mapping their occurrences in Angola, we present hotspots of geoxyle endemism, and then discuss the current state of knowledge, as well as threats and conservation needs for geoxyles.

METHODS

The geoxyle taxa enumerated in this review were compiled based on the catalogue of Angolan plant species which indicates most endemic species (Figueiredo & Smith 2008), our own ongoing vegetation surveys conducted in Bié, Huíla, Moxíco and Cuando Cubango provinces since 2011, and a thorough search of geoxyle literature (White 1976, Maurin *et al.* 2014, Revermann *et al.* 2017, Goyder *et al.* 2018, Zigelski *et al.* 2019a). We furthermore checked whether newly described and revised species from Angola match the definition of a geoxyle (Robbrecht *et al.* 1996, Dessein *et al.* 2003, Darbyshire *et al.* 2019, 2021, Frazão *et al.* 2020). It was not always clear if a species is a geoxyle because species descriptions were often vague and insufficient with regard to belowground parts. In many cases information was limited to terms like "perennial", "with a woody base" or "growing from a woody rootstock". We thus applied a broader definition (species with a woody base) and a stricter definition (species with woody underground organs and with congeneric tree relatives) and categorised the species accordingly (Table 1). Taxa which also occur outside of Angola or are endemic to Angola but restricted to the lowlands (≤ 1,200 masl) were excluded, leaving a total of 126 highland taxa. Table 2 provides information on the plant families with geoxyle taxa in Angola, and Appendix 1 lists all endemic geoxyle taxa occurring on the Angolan Planalto. For these taxa we retrieved georeferenced occurrence data from the Vegetation Database of the Okavango Basin (ID AF-00-009) in the Global Index of Vegetation-Plot Databases (Dengler *et al.* 2011), vegetation databases from Angolan Biodiversity Observatories (SASSCAL ObservationNet 2023), collections stored at the herbarium LUBA in Lubango (Angola) and the Global Biodiversity Information Facility (GBIF 2021). For the latter two we manually georeferenced entries which had precise enough locality descriptions. A total of 1,630 georeferenced occurrence records were obtained and these were mapped using standard settings for kernel density estimation in QGIS 3.10.14 (QGIS.org 2023).

ENDEMIC GEOXYLE SPECIES

Figure 2 shows the distribution of the 126 highland geoxylic taxa in Angola. A similar number of taxa are known from the Nyika Plateau in Malawi, which is

Table 1: *Number of geoxyle taxa endemic to the Angolan Planalto, and endemic to Angola but also occurring beyond the Angolan Planalto at lower altitudes.*

	Taxa endemic to the Angolan Planalto		**Taxa endemic to Angola**	
Geoxyle characteristic*	Number of endemic taxa	Number of families represented	Number of endemic taxa	Number of families represented
i) Species with a woody base	91	23	126	23
ii) Species with a woody base and a woody underground storage organ	50	16	77	16
iii) Species with a woody base, woody underground storage and tree relatives	22	10	32	13

* As species descriptions are often vague and insufficient with regard to belowground parts, we compiled the table with increasingly strict definitions of geoxyles: (i) species with "a woody base" can be termed geoxyles in the broad sense, this group may also include perennial herbs; (ii) species with woody underground storage organs (USO) have a woody base and extended belowground woody structures; and (iii) species have a woody base, USOs and congeneric tree relatives which are geoxyles in the strict sense.

also part of the Zambezian phytochorion, though only 10 geoxylic species (in the broad sense) are endemic to the plateau (Meller 2022). Hotspots are evident on the Humpata plateau near Lubango, and on the Bié and Huambo high plains. Table 3 lists endemic geoxyle taxa occurring on the Angolan Planalto, and indicates which species are strict highland endemics. Although the high plain of southeastern Angola is also known to be particularly rich in geoxyles (Goyder *et al.* 2018, Zigelski *et al.* 2018, 2019a), its species pool differs from that of the Angolan Planalto because most highland geoxyles do not extend far into the eastern areas (Figure 2B). This concurs with the findings of Linder (2001), who identified two centres of plant endemism and diversity in Angola, one extending eastwards from central Angola across Katanga and Zambia, the other on the Humpata Plateau.

Meller *et al.* (2022b) have shown that multiple biogeographic origins and environmental heterogeneity promote geoxyle diversity in Angola. The high number of families that contribute geoxyle species also adds to the diversity (Tables 1 and 2), as

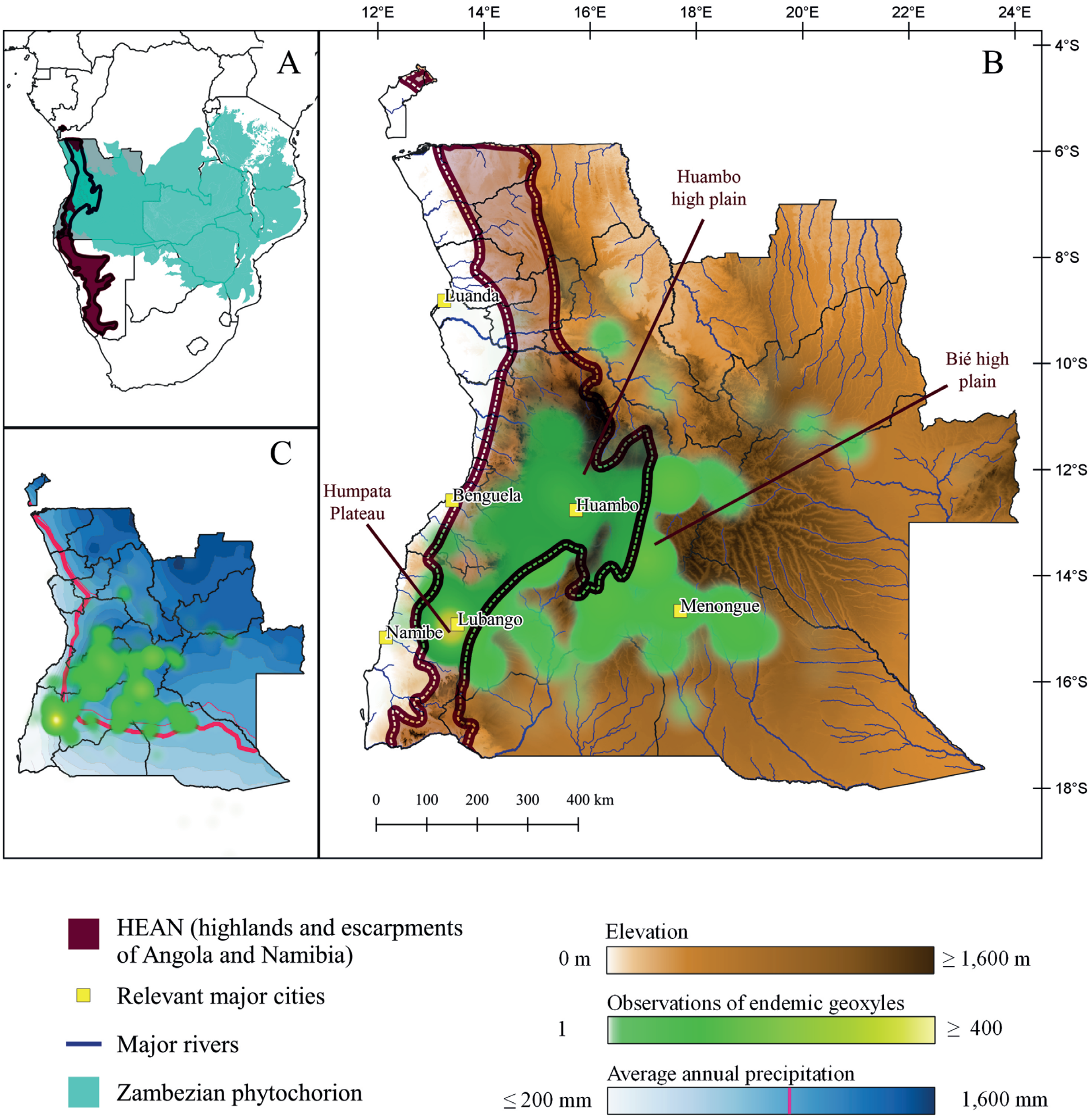

Figure 2: *Distribution of geoxyle taxa endemic to the Angolan Planalto. A) Location of the Zambezian centre of endemism (phytochorion) (cyan) in relation to Angola (shaded) and the highlands and escarpments of Angola and Namibia (HEAN). B) Angola in detail, showing topography with the HEAN boundary, and the density of collections and observations of 126 endemic geoxyle taxa. C) Distribution of average annual precipitation across Angola, overlaid with geoxyle density, showing that highland-specific geoxyles do not generally occur where average annual precipitation falls below 800 mm (pink line).*

Table 2: *Families with the most geoxyle taxa in Angola. The number of highland endemic geoxyles in families with at least five geoxyle taxa in the broad sense is given. For comparison, the total number of geoxyle taxa in these families that occur in Angola (including non-endemics) is given in brackets. USO = underground storage organ.*

	Number of highland endemic geoxyle species (total number of geoxyle species)		
Family	**With a woody base**	**With a woody USO**	**With congeneric tree relative**
Fabaceae	28 (69)	13 (49)	2 (11)
Rubiaceae	10 (45)	6 (40)	5 (38)
Acanthaceae	11 (15)	3 (7)	0 (0)
Lamiaceae	7 (17)	2 (13)	1 (3)
Euphorbiaceae	5 (12)	5 (11)	2 (10)
Malvaceae	5 (11)	5 (11)	1 (6)
Other*	25 (110)	16 (98)	11 (65)
Total	91 (279)	50 (229)	22 (133)

*Some important geoxyle families have fewer than five highland endemics and are therefore included in the group "other"; this group includes Anacardiaceae (three highland endemic taxa out of a total of eleven taxa), Apocynaceae (no highland endemic taxa out of a total of five taxa), Ochnaceae (no highland endemic taxa out of a total of six taxa) and Proteaceae (four highland endemic taxa out of a total of nine taxa).

phylogenetic diversity often is a prerequisite for overall species diversity (Enquist *et al.* 2002). Environmental differences between the higher- and lower-lying areas, particularly regarding edaphic conditions and disturbance regimes, could thus cause distinct geoxyle communities. Many geoxyle species have specific requirements with regard to substrates (Revermann *et al.* 2017). From the coastal plain in western Angola elevations increase, the topography is rugged and weathered plinthosols and shallow substrates on unweathered bedrock predominate (Huntley 2019). The southern and eastern parts of Angola, on the other hand, are characterised by gently undulating landscapes covered by deep and nutrient-poor deposits of Kalahari sands that extend eastwards into Zambia and southwards into Namibia and Botswana. In these sandy areas in southern and eastern Angola, quantity and seasonality of rainfall follows a north–south gradient, thereby forming a natural boundary for highland-specific geoxyles at the 800 mm isopleth of annual average rainfall (Figure 2C). Rainfall above 800 mm is enough for sufficient, continuous fuel loads (cured grasses) to support frequent fires (Govender *et al.* 2006, Archibald *et al.* 2010).

However, there are differences in the exposure to other aboveground disturbances along the east–west gradient. The higher lying areas of the Angolan Planalto and Humpata Plateau are prone to localised, frequent frosts in the dry season (up to 40 per year) which affect the open grasslands in the valleys, in particular, because the cold air can pool there (Finckh *et al.* 2016, 2021). During the Pliocene (5.3–2.6 mya), and particularly in the Pleistocene (2.6 million to 11,700 years ago), Angola had a cooler and more arid climate, and probably experienced more frequent and more severe nocturnal frost events (deMenocal 1995, Herbert *et al.* 2016). Strikingly, the highest areas along the western escarpment now receive very little frost and it only occurs in enclosed valleys (SASSCAL WeatherNet 2023, pers. obs. P Meller, M Finckh), probably due to the mild oceanic influence.

Several ecological theories may help to explain the high number of highland endemic geoxyle taxa, for example, plant and/or seed dispersal has been limited in the past (Freestone & Inouye 2006), climatic conditions have been stable over a long time (Lovett & Friis 1996) and/or soils in the highlands are heterogeneous at a small scale (Hulshof & Spasojevic 2020). A combined effect is probable, because the topography of the highlands leads to only slightly connected small-scale mosaics of forests, woodlands, grasslands and wetlands, an environment that seems to promote evolutionary processes. However, it should also be noted that historically the western part of Angola has been far better covered by collectors than the eastern part (Sosef *et al.* 2017, Goyder & Gonçalves 2019). Some of the geoxyle hotspots in Figure 2 reflect historical collection sites (e.g. Morro de Lopollo near Lubango) and expedition routes.

THREATS AND CONSERVATION

Inherently, most aboveground disturbances are not threatening to geoxyles because they are well-adapted to them. Their belowground storage organs and bud banks are vulnerable, however, because once these are critically damaged, geoxyles lose their carbon reserves and resprouting ability (Zaloumis & Bond 2016, Buisson *et al.* 2019). These critical parts are mostly located in the topsoil, in the first ~30 cm below the surface (Gomes *et al.* 2021), which is sufficient to buffer short thermal peaks caused by the passage of fire (Auld & Bradstock 1996), as well as nocturnal frost pulses lasting several hours (Revermann 2013); soil temperature at 5–10 cm deep only deviates slightly in both situations. However, the geoxyles' location in the topsoil might not protect them from physical impacts. Historically, the Angolan Planalto had low densities of meso- and megaherbivores (Huntley *et al.* 2019), which implies that geoxyle grasslands there were probably not heavily affected by grazing or trampling. In Cangandala National Park, herds of giant sable antelope (*Hippotragus niger variani*) have been seen

Table 3: *Endemic geoxyle taxa occurring on the Angolan Planalto. Only taxa with a congeneric tree relative are listed here; a full list of endemic geoxyle taxa is provided in Appendix 1. For each species, geoxyle category indicates whether it is a geoxyle in a broad sense (with a woody base), or strict sense (with a woody underground storage organ), and whether it is a strict highland endemic (Y = yes; N = no). Close tree relatives from south-central Africa are also provided, however, since phylogenetic studies are lacking for most geoxyle taxa, the tree taxa listed here should be regarded as examples and not necessarily as the actual closest tree relative. Distribution indicates if species are restricted to particular high plains, escarpments or localities; wider distributions within Angola are presented as an alphabetical list of provinces abbreviated as follows: BE – Benguela; BI – Bié; CC – Cuando Cubango; CS – Cuanza-Sul; CU – Cunene; HI – Huíla; HU – Huambo; MA – Malanje; MO – Moxico; and NA – Namibe.*

Taxon	**Family**	**Geoxyle category**	**Highland endemic**	**Close tree relative(s)**	**Distribution**
Baphia sp. nov.	Fabaceae	strict	N	*Baphia bequaertii*	BI, CC, MO
Clutia benguelensis Müll.Arg.	Euphorbiaceae	strict	Y	*Clutia abyssinica*	BE, BI, HI, HU
Combretum argyrotrichum Welw. ex M.A.Lawson	Combretaceae	strict	Y	*Combretum zeyheri*	Humpata Plateau, HU high plain
Combretum viscosum Exell	Combretaceae	strict	Y		BE, BI, HI, HU
Cryptosepalum sp. nov. aff. *maraviense*	Fabaceae	strict	Y	*Cryptosepalum exfoliatum*	BI high plain
Dissotis benguellensis A.Fern. & R.Fern.	Melastomataceae	broad	Y	*Dissotis melleri*	HU, Serra do Môco
Dissotis carrissoi A.Fern. & R.Fern.	Melastomataceae	broad	N		CS, HU
Erythrina pygmaea Torre	Fabaceae	strict	Y	*Erythrina abyssinica*	Humpata Plateau
Euclea angolensis Gürke	Ebenaceae	strict	Y	*Euclea divinorum*	Humpata Plateau
Euphorbia asclepiadea Milne-Redh.	Euphorbiaceae	broad	N	*Euphorbia matabelensis*	BI high plain
Euphorbia parifolia N.E.Br.	Euphorbiaceae	strict	Y		Humpata Plateau, Tundavala
Fadogia caespitosa Robyns	Rubiaceae	strict	N	*Fadogia erythroploea*	Humpata Plateau
Fadogia chrysantha K.Schum.	Rubiaceae	strict	Y		HU high plain
Fadogia graminea Wernham	Rubiaceae	strict	N		BI high plain
Fadogia punctulata Robyns	Rubiaceae	strict	Y		HU high plain
Fadogia stenophylla Welw. ex Hiern	Rubiaceae	strict	N		Humpata Plateau, Lubango
Gnidia fruticulosa Gilg	Thymelaeaceae	broad	Y	*Gnidia glauca*	Humpata Plateau
Gnidia newtonii Gilg	Thymelaeaceae	broad	Y		Humpata Plateau
Gnidia rendlei Hiern	Thymelaeaceae	broad	Y		Humpata Plateau, Mumpulla
Gnidia welwitschii Hiern	Thymelaeaceae	broad	Y		Humpata Plateau
Grewia suffruticosa K.Schum.	Malvaceae	strict	Y	*Grewia bicolor*	Humpata Plateau
Hypericum abilianum N.Robson	Hypericaceae	broad	Y		Humpata Plateau
Julbernardia gossweileri (Baker f.) Torre & Hillc.	Fabaceae	strict	N	*Julbernardia paniculatum*	CC, HI, HU, MA

Lannea gossweileri Exell & Mendonça	Anacardiaceae	strict	Y	*Lannea discolor*	BI high plain
Lannea rubra Hiern (Engl.)	Anacardiaceae	strict	Y		Humpata Plateau, Tundavala
Leptactina prostrata K.Schum.	Rubiaceae	strict	N	*Leptactina platyphylla*	BI high plain, MO
Ozoroa xylophylla (Engl. & Gilg) R.Fern. & A.Fern.	Anacardiaceae	strict	Y	*Ozoroa insignis*	BI high plain and Humpata Plateau
Pavetta nana K.Schum.	Rubiaceae	strict	Y	*Pavetta gardeniifolia*	Humpata Plateau, Tchivinguiro
Phyllanthus microdendron Müll.Arg.	Phyllanthaceae	strict	Y	*Phyllanthus muellerianus*	BI high plain
Protea dekindtiana Engl.	Proteaceae	strict	Y	*Protea gaguedii*	Humpata Plateau, Tchivinguiro
Protea ongotium Beard	Proteaceae	strict	Y		BI high plain and Humpata Plateau
Protea paludosa subsp. *paludosa* Hiern (Engl.)	Proteaceae	strict	Y		BI high plain and Humpata Plateau
Protea poggei subsp. *haemantha* (Engl. & Gilg) Chisumpa & Brummitt	Proteaceae	strict	N		BI high plain, MO
Protea poggei subsp. *heliophila* Chisumpa & Brummitt	Proteaceae	strict	Y		HU high plain
Psychotria moninensis (Hiern) E.M.A.Petit	Rubiaceae	strict	N	*Psychotria succulenta*	BE, BI, CC, HI, HU, MA
Psychotria welwitschii (Hiern) Bremek.	Rubiaceae	strict	Y		HU, HI and NA escarpment
Tricalysia angolensis A.Rich. ex DC.	Rubiaceae	strict	N	*Tricalysia elliotii*	BI, CC, CU high plains and Humpata Plateau
Vangueria cistifolia var. *cistifolia* (Welw. ex Hiern) Lantz	Rubiaceae	strict	N	*Vangueria infausta*	BI, HI, MA
Vangueria fulva (Robyns) Lantz	Rubiaceae	strict	Y		BI high plain and Humpata Plateau
Vitex caespitosa Exell	Lamiaceae	strict	Y	*Vitex ferruginea*	BI, BE, HU

feeding on geoxyles in grasslands after fire, when grasses have not yet resprouted in the dry season (pers. obs. A Gomes). However, it is unclear what effect modern herbivory and trampling by cattle has on geoxyles in Angola. Land-use changes and landscape transformations in Angola have accelerated in the past two decades and are currently happening without regulation (Mendelsohn 2019). In the Cerrado in Brazil, another biome characterised by a high geoxyle diversity, much damage has been done to the natural vegetation, including geoxyles, with the transformation from natural grasslands into intensively used rangelands or into agricultural fields (Grecchi *et al.* 2014, Velazco *et al*. 2019).

The biggest threat to geoxyles lies in the transformation of natural tropical grasslands to intensive land-use types. Once trampling or ploughing damages their belowground parts irreversibly, geoxyle species cannot easily recuperate. Their strategy is to grow slowly, to survive and live long (Alves *et al.* 2013, B van Wyk pers. comm.), whereas propagation via seeds seems only secondary and with a low rate of success, since geoxyle seedlings seem to be very rare (pers. obs. P Meller). This means that even after an agricultural field has been abandoned, it may take a very long time for geoxyles to recolonise the area. To date, agriculture in more remote parts of Angola is only starting to become industrialised, and most agricultural practices still rely on combinations of hard manual work, animal traction and/or fire. However, urbanisation and technical progress promote the mechanisation of agriculture, which in turn makes it easier to convert land pervaded by massive belowground woody structures, as seen for instance on the Bié and Huambo plateaus (Figure 3, pers. obs. M Finckh, A Gomes, P Meller).

Analogously, misguided attempts to afforest tropical grasslands in order to sequester atmospheric CO_2 (Bastin *et al.* 2019, Bond *et al.* 2019) endanger geoxyles and make little sense because intact geoxyle grasslands can store carbon amounts comparable to old-growth woodlands (Gomes *et al.* 2021). Even if the geoxyles' belowground structures are left unharmed,

Figure 3: *Tractor-ploughed fields in geoxyle grasslands near Chitembo, Bié, appeared in July 2021 (top photos). A plough pulled by a tractor is deep and strong enough to destroy the massive belowground geoxyle structures. Ploughed fields are then planted with crops like cassava, beans or maize (bottom photo). The maize field in the lower photo was ploughed in 2015 but had already been abandoned four years later because productivity decreases rapidly in these nutrient-poor soils.*

once they are overshadowed by trees, the shade-intolerant geoxyles rapidly become outcompeted (Zaloumis & Bond 2016, Buisson *et al.* 2019). Like intensified agriculture, this destroys biodiverse, old-growth natural grasslands (Bond 2016).

It is clear that geoxylic species face imminent threats in Angola due to accelerating land use change and intensification. For example, nearly 800,000 ha of miombo woodland, including geoxyle habitats, were converted to croplands on the Angolan Planalto between 2002 and 2015 (Palacios *et al.* 2015, Mendelsohn 2019). Lack of knowledge about geoxyle diversity makes it difficult to estimate specific conservation needs, because many geoxyle species are poorly known and/or described, and the range extent and population sizes of most species are still unknown. As a result, threat status assessments (IUCN Red List) are rarely available. Of the 126 taxa occurring on the Angolan Planalto, 119 taxa (94.4%) are either Data Deficient or not assessed. The high rate of localised endemics facing land-use intensification, however, indicates a substantial threat to at least some of the geoxyle species, such as *Barleria kacondensis* subsp. *glabrescens* which is classified as EN B1ab(iii), i.e., “Endangered, with extent of occurrence < 100 km² and further decline” (Darbyshire *et al.* 2021) and *Bolusia ervoides* which has been described as a “rare species and is known from only few collections” (van Wyk *et al.* 2010).

GAPS IN KNOWLEDGE AND PRIORITIES FOR RESEARCH

As described, several knowledge gaps and research priorities are already apparent: the impact of herbivory on geoxyle grasslands cannot be assessed without further research, and the same is true for the threats and conservation needs of individual geoxyle species and communities. The diversity, richness and multiple origins of geoxyle species make it difficult to study them as a whole (Meller *et al.* 2022b), so we advocate not to treat them across-the-board as a uniform plant growth form, but as a conglomeration of species that adapted convergently in response to similar environmental drivers.

Geoxyle grasslands are characterised by the low agricultural potential of the soils on which they occur, and the fact that different soil types bear different geoxyle communities (Revermann *et al.* 2017). Generally, these soils are weathered, well-drained, nutrient-poor and of high sand content (> 80%); they are acidic (~pH 4) with a low cation exchange capacity (< 20 cmolc/dm³) and low base saturation (71%–78%) (Gröngröft 2013, Gomes *et al.* 2021). This is also evident from other co-occurring plant species that are adapted to low nutrient contents, such as orchids. From pristine species-rich grassland ecosystems worldwide it is known that the application of nitrogen and phosphorus fertilisers leads to diversity losses and homogenisations in grasslands (Tilman & Downing 1994, Harpole & Tilman 2007). If industrial agriculture in Angolan geoxyle grasslands intensifies further, it is likely that the application of fertilisers will have a similar effect on geoxyle diversity in the long term. Research on these issues is urgently needed.

The high number of endemic species and their often localised ranges raise the question of genetic diversity and connectedness between populations. To our knowledge, there have been no studies on population genetics of Afrotropical geoxyles to date, except for one study on the widely distributed and polymorphic *Syzygium guineense* complex, which includes geoxylic forms, and where gene flow between geoxyle, shrub and tree forms occurs over wide ranges (Zigelski *et al.* 2019b). Detailed studies on the genetic diversity, or isolation, of specific geoxyle populations are missing, which is concerning because the influence of the geoxyles’ supposedly limited sexual reproduction cannot be assessed. Furthermore, demographic studies of geoxyle species are practically non-existent, with one exception (Chidumayo 2019), making it hard to understand and counteract the observed rarity of seedlings. Such knowledge is crucial for conservation and restoration purposes, particularly in the light of impending grassland degradations and fragmentations.

There are manifold research deficiencies regarding African geoxyles, although Burtt Davy published the first comprehensive review 100 years ago (Davy 1922), followed by treatises from White (1976), Maurin *et al.* (2014) and Zigelski *et al.* (2019a). These articles, however, focus predominantly on ecological and evolutionary aspects rather than the complexity of the geoxylic growth form. Scientific information on the life cycle of geoxyles would make conservation and management plans more sustainable and holistic. Aspects such as animal–geoxyle interactions, plant–fungi and plant–microbe mutualisms, pollination and pollinators, dispersal mechanisms, growing rates, and success rates of generative reproduction (and how to improve it) need to be investigated. To conclude, we see imminent threats of destruction and loss of a landscape type which is home to unique plant evolution, before we even have started to grasp and comprehend its functioning, diversity, history, biotic interactions and ecosystem services.

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REFERENCES

Alves RJV, Silva NGD, Fernandes Junior AluJ, Guimaraes AR (2013) Longevity of the Brazilian underground tree *Jacaranda decurrens* Cham. *Anais da Academia Brasileira de Ciências* 85(2): 671–678. https://doi.org/10.1590/S0001-37652013005000038.

Archibald S, Scholes RJ, Roy DP, Roberts G, Boschetti L (2010) Southern African fire regimes as revealed by remote sensing. *International Journal of Wildland Fire* 19(7): 861. https://doi.org/10.1071/WF10008.

Auld TD, Bradstock RA (1996) Soil temperatures after the passage of a fire: do they influence the germination of buried seeds? *Austral Ecology* 21(1): 106–109. https://doi.org/10.1111/j.1442-9993.1996.tb00589.x.

Bastin J-F, Finegold Y, Garcia C, Mollicone D, Rezende M, Routh D, Zohner CM, Crowther TW (2019) The global tree restoration potential. *Science* 365(6448): 76–79. https://doi.org/10.1126/science.aax0848.

Bond WJ (2016) Ancient grasslands at risk. *Science* 351 (6269): 120–122. https://doi.org/10.1126/science.aad5132.

Bond WJ, Stevens N, Midgley GF, Lehmann CER (2019) The trouble with trees: afforestation plans for Africa. *Trends in Ecology & Evolution* 34(11): 963–965. https://doi.org/10.1016/j.tree.2019.08.003.

Bonnefille R (2011) Rainforest responses to past climatic changes in tropical Africa. In: Bush M, Flenley J, Gosling W (eds) *Tropical Rainforest Responses to Climatic Change*. 125–184. Springer Berlin Heidelberg, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-05383-2_5.

Buisson E, Le Stradic S, Silveira FAO, Durigan G, Overbeck GE, Fidelis A *et al.* (2019) Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. *Biological Reviews* 94(2): 590–609. https://doi.org/10.1111/brv.12470.

Chidumayo EN (2019) Biomass and population structure of a geoxyle, *Lannea edulis* (Sond.) Engl., at a savanna woodland site in Zambia. *South African Journal of Botany* 125: 168–175. https://doi.org/10.1016/j.sajb.2019.07.027.

Clayton WD, Cope TA (1980) The chorology of Old World species of Gramineae. *Kew Bulletin* 35(1): 135. https://doi.org/10.2307/4117012.

Darbyshire I, Tripp EA, Chase FM (2019) A taxonomic revision of Acanthaceae tribe Barlerieae in Angola and Namibia. Part 1. *Kew Bulletin* 74(5): 1–85. https://doi.org/10.1007/s12225-018-9791-0.

Darbyshire I, Manzitto-Tripp EA, Chase FM (2021) A taxonomic revision of Acanthaceae tribe Barlerieae in Angola and Namibia. Part 2. *Kew Bulletin* 76(2): 127–190. https://doi.org/10.1007/s12225-021-09928-5.

Davy JB (1922) The suffrutescent habit as an adaptation to environment. *The Journal of Ecology* 10(2): 211. https://doi.org/10.2307/2255742.

DeMenocal PB (1995) Plio-Pleistocene African climate. *Science* 270(5233): 53–59. https://doi.org/10.1126/science.270.5233.53.

Dengler, J, Jansen, F, Glöckler, F, Peet, RK, De Cáceres, M, Chytrý, M, *et al*. (2011) The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *Journal of Vegetation Science* 22(4): 582–597.

Dessein S, Ntore S, Robbrecht E, Smets E (2003) Pollen and seeds reveal that *Spermacoce thymoidea* s.l. (African Rubiaceae, Spermacoceae) represents three endemic or disjunct species from the Zambezian high plateaus. *Systematic Botany* 28(1): 130–144.

Enquist BJ, Haskell JP, Tiffney BH (2002) General patterns of taxonomic and biomass partitioning in extant and fossil plant communities. *Nature* 419: 610–613. https://doi.org/10.1038/nature01069.

Fidelis A, Appezzato-da-Glória B, Pillar VD, Pfadenhauer J (2014) Does disturbance affect bud bank size and belowground structures diversity in Brazilian subtropical grasslands? *Flora – Morphology, Distribution, Functional Ecology of Plants* 209(2): 110–116. https://doi.org/10.1016/j.flora.2013.12.003.

Figueiredo E, Smith G (2008) Plants of Angola / Plantas de Angola. *Strelitzia* 22.

Finckh M, Revermann R, Aidar MPM (2016) Climate refugees going underground – a response to Maurin *et al*. (2014). *New Phytologist* 209(3): 904–909. https://doi.org/10.1111/nph.13567.

Finckh M, Wendefeuer J, Meller P (2021) Frost-driven lower treelines in Angola and their implications for tropical forest–grassland mosaics. *Journal of Vegetation Science* 32(5). https://doi.org/10.1111/jvs.13084.

Frazão R, Catarino S, Goyder D, Darbyshire I, Magalhães MF, Romeiras MM (2020) Species richness and distribution of the largest plant radiation of Angola: *Euphorbia* (Euphorbiaceae). *Biodiversity and Conservation* 29(1): 187–206. https://doi.org/10.1007/s10531-019-01878-6.

Freestone AL, Inouye BD (2006) Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology* 87(10): 2425–2432. https://doi.org/10.1890/0012-9658(2006)87[2425:DLAEHS]2.0.CO;2.

GBIF (2021) GBIF occurrence download. https://doi.org/10.15468/DL.43FWMF.

Gomes AL, Revermann R, Gonçalves FMP, Lages F, Aidar MPM, Finckh M, Jürgens N (2019) Tree or not a tree: differences in plant functional traits among geoxyles and closely related tree species. *South African Journal of Botany* 127: 176–184. https://doi.org/10.1016/j.sajb.2019.08.044.

Gomes AL, Revermann R, Gonçalves FMP, Lages F, Aidar MPM, Sanguino Mostajo GA, Finckh M (2021) Suffrutex grasslands in south-central Angola: belowground biomass, root structure, soil characteristics and vegetation dynamics of the 'underground forests of Africa'. *Journal of Tropical Ecology* 37(3): 136–146. https://doi.org/10.1017/S0266467421000298.

Govender N, Trollope WSW, Van Wilgen BW (2006) The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* 43(4): 748–758. https://doi.org/10.1111/j.1365-2664.2006.01184.x.

Goyder DJ, Barker N, Bester SP, Frisby A, Janks M, Gonçalves FMP (2018) The Cuito catchment of the Okavango system: a vascular plant checklist for the Angolan headwaters. *PhytoKeys* 113: 1–31. https://doi.org/10.3897/phytokeys.113.30439.

Goyder DJ, Gonçalves FMP (2019) The flora of Angola: collectors, richness and endemism. In: Huntley BJ, Russo V, Lages F, Ferrand N (eds) *Biodiversity of Angola*. 79–96. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-03083-4_5.

Grecchi RC, Gwyn QHJ, Bénié GB, Formaggio AR, Fahl FC (2014) Land use and land cover changes in the Brazilian Cerrado: a multidisciplinary approach to assess

the impacts of agricultural expansion. *Applied Geography* 55: 300–312. https://doi.org/10.1016/j.apgeog.2014.09.014.
Grobler BA, Cowling RM (2021) The composition, geography, biology and assembly of the coastal flora of the Cape Floristic Region. *PeerJ* 9: e11916. https://doi.org/10.7717/peerj.11916.
Gröngröft A, J Luther-Mosebach, L Landschreiber, A Eschenbach (2013) Cusseque - Soils. *Biodiversity and Ecology* 5: 51–54. https://doi.org/10.7809/b-e.00245
Harpole WS, Tilman D (2007) Grassland species loss resulting from reduced niche dimension. *Nature* 446(7137): 791–793. https://doi.org/10.1038/nature05684.
Herbert TD, Lawrence KT, Tzanova A, Peterson LC, Caballero-Gill R, Kelly CS (2016) Late Miocene global cooling and the rise of modern ecosystems. *Nature Geoscience* 9(11): 843–847. https://doi.org/10.1038/ngeo2813.
Hulshof CM, Spasojevic MJ (2020) The edaphic control of plant diversity. *Global Ecology and Biogeography* 29(10): 1634–1650. https://doi.org/10.1111/geb.13151.
Huntley BJ (2019) Angola in outline: Physiography, climate and patterns of biodiversity. In: Huntley BJ, Russo V, Lages F, Ferrand N (eds) *Biodiversity of Angola*. 15–42. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-03083-4_2.
Huntley BJ, Beja P, Vaz Pinto P, Russo V, Veríssimo L, Morais M (2019) Biodiversity conservation: history, protected areas and hotspots. In: Huntley BJ, Russo V, Lages F, Ferrand N (eds) *Biodiversity of Angola*. 495–512. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-03083-4_18.
Linder HP (2001) Plant diversity and endemism in sub-Saharan tropical Africa: African phytogeography. *Journal of Biogeography* 28(2): 169–182. https://doi.org/10.1046/j.1365-2699.2001.00527.x.
Lovett JC, Friis I (1996) Patterns of endemism in the woody flora of north-east and east Africa. In: van der Maesen LJG, van der Burgt XM, van Medenbach de Rooy JM (eds) *The biodiversity of African plants*. 582–601. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-009-0285-5_72.
Maurin O, Davies TJ, Burrows JE, Daru BH, Yessoufou K, Muasya AM, Bank M, Bond WJ (2014) Savanna fire and the origins of the 'underground forests' of Africa. *New Phytologist* 204(1): 201–214. https://doi.org/10.1111/nph.12936.
Meerts P (2017) Geoxylic suffrutices of African savannas: short but remarkably similar to trees. *Journal of Tropical Ecology* 33(4): 295–298. https://doi.org/10.1017/S0266467417000165.
Meller (2022) *Diversity, ecology and origin of geoxylic plants in the Western Zambezian Floristic Region*. Doctoral dissertation, University of Hamburg. pp. 151. https://ediss.sub.uni-hamburg.de/handle/ediss/9847
Meller P, Frazão R, Lages F, Jürgens N, Finckh M (2022a) Tipping the scales: how fire controls the balance among functional groups in Angolan grasslands. *African Journal of Range & Forage Science* 39(1): 56–69. https://doi.org/10.2989/10220119.2021.2012822.
Meller P, Stellmes M, Fidelis A, Finckh M (2022b) Correlates of geoxyle diversity in Afrotropical grasslands. *Journal of Biogeography* 49(2): 339–352. https://doi.org/10.1111/jbi.14305.
Mendelsohn, JM (2019) Landscape changes in Angola. In: Huntley B, Russo V, Lages F, Ferrand N (eds) *Biodiversity of Angola*. 123–137. Springer International Publishing Cham. https://doi.org/10.1007/978-3-030-03083-4_8.
Mendelsohn JM, Huntley BJ (2023) Introducing the highlands and escarpments of Angola and Namibia. In: Mendelsohn JM, Huntley BJ, Vaz Pinto P (eds) Monograph on endemism in the highlands and escarpments of Angola and Namibia. *Namibian Journal of Environment* 8: 7–22.
Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC *et al.* (2001) Terrestrial ecoregions of the world: a new map of life on earth. *BioScience* 51(11): 933. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2.
Ott JP, Klimešová J, Hartnett DC (2019) The ecology and significance of below-ground bud banks in plants. *Annals of Botany* 123(7): 1099–1118. https://doi.org/10.1093/aob/mcz051.
Palacios G, Lara-Gomez M, Márquez A, Vaca JL, Ariza D, Lacerda V, Navarro-Cerrillo RM (2015) *Spatial dynamic and quantification of deforestation and degradation in Miombo Forest of Huambo Province (Angola) during the period 2002–2015*. Unpublished report: SASSCAL Project Proceedings, Report Task 137, Huambo, Angola. pp. 40–45.
Pausas JG, Lamont BB, Paula S, Appezzato-da-Glória B, Fidelis A (2018) Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist* 217(4): 1435–1448. https://doi.org/10.1111/nph.14982.
Pennington RT, Hughes CE (2014) The remarkable congruence of New and Old World savanna origins. *New Phytologist* 204(1): 4–6. https://doi.org/10.1111/nph.12996.
QGIS.org (2023) QGIS Geographic Information System. QGIS Association. http://www.qgis.org.
Revermann R (2013) Cusseque – micro-climatic conditions. *Biodiversity and Ecology* 5: 47. https://doi.org/10.7809/b-e.00244.
Revermann R, Gonçalves FM, Gomes AL, Finckh M (2017) Woody species of the Miombo woodlands and geoxylic grasslands of the Cusseque area, south-central Angola. *Check List* 13(1): 2030. https://doi.org/10.15560/13.1.2030.
Robbrecht E, Huysmans S, Figueiredo E (1996) The generic status of *Oxyanthus gossweileri* (Rubiaceae) from Angola. *South African Journal of Botany* 62(1): 17–22. https://doi.org/10.1016/S0254-6299(15)30572-X.
SASSCAL ObservationNet (2023) http://www.sasscalobservationnet.org.
SASSCAL WeatherNet (2023) http://www.sasscalweathernet.org.
Sosef MSM, Dauby G, Blach-Overgaard A, Van Der Burgt X, Catarino L, Damen T *et al.* (2017) Exploring the floristic diversity of tropical Africa. *BMC Biology* 15(1): 15. https://doi.org/10.1186/s12915-017-0356-8.
Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. *Nature* 367(6461): 363–365. https://doi.org/10.1038/367363a0.
Trauth MH, Larrasoaña JC, Mudelsee M (2009) Trends, rhythms and events in Plio-Pleistocene African climate. *Quaternary Science Reviews* 28(5–6): 399–411. https://doi.org/10.1016/j.quascirev.2008.11.003.
Van Wyk B-E, Venter M, Boatwright JS (2010) A revision of the genus *Bolusia* (Fabaceae, Crotalarieae). *South African Journal of Botany* 76(1): 86–94. https://doi.org/10.1016/j.sajb.2009.08.010.
Velazco SJE, Villalobos F, Galvão F, De Marco Júnior P (2019) A dark scenario for Cerrado plant species: effects of future climate, land use and protected areas

ineffectiveness. *Diversity and Distributions* 25(4): 660–673. https://doi.org/10.1111/ddi.12886.

White F (1976) The underground forests of Africa: a preliminary review. *Gardens' Bulletin, Singapore* 29: 55–71.

White F (1983) *The vegetation of Africa: a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa*. Unesco, Paris.

Wigley BJ, Staver AC, Zytkowiak R, Jagodzinski AM, Wigley-Coetsee C (2019) Root trait variation in African savannas. *Plant and Soil* 441(1–2): 555–565. https://doi.org/10.1007/s11104-019-04145-3.

Willis CK, Burrows JE, Fish L, Phiri PSM, Chikuni AC, Golding J (2001) Developing a greater understanding of the flora of the Nyika. *Systematics and Geography of Plants* 71(2): 993. https://doi.org/10.2307/3668733.

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292(5517): 686–693. https://doi.org/10.1126/science.1059412.

Zaloumis NP, Bond WJ (2016) Reforestation or conservation? The attributes of old growth grasslands in South Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371(1703): 20150310. https://doi.org/10.1098/rstb.2015.0310.

Zigelski P, Gomes A, Finckh M (2019a) Suffrutex dominated ecosystems in Angola. In: Huntley BJ, Russo V, Lages F, Ferrand N (eds) *Biodiversity of Angola*. 109–121. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-03083-4_7.

Zigelski P, Lages F, Finckh M (2018) Seasonal changes of biodiversity patterns and habitat conditions in a flooded savanna – the Cameia National Park Biodiversity Observatory in the Upper Zambezi catchment, Angola. *Biodiversity & Ecology* 6: 438–447. https://doi.org/10.7809/b-e.00356.

Zigelski P, Rudolph B, Oldeland J, Lages F, Jürgens N, Finckh M (2019b) The tough, the wet and the hidden: evolutionary strategies of a polyploid tropical tree in a changing environment. *Perspectives in Plant Ecology, Evolution and Systematics* 38: 1–12. https://doi.org/10.1016/j.ppees.2019.03.001.

Appendix 1: *Full list of endemic geoxyle taxa occurring on the Angolan Planalto (extended version of Table 3). For each species, the geoxyle category indicates whether it is a geoxyle in a broad sense (with a woody base), or strict sense (with a woody underground storage organ); also indicated, is whether it is a strict highland endemic and whether it has a close congeneric tree relative (Y = yes; N = no). Distribution indicates if species are restricted to particular plateaus, escarpments or localities; wider distributions within Angola are presented as an alphabetical list of provinces abbreviated as follows: BE – Benguela; BI – Bié; CC – Cuando Cubango; CN – Cuanza-Norte; CS – Cuanza-Sul; CU – Cunene; HI – Huíla; HU – Huambo; LS – Lunda-Sul; MA – Malanje; MO – Moxíco; and NA – Namibe*

Taxon	**Family**	**Geoxyle category**	**Highland endemic**	**Close tree relative(s)**	**Distribution**
Acalypha dumetorum Müll.Arg.	Euphorbiaceae	broad	N	N	BE
Acalypha eriophylla Hutch.	Euphorbiaceae	broad	Y	N	BI high plains
Acalypha eriophylloides S.Moore	Euphorbiaceae	broad	Y	N	BI high plains
Acalypha gossweileri S.Moore	Euphorbiaceae	broad	N	N	CN, Cazengo
Acalypha huillensis Pax & K.Hoffm.	Euphorbiaceae	broad	Y	N	Humpata Plateau
Adenodolichos mendesii Torre	Fabaceae	broad	Y	N	BI high plains
Aeschynomene benguellensis Torre	Fabaceae	broad	Y	N	BE, BI, HI, HU
Aeschynomene debilis Baker	Fabaceae	broad	Y	N	Humpata Plateau
Aeschynomene dimidiata subsp. *dimidiata* Baker	Fabaceae	broad	N	N	CC, HI, HU, LS, MA
Ampelocissus dekindtiana Gilg	Vitaceae	broad	Y	N	Humpata Plateau, Tchivinguiro
Antizoma angolensis Exell & Mendonça	Menispermaceae	broad	Y	N	HU high plains
Baphia sp. nov.	Fabaceae	strict	N	Y	CC, BI, MO
Barleria antunesii Lindau	Acanthaceae	broad	Y	N	Humpata Plateau
Barleria buddleoides S.Moore	Acanthaceae	broad	N	N	CC, HI
Barleria crabbeoides I.Darbysh.	Acanthaceae	broad	Y	N	Humpata Plateau, Lubango
Barleria eburnea I.Darbysh.	Acanthaceae	broad	N	N	BI high plains and Humpata Plateau
Barleria imatensis I.Darbysh.	Acanthaceae	broad	N	N	Humpata Plateau, Tchivinguiro
Barleria kacondensis subsp. *glabrescens* I.Darbysh.	Acanthaceae	broad	Y	N	HU high plains
Barleria kacondensis subsp. *kacondensis* S.Moore	Acanthaceae	broad	Y	N	BI high plains and Humpata Plateau
Barleria polyneura S.Moore	Acanthaceae	broad	N	N	Humpata Plateau
Barleria violascens var. *humpatana* I.Darbysh.	Acanthaceae	broad	Y	N	Humpata Plateau, Monino
Basananthe nummularia Welw.	Passifloraceae	broad	Y	N	Humpata Plateau, Lopollo
Bolusia ervoides (Baker) Torre	Fabaceae	broad	Y	N	Humpata Plateau, Lopollo

Ceratoteca reniformis Abels	Pedaliaceae	broad	N	N	BE, CS, HI, HU, MA
Chamaecrista huillensis (Mendonca & Torre) Lock	Fabaceae	broad	N	N	CC, HI, NA
Chamaecrista newtonii (Mendonca & Torre) Lock	Fabaceae	broad	Y	N	BE, HI
Clutia benguelensis Müll.Arg.	Euphorbiaceae	strict	Y	Y	BE, BI, HI, HU
Combretum argyrotrichum Welw. ex M.A.Lawson	Combretaceae	strict	Y	Y	HU high plains, Humpata Plateau
Combretum viscosum Exell	Combretaceae	strict	Y	Y	BE, BI, HI, HU
Crossandra angolensis S.Moore	Acanthaceae	broad	Y	N	BE
Crotalaria bondii Torre	Fabaceae	broad	Y	N	Humpata Plateau
Crotalaria griseofusca Baker f.	Fabaceae	broad	Y	N	BI high plains
Crotalaria ivantalensis Baker	Fabaceae	broad	Y	N	HI, NA
Crotalaria mendesii Torre	Fabaceae	broad	N	N	CU, HI
Crotalaria pittardiana Torre	Fabaceae	broad	N	N	BE, CU, HI, HU
Crotalaria pseudovirgultatis Torre	Fabaceae	broad	Y	N	Humpata Plateau, Lubango
Crotalaria subsessilis Harms	Fabaceae	broad	N	N	CC
Cryptosepalum sp. nov. aff. *maraviense*	Fabaceae	strict	Y	Y	BI high plains
Dissotis benguellensis A.Fern. & R.Fern.	Melastomataceae	strict	Y	Y	HU, Serra do Môco
Dissotis carrissoi A.Fern. & R.Fern.	Melastomataceae	strict	N	Y	CS, Huambo
Dolichos dongaluta Baker	Fabaceae	broad	Y	N	BI high plains
Dolichos elatus Baker	Fabaceae	broad	N	N	BE, MA
Droogmansia dorae var. *dorae* Torre	Fabaceae	broad	Y	N	BI high plains
Droogmansia gossweileri Torre	Fabaceae	broad	Y	N	HU high plains
Droogmansia vanderystii De Wild.	Fabaceae	broad	N	N	CS, HU
Eminia benguellensis Torre	Fabaceae	broad	N	N	BE, HI, HI, LS, MA
Eriosema albo-griseum Baker f.	Fabaceae	broad	Y	N	Humpata Plateau, Tundavala
Eriosema cyclophyllum Baker f.	Fabaceae	broad	Y	N	BI high plains and Humpata Plateau
Eriosema gossweileri Baker f.	Fabaceae	broad	Y	N	Humpata Plateau, Tundavala
Eriosema pygmaeum Baker	Fabaceae	broad	N	N	Humpata Plateau
Eriosema speciosum Baker	Fabaceae	broad	N	N	CN, BE, HI, HU
Erythrina pygmaea Torre	Fabaceae	strict	Y	Y	Humpata Plateau
Euclea angolensis Gürke	Ebenaceae	strict	Y	Y	Humpata Plateau

Euphorbia asclepiadea Milne-Redh.	Euphorbiaceae	strict	N	Y	BI high plains
Euphorbia parifolia N.E.Br.	Euphorbiaceae	strict	Y	Y	Humpata Plateau, Tundavala
Fadogia caespitosa Robyns	Rubiaceae	strict	N	Y	Humpata Plateau
Fadogia chrysantha K.Schum.	Rubiaceae	strict	Y	Y	HU high plains
Fadogia graminea Wernham	Rubiaceae	strict	N	Y	BI high plains
Fadogia punctulata Robyns	Rubiaceae	strict	Y	Y	HU plateau
Fadogia stenophylla Welw. ex Hiern	Rubiaceae	strict	N	Y	Humpata Plateau, Lubango
Fuerstia adpressa A.J.Paton	Lamiaceae	broad	Y	N	BE, HI
Fuerstia rigida (Benth.) A.J.Paton	Lamiaceae	broad	Y	N	Humpata Plateau, Lopollo
Ganguelia gossweileri (S.Moore) Robbr.	Rubiaceae	broad	Y	N	BI high plains
Gnidia fruticulosa Gilg	Thymelaeaceae	strict	Y	Y	Humpata Plateau
Gnidia newtonii Gilg	Thymelaeaceae	strict	Y	Y	Humpata Plateau
Gnidia rendlei Hiern	Thymelaeaceae	strict	Y	Y	Humpata Plateau, Mumpulla
Gnidia welwitschii Hiern	Thymelaeaceae	strict	Y	Y	Humpata Plateau
Grewia suffruticosa K.Schum.	Malvaceae	strict	Y	Y	Humpata Plateau
Hypericum abilianum N.Robson	Hypericaceae	strict	Y	Y	Humpata Plateau
Indigofera corallinosperma Torre	Fabaceae	broad	Y	N	Humpata Plateau
Indigofera huillensis Baker f.	Fabaceae	broad	Y	N	BE, HI
Indigofera mendesii Torre	Fabaceae	broad	Y	N	Humpata Plateau
Indigofera nummularia Baker	Fabaceae	broad	Y	N	BE, HU
Indigofera paraoxalidea Torre	Fabaceae	broad	Y	N	Humpata Plateau
Jamesbrittenia angolensis Hilliard	Scrophulariaceae	broad	Y	N	Humpata Plateau, Tundavala
Julbernardia gossweileri (Baker f.) Torre & Hillc.	Fabaceae	strict	N	Y	CC, HI, HU, MA
Lannea gossweileri Exell & Mendonça	Anacardiaceae	strict	Y	Y	BI high plains
Lannea rubra Hiern (Engl.)	Anacardiaceae	strict	Y	Y	Humpata Plateau, Tundavala
Lepidagathis gossweileri S.Moore	Acanthaceae	broad	Y	N	BE, HI
Leptactina prostrata K.Schum.	Rubiaceae	strict	N	Y	BI high plains, MO
Linariopsis prostrata Welw.	Pedaliaceae	broad	Y	N	HI
Macrotyloma bieense (Torre) Verdc.	Fabaceae	broad	Y	N	Humpata Plateau, Tchivinguiro

Meineckia phyllanthoides subsp. *trichopoda* (Müll.Arg.) G.L.Webster	Euphorbiaceae	broad	N	N	northwest Angola
Oldenlandia sipaneoides K.Schum.	Rubiaceae	broad	Y	N	Humpata Plateau, Lopollo
Orthosiphon violaceus Briq.	Lamiaceae	broad	Y	N	Humpata Plateau, Lopollo
Ozoroa xylophylla (Engl. & Gilg) R.Fern. & A.Fern.	Anacardiaceae	strict	Y	Y	BI high plains and Humpata Plateau
Pavetta nana K.Schum.	Rubiaceae	strict	Y	Y	Humpata Plateau, Tchivinguiro
Pentanisia rubricaulis (K.Schum.) Kårehed & B.Bremer	Rubiaceae	broad	Y	N	BI high plains, HI, HU
Phaulopsis lankesterioides (Lindau) Lindau	Acanthaceae	broad	Y	N	BE, HI, HU
Phyllanthus microdendron Müll.Arg.	Phyllanthaceae	strict	Y	Y	BI high plains
Polygala huillensis Welw. ex Oliv.	Polygalaceae	broad	Y	N	Humpata Plateau, Lopollo
Protea dekindtiana Engl.	Proteaceae	strict	Y	Y	Humpata Plateau, Tchivinguiro
Protea ongotium Beard	Proteaceae	strict	Y	Y	BI high plains and Humpata Plateau
Protea paludosa subsp. *paludosa* Hiern (Engl.)	Proteaceae	strict	Y	Y	BI high plains and Humpata Plateau
Protea poggei subsp. *haemantha* (Engl. & Gilg) Chisumpa & Brummitt	Proteaceae	strict	N	Y	BI highlands, MO
Protea poggei subsp. *heliophila* Chisumpa & Brummitt	Proteaceae	strict	Y	Y	HU high plains
Pseudeminia benguellensis (Torre) Verdc.	Fabaceae	broad	N	N	CC, BE, HI, HU
Psychotria moninensis (Hiern) E.M.A.Petit	Rubiaceae	strict	N	Y	CC, BE, BI, HI, HU, MA
Psychotria welwitschii (Hiern) Bremek.	Rubiaceae	strict	Y	Y	HI, HU and NA escarpment
Spermacoce aprica (Hiern) Govaerts	Rubiaceae	broad	Y	N	Humpata Plateau, Ivantala
Spermacoce terminaliflora R.D.Good	Rubiaceae	broad	N	N	Humpata Plateau
Spermacoce thymoidea (Hiern) Verdc.	Rubiaceae	broad	Y	N	Humpata Plateau
Sphedamnocarpus barbosae Launert	Malpighiaceae	broad	Y	N	HU high plains
Stachys huillensis Hiern	Lamiaceae	broad	Y	N	Humpata Plateau
Stomatanthes tundavalaensis D.J.N.Hind	Asteraceae	broad	Y	N	Humpata Plateau
Tephrosia gossweileri Baker f.	Fabaceae	broad	Y	N	BE, BI, HI, HU
Tephrosia huillensis Baker	Fabaceae	broad	Y	N	HI, HU highland
Tephrosia melanocalyx Baker	Fabaceae	broad	Y	N	Humpata Plateau, Lopollo
Tephrosia newtoniana Torre	Fabaceae	broad	Y	N	Humpata Plateau, Tundavala
Tephrosia rigidula Baker	Fabaceae	broad	N	N	BE, CU, HI, HU
Tephrosia tundavalensis Bamps	Fabaceae	broad	Y	N	Humpata Plateau, Tundavala

Thesium lycopodioides Gilg	Santalaceae	broad	Y	N	BI high plains
Thesium triste A.W.Hill	Santalaceae	broad	N	N	CC, HI, MA
Thunbergia cycnium S.Moore	Acanthaceae	broad	Y	N	BI high plains
Thunbergia huillensis S.Moore	Acanthaceae	broad	Y	N	BI high plains and Humpata Plateau
Thunbergia retefolia S.Moore	Acanthaceae	broad	Y	N	BI high plains
Tinnea benguellensis Gürke	Lamiaceae	broad	N	N	BI high plains, MO
Tinnea gossweileri Robyns & Lebrun	Lamiaceae	broad	Y	N	HU high plains
Tricalysia angolensis A.Rich. ex DC.	Rubiaceae	strict	N	Y	CC, CU, BI high plains and Humpata Plateau
Triumfetta gossweileri Exell & Mendonça	Malvaceae	broad	Y	N	BI high plains and Humpata Plateau
Triumfetta hundtii Exell & Mendonça	Malvaceae	broad	Y	N	BE, Caconda
Triumfetta macrocoma K.Schum.	Malvaceae	broad	Y	N	Humpata Plateau, Tchivinguiro
Triumfetta rhodoneura K.Schum.	Malvaceae	broad	Y	N	Humpata Plateau
Vangueria cistifolia var. *cistifolia* (Welw. ex Hiern) Lantz	Rubiaceae	strict	N	Y	BI, HI, MA
Vangueria fulva (Robyns) Lantz	Rubiaceae	strict	Y	Y	BI high plains and Humpata Plateau
Vitex caespitosa Exell	Lamiaceae	strict	Y	Y	BI, BE, HU