



# Correlates of geoxyle diversity in Afrotropical grasslands

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## Abstract

**Aim:** Tropical old-growth grasslands are increasingly acknowledged as biodiverse ecosystems, but they are understudied in many aspects. Geoxyle species are a key component in many of these ecosystems, their belowground storage organs and bud banks are functionally diverse and contribute to the grasslands' resilience. However, the drivers of the geoxyles' evolution and (belowground) diversity are little understood. Thus, we combined analyses on the key aspects of diversity, belowground functionality, ancestry, and ecology of geoxyles to provide the first comprehensive understanding of this often overlooked growth form.

**Location:** Southern hemisphere Africa, particularly Angola as a part of the Zambezi phytochorion.

**Taxon:** Geoxyle species.

**Methods:** We assessed belowground bud bank types and biogeographic origins of geoxyles in grass-dominated vegetation types on the Angolan plateau, covering a broad altitudinal, climatic and geological range. Geoxyles were sampled extensively at three different sites, yielding 118 taxa covering about 59% of the Angolan geoxyle flora. Based on the current distribution of these species in Africa below the equator, we analysed their origins and environmental correlates in a taxonomic, functional and biogeographic context.

**Results:** Geoxyle species numbers and species communities differed strongly among sites, but functional types showed very similar spectra. Geoxyles evolved in multiple lineages and originated in different biomes, and functional types were unevenly associated with lineages and biomes. Furthermore, functional types correlate to specific environmental driver combinations.

**Main conclusions:** Functional diversity is not directly linked to species diversity, but is a result of multiple biogeographic origins that contributed functionally differently preadapted lineages to the Zambezi flora. Thus, geoxyles can occur under different environmental conditions, but require seasonal climates, and open grassy ecosystems subjected to fire, frost and likely herbivory. We highlight the importance of frost as a correlate of geoxyle diversity and emphasize the need for further studies to understand this important and complex growth form.

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## KEYWORDS

belowground bud bank, climate seasonality, disturbance, frost in tropics, functional diversity, geoxyle, species diversity, tropical old-growth grassland, underground storage organ

## 1 | INTRODUCTION

Worldwide, tropical grasslands and savannas, previously often perceived as a result of anthropogenic deforestation, are increasingly recognized as old-growth, species- and endemism-rich ecosystems with a long evolutionary history (Parr et al., 2014; Pennington et al., 2018; Veldman, 2016; Veldman, Buisson, et al., 2015). They provide important ecosystem services, such as underground carbon storage (Grace et al., 2006; Jones et al., 2019), and sustenance for human communities (Lehmann & Parr, 2016; Pennington et al., 2018). Several authors recently stressed the need to increase our knowledge about these ecosystems to establish sustainable management and conservation planning. This knowledge becomes particularly urgent since tropical grasslands are increasingly threatened by climate change (García Criado et al., 2020; Scheiter & Higgins, 2009), agricultural expansion and ecosystem-altering management like fire suppression and afforestation (Abreu et al., 2017; Bastin et al., 2019; Buisson et al., 2019; Veldman, Overbeck, et al., 2015).

Tropical grasslands are ecosystems with a flora highly adapted to specific disturbances. Geoxyles ('underground trees', geoxylic suffrutices), are a particular key element: subshrubs with short-lived reproductive aerial branches and extended woody belowground organs, such as roots, rhizomes or tubers (Maurin et al., 2014; Pausas et al., 2018; White, 1976; Zigelski et al., 2019), which serve as underground storage organs (USOs) and belowground bud banks (BBBs). Both functions are essential for resprouting after disturbance (Ott et al., 2019; Pausas et al., 2018). By locating their woody biomass and buds belowground and minimizing their aboveground shoots, these species are well adapted to seasonality and fire, herbivory and frost (Finckh et al., 2016; Maurin et al., 2014; Wigley et al., 2019). Periodical aboveground disturbances are regarded as a key necessity for the occurrence of geoxyles; otherwise, they are easily out-competed (Fidelis et al., 2014). The impacts of herbivory, frost and fire on tropical grassland evolution and maintenance are currently hotly debated (Botha et al., 2020; Lamont et al., 2017; Midgley et al., 2010; Staver & Bond, 2014).

The architecture of the underground structures of geoxyle species is diverse and has recently been conceptualized by Pausas et al. (2018). Geoxyles form different BBB types, defined by bud locations on roots, storage organs or propagation organs, among others. This morphological diversity also implies different functional roles of BBB types because species with rhizomes (allowing for vegetative propagation) follow different life strategies than species with storage tubers only (allowing for persistence) (Ott et al., 2019; Pausas et al., 2018). Under natural conditions, geoxyles contribute strongly to the functionality and resilience of their habitats because of their resprouting ability (Fidelis et al., 2014; Zaloumis & Bond, 2016). Therefore, detailed analyses of geoxyles and their ancestral

background are crucial to understanding patterns of functional diversity and evolution at a broader scale.

Geoxyles are best known from biodiversity hot spots in the Cerrado and in south-central Africa (Pennington & Hughes, 2014). In the latter, particularly the parts of Angola, the Democratic Republic of the Congo and Zambia that belong to the Zambeian phytochorion represent a biodiversity and endemism hotspot for geoxyles (Maurin et al., 2014; Revermann et al., 2017; White, 1983). Many geoxyles of this area are taxonomically closely related to tree species (Meerts, 2017; White, 1976). Whilst Maurin et al. (2014) placed many of the geoxyle species into 'savanna lineages', other authors point to further sources of the Zambeian geoxyle species pool, e.g. tropical forests (Finckh et al., 2016) or the Mediterranean Cape region (Lamont et al., 2017). Multiple biogeographic origins thus seem plausible but remain untested so far.

Since the Miocene (ca 15 Ma), Africa has experienced major climatic changes due to global cooling, increasing seasonality and aridification (Herbert et al., 2016; Trauth et al., 2009; Zachos et al., 2001). These changes led to the fragmentation of tropical closed-canopy forests and the spread of open habitats (Bond & Keeley, 2005; Bonnefille, 2011; Cerling et al., 1997). The convergent emergence of geoxyles in south-central Africa started together with these environmental changes in the Pliocene, and intensified particularly during the Pleistocene, 2 Ma (Lamont et al., 2017; Maurin et al., 2014). The climatic changes and vegetation developments promoted the frequent occurrence of nocturnal frosts in the dry season in subtropical and tropical highland regions (Finckh et al., 2016, 2021; Herbert et al., 2016). Frost occurrence and severity were predicted to have been even stronger during the Pleistocene (Demenocal, 1995; Finckh et al., 2021). Moreover, the spread of open grassy biomes in Africa is linked to the occurrence of fire (Bond & Keeley, 2005), though fire frequencies were much lower until prehistoric societies reached populations and densities big enough to change natural fire regimes, 200–400 ka (Archibald et al., 2012; Bird & Cali, 1998). The emergence of grassy biomes in Africa ca 15 Ma also coincides with the spread of (mega)herbivores (Charles-Dominique et al., 2016), which still roam grasslands and savannas.

To date, Afrotropical grassland ecosystems dominated by geoxyles (herein referred to as geoxyle grasslands) are understudied; little is known about their floristic composition, evolutionary and biogeographic origins and environmental drivers. Since anthropogenic fires are common, these grasslands are often regarded as fire-controlled savannas, whereas frost is rarely considered. Herbivory may also play a role in the structural and floristic composition of geoxyle grasslands as it does in drier savanna ecosystems (Archibald et al., 2019; Asner et al., 2009). Moreover, the aboveground effects of these drivers (topkill, biomass removal, fuel provision and consumption) have an impact on the belowground makeup of these



ecosystems at the community level, of which little is known. So far, a few studies have targeted the underground response of savanna tree species (Wigley et al., 2019) or that of geoxyles from the Cerrado (Apezato-da-Glória et al., 2008; Pilon et al., 2021; Zupo et al., 2021) to herbivory, fire and soil properties. What is lacking are studies that relate the diversity and composition of Afrotropical geoxyles with their belowground functional traits, evolutionary ancestry, and environmental drivers.

Our paper aims at addressing these knowledge gaps in a multifaceted approach, based on field inventories in the western Zambeian phytocorion and subcontinental floristic and environmental data from southern hemisphere Africa. We aim to integrate the diversity, belowground functionality, ancestry and ecology of Afrotropical geoxyles for a comprehensive understanding of this growth form. In particular, we hypothesize that (i) geoxyle species diversity enhances belowground functional diversity, (ii) multiple biogeographic origins promote both belowground functional and species diversity, (iii) environmental factors and in particular disturbances like fire, frost and herbivory determine the belowground functional type of a geoxyle and their distribution.

## 2 | MATERIALS AND METHODS

### 2.1 | Study region and data collection

We sampled data on geoxyle species and BBB-types in grasslands at three long-term biodiversity monitoring sites of the SASSCAL Observation Network (<http://www.sasscalobservationnet.org>) across central Angola: at high elevation on the escarpment near Lubango, Huíla province (Tundavala, S72); at the foothills of the

Angolan Plateau in the Bicular National Park, Huíla province (Bicular NP, S75) and at mid-altitude on the Bié Plateau, Bié province (Cussequé, S74) (Table 1; Figure S7). Each site represents a different ecoregion and they are all characterized by frequent disturbances of different types. At each site, a permanent 1-km<sup>2</sup> observatory has been established according to the SASSCAL guidelines. During field visits to these sites from 2017 to 2020, we repeatedly searched the geoxyle grasslands within the observatories to identify all occurring geoxyles and assemble species lists for each site.

We excavated at least one well-developed specimen of all tentative geoxyle species and categorized their belowground organ type according to the key of Pausas et al. (2018). (Figure S7). We included all species with a woody BBB type in this study (because 'geo-' = underground, '-xyle' = woody), i.e. lignotuber (Li), xylopodium (Xy), root crown (RC), bud-bearing root (Ro) and woody rhizome (WR). In this way, we include some species that were not included by White (1976) or Maurin et al. (2014), as they considered only species with close tree relatives. We indicated in Table S1 which taxa have close congeneric tree relatives.

Species that are not obligate geoxyles and can attain tree form under favourable conditions were excluded from this study. In this way, we compiled a list of 118 obligate geoxyle taxa with woody BBB types. Not all of them could be completely identified; 116 species were identified to species/subspecies/variety level, encompassing 23 species endemic to Angola (19.5%). Eight taxa could be identified only to genus level (two of them yet-undescribed species) and one species could not be placed at all. All taxa are listed in Table S1.

For all identified geoxyle species at our study sites, we retrieved georeferenced locations from the Global Biodiversity Information Facility (GBIF), including synonyms ([queryIDhttps://doi.org/10.15468/dl.83zf38](https://doi.org/10.15468/dl.83zf38)). The species names were checked beforehand and when

**TABLE 1** Comparison of research sites in Angola. MAP, mean annual precipitation; MAT, annual mean temperature; both bioclimatic variables derived from WorldClim 2 (Fick & Hijmans, 2017). WWF ecoregion classification according to Olson et al. (2001). The disturbance regime was assessed through long-standing observations, the use of permanently installed microclimate temperature loggers (Gemini Tinytag Plus 2) since 2012 (Cussequé; Finckh et al., 2021) and 2018 (Bicular, Tundavala), and interviews with local people

Site	Bicular	Cussequé	Tundavala
Latitude	-15.100°	-13.705°	-14.800°
Longitude	14.836°	17.053°	13.407°
Altitude (m)	1240	1550	2240
MAP (mm)	862	1110	980
MAT (°C)	20.6	19.5	15.8
Soil type	Deep arenosols <sup>a</sup>	Weathered ferralsols <sup>b</sup> , alluvial arenosols <sup>a</sup>	Shallow ferralsols <sup>b</sup> , bedrock
Ecoregion	Zambeian Baikiaea woodlands	Angolan Miombo woodland	Angolan montane forest-grassland mosaic
Fire regime	Annual/biennial high-intensity surface fires (patchy) (July/August)	Annual surface fires of varying intensity (patchy) (July)	Annual low-intensity surface fires (August/September)
Frost regime	About 40 frost nights/year (May-September)	About 40 frost nights/year (May-September)	0-1 frost nights/year (July-September)
Herbivory	Wild (mega)herbivores (elephants, ungulates)	Small wild herbivores (≤20 kg body mass)	Cattle grazing

<sup>a</sup>Nutrient-poor and coarse-grained soils consisting mostly of unconsolidated sands.

<sup>b</sup>Deeply weathered red or yellow soils of the humid tropics, high content of sesquioxides and low-activity clays.

necessary updated according to the International Plant Names Index (IPNI) and theplantlist.org. Furthermore, we added our own georeferenced observations of geoxyle species across Angola (TFO GVID database ID: AF-00-0009). The compiled data were checked for errors and duplicates, and all observations from north of the equator and from islands (including Madagascar) were excluded.

For all occurrence coordinates, we assembled a comprehensive spectrum of environmental data. The 10-day, 1-km normalized difference vegetation index (NDVI) long-term statistics version 2 collection (1999–2017) was acquired from the PROBA-V product distribution portal (<http://www.vito-eodata.be>). The NDVI is related to the greenness and productivity of vegetation, and we derived the median and the intra-annual standard deviation to include information on vegetation productivity and its variability. Covering an observation period from 2000 to 2018, information on the fire regime was included, such as fire frequency and intensity. These products are based on the MODIS Active Fire Product MOD14A1 collection 6 (Giglio & Justice, 2015) and the Burned Area Product MCD64A1 collection 6 (Giglio et al., 2015), the former with a spatial resolution of 1 km by 1 km and the latter with that of 500 m by 500 m. A detailed description of the methodology used to derive the fire parameters can be found in Stellmes et al. (2013).

We selected climatic parameters known to influence the vegetation in the study area (i.e. precipitation, temperature and seasonality). Data were acquired from WorldClim 2 (Fick & Hijmans, 2017) and have a spatial resolution of 1 km by 1 km. For frost occurrence, we used the CRU TS 4.04 data set with a 0.5° resolution (Harris et al., 2020).

To cover the edaphic influence on vegetation, parameters of soil texture were chosen from the SoilGrids250m data provider (Hengl, Mendes de Jesus, et al., 2017), reflecting resistance to roots, water retention, aeration and nutrient content. Moreover, we selected information on the soil nutrients phosphorus and nitrogen, made available by Soil Nutrient Grids (Hengl, Leenaars, et al., 2017). Edaphic data sets were acquired in 250-m spatial resolution.

Initially, we chose more than 20 potentially relevant environmental parameters and tested for linear correlation. Many parameters were highly correlated, so we retained only eight variables with correlation below Pearson  $r^2 = 0.65$ , calculated with package

'corrplot' (Wei et al., 2017) in R 4.0.3 (R Core Team, 2020) (Table 2, Table S2).

Using QGIS 2.18.18 and R package 'raster' (Hijmans et al., 2015), we aligned and resampled all environmental rasters to the same resolution (1 km) by averaging the pixels of finer-resolved rasters. Finally, all rasters were trimmed to the same extent (1°N to 35°S and 7°E to 45°E).

For each geoxyle data point, we extracted the values from these environmental rasters. The resulting data set was checked for duplicates and freed of incomplete observations, yielding environmental characteristics of 6599 unique data points of fully identified geoxyle species. All following data analyses were conducted in R 4.0.3 (R Core Team, 2020) with necessary packages named, if not stated otherwise. To minimize potential biases caused by spatial autocorrelations and uneven species sample sizes, we thinned this data set using package 'spThin' (Aiello-Lammens et al., 2015) so that selected data points of the same BBB type were spaced at least 1-km apart. Thinning yielded 5169 data points: 615 for lignotubers, 1880 for root crowns, 2355 for woody rhizomes, 143 for bud-bearing roots and 176 for xylopodia.

## 2.2 | Data analysis

### 2.2.1 | Species and functional diversity measures

Using the compiled list of geoxyle species from Bicular, Cusseque and Tundavala, we calculated the overall species richness and turnover among sites with Whittaker's  $\beta$ -diversity index ( $\beta_{WV}$ ) (Whittaker, 1960). The frequencies per BBB type per site were tested with  $\chi^2$  and post hoc Fisher tests (package 'fifer' [Fife & Fife, 2017]) to check for differences in functional composition among sites.

### 2.2.2 | Ancestral background of geoxyles

Analogously, BBB-type composition and site preferences were compared per plant family using the same tests to illustrate the taxonomic

TABLE 2 List of selected environmental factors used in this study. The code for each bioclimatic variable is provided in parentheses

Type	Variable	Code	Source
Climatic	Precipitation seasonality (%) (coefficient of variation) (BIO 15)	PS	Fick and Hijmans (2017)
	Annual mean temperature (°C) (BIO 1)	MAT	
	Mean annual precipitation (mm) (BIO 12)	MAP	
	Isothermality (%) (diurnal:annual temperature range) (BIO 3)	ISOT	
Edaphic	Clay content 5–15 cm (%)	CLAY	Hengl, de Jesus, et al. (2017)
Disturbance	Mean annual frost days 1990–2019	FROST	Harris et al. (2020)
	Fire frequency 2000–2018	F.freq	Updated after Stellmes et al. (2013)
Productivity	Median NDVI 1999–2017	NDVI <sub>med</sub>	Derived from PROBA-V data from <a href="http://www.vito-eodata.be">http://www.vito-eodata.be</a>

range. To assess biogeographic origin, we based our analysis on the chorological classification of White (1993), who defined phytochoria (sing., phytochorion) in Africa as biogeographic regions of high floristic diversity and endemism. For all geoxyle genera, we identified in which phytochoria south of the Sahara they show the highest species diversity and occurrence. Genera can belong to more than one phytochorion, and all geoxyle species from a given genus got the same phytochorial affiliations. Details about the genera's biogeographic origin and distribution were retrieved from sources listed in Table S3. For large pantropical genera, we narrowed the focus to African diversity patterns only. We merged White's phytochoria to larger classes (as shown in Table S6) and use the term *biome* for these subsumed classes in this sense throughout our manuscript.

Subsequently, we summarized the geoxyles' biogeographic affiliations at species level per BBB type, site and plant family. We did this with absolute numbers and tested with  $\chi^2$  and post hoc Fisher tests, whether or not different patterns emerged. Patterns and interlinks were visualized with packages 'ggplot2' (Wickham, 2016) and 'networkD3' (Allaire et al., 2017), with subsequent editing in GIMP 2.10.22 (The GIMP Development Team, 2020).

### 2.2.3 | Environmental analysis

We used subcontinental distribution data to infer environmental associations of geoxyles that occur at our Angolan study sites. This approach draws on ecological niche modelling (Araújo & Peterson, 2012; Hampe, 2004) and aims to recognize environmental patterns of geoxyle grasslands. To test whether environmental associations of geoxyles show functional (differences between BBB types) or biogeographic patterns (differences between biomes of origin), we used the following approach.

First, we assessed the specific contribution to species' ordination (and, therefore, environmental separation of species pools) of each variable in a covariance-based principal component analysis (PCA). The basis for calculation was a species-by-variable matrix with the thinned data points ( $n = 5169$ ). Beforehand, the data were standardized to a mean of 0, with a standard deviation of 1, to meet the requirements of this analysis. The resulting variable contributions were screened for significant impact on the ordination of the data. This analysis was done using packages 'FactoMineR' (Lê et al., 2008) and 'corrplot' (Wei et al., 2017). Subsequently, we visualized whether species' ordination is influenced by BBB type or biogeographic origin. We plotted the PCA once for each functional and biogeographic grouping, adding the 95% confidence ellipses for each group, respectively, and checked for the overlap of confidence intervals.

Finally, we visualized the probability of species occurrence along each of the eight parameter gradients, using violin plots. The violins are based on Gaussian kernel density estimations (implemented in the `geom_violin` of 'ggplot2') and allow to visualize and compare the amount and distribution of data per parameter. In this way, we defined the *environmental envelopes* available for the Angolan geoxyle species pool and obtained the position of each site, plus the

average position of each BBB type, within this environmental space. We tested for differences among BBB types, using Welch's ANOVA, to account for the heteroscedastic data. Since our data are partly skewed and non-normally distributed, we applied appropriate transformations to each parameter and checked whether the outcomes differ from the untransformed parameters. Most parameters did not need to be transformed; only one parameter, annual frost days, was too skewed to keep it untransformed. We, therefore, analysed the inverse of (annual frost days + 0.1).

## 3 | RESULTS

### 3.1 | Species and functional diversity

In total, we observed 118 geoxyle taxa with woody BBB types from 33 plant families at the three sites, Bicular, Cusseque and Tundavala (Table S1). The size of the geoxyle species pool differed greatly between sites; Cusseque had more than twice the number of taxa found in Tundavala. Table 3 illustrates the small overlap between the species pools. Only five geoxyle species (i.e. 4.2%) were found at all sites. Geoxyles make out about one-fifth to one-third of the overall eudicot species pool. Cusseque had the highest geoxyle (and overall) species richness and most species that were not found at the other sites (42.7%).

The species turnover among the three sites is high. Cusseque and Tundavala shared a similar number of species ( $\beta_{W\text{ Cus-Tun}} = 0.714$ ) as Cusseque and Bicular ( $\beta_{W\text{ Cus-Bic}} = 0.729$ ), whereas the species pools of Bicular and Tundavala differed more strongly ( $\beta_{W\text{ Bic-Tun}} = 0.811$ ). At all three sites, woody rhizomes are the dominant BBB type, followed by lignotubers and root crowns, whereas xylopodia and bud-bearing roots are present in only a few species. Although the intersection of the species pools is small, the proportion of BBB types does not differ between sites ( $\chi^2 = 5.949$ ; d.f. = 8;  $p = 0.653$ ) (Table 3).

### 3.2 | Ancestral background of geoxyles

Less than half of the geoxyles had congeneric tree relatives (49 taxa, 41.5%), and the BBB type proportions among geoxyles with tree relatives differed from those without (Table 3). Tree-related geoxyles almost exclusively possess lignotubers or woody rhizomes. The latter is present in 67.3% of tree-related geoxyle taxa, compared to a share of 50.8% overall, and 39.1% in the tree-unrelated geoxyle pool. Twenty-three families contribute tree-related geoxyle taxa, but some families which contribute many geoxyle taxa to the grassland flora are missing, e.g. Asteraceae or Santalaceae.

Overall, some families, such as Ochnaceae, Proteaceae and Rubiaceae, show a strong tendency towards specific BBB types (Figure 1). In many cases, however, we observed mixed spectra. Most geoxyle species belong to the Fabaceae family (25.2% of all species), particularly to the subfamily Papilionoideae (21.7%). Fabaceae is the



only family that includes all BBB types, even the less frequent bud-bearing roots and xylopodia.

Testing for differences in the BBB-type composition of major families (with at least four species) yielded an overall unequal composition ( $\chi^2 = 48.780$ ; d.f. = 28;  $p = 0.009$ ). In pairwise comparisons, the strongest differences were measured between lignotubers and woody rhizomes and between lignotubers and root crowns and

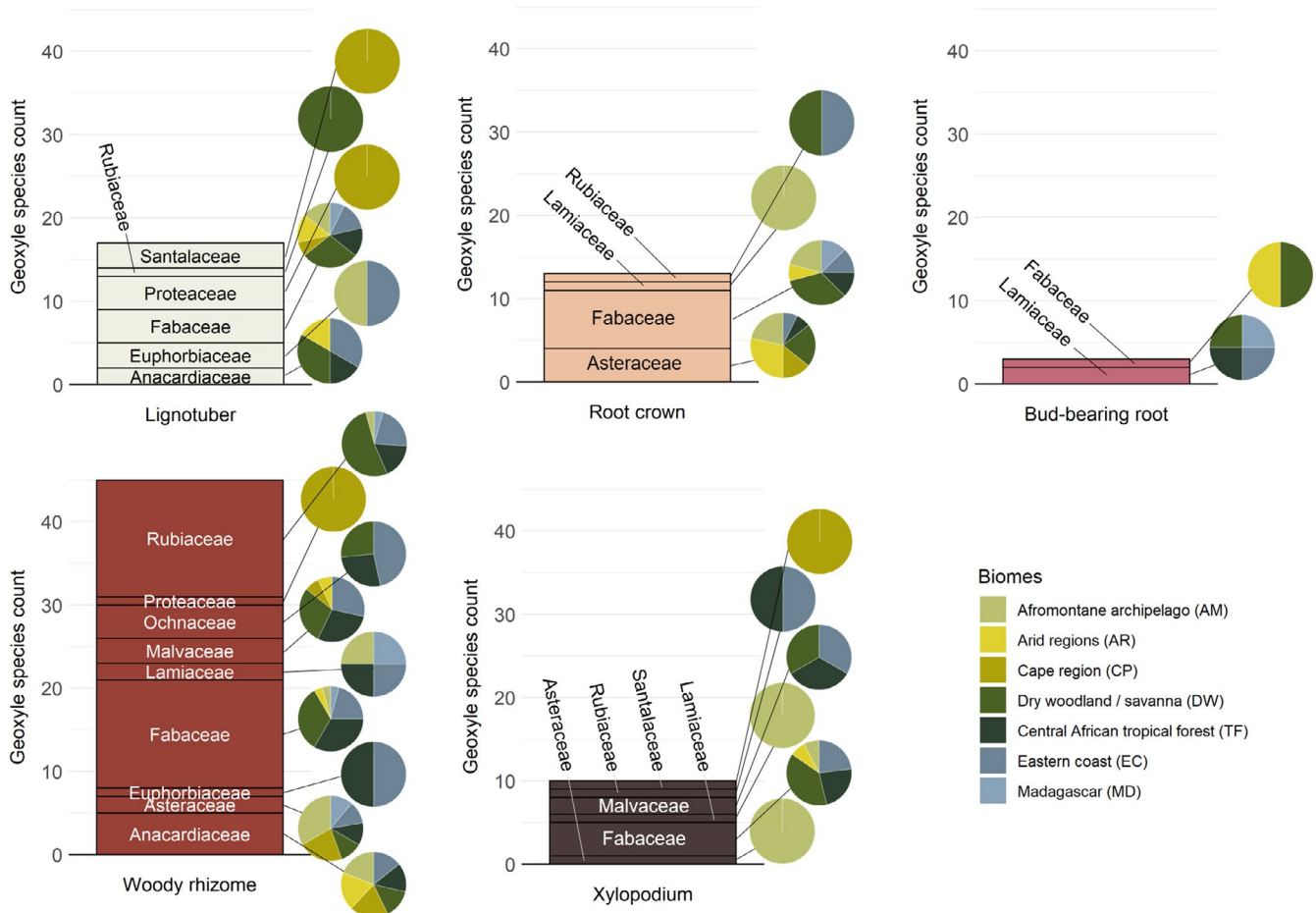
occurred particularly in Rubiaceae versus Proteaceae, Asteraceae and Euphorbiaceae, as well as Proteaceae versus Lamiaceae and Ochnaceae (Figure 1; Table S4). However, these differences were significant only with unadjusted  $p$ -values.

Regarding their biogeographic origin, it stands out that most geoxyle genera have a strong link to forest and woodland biomes, with 25.8% linked to Dry woodlands (DW), followed by 21.4% each with

**TABLE 3** Overview of geoxyle species and BBB types among sites, and overall. The first three columns show the share of geoxyle species among sites, with the number of species unique to each site on the diagonal. The following columns indicate the total number of geoxyle species and to which BBB types they belong. For comparison, the total species richness of eudicot species per site is also given

	Bic	Cus	Tun	At all sites	Geoxyle spp. per site	Li	RC	Ro	WR	Xy	Eudicot spp. per site
Bicuar	22	16	7	5	40	7	8	2	21	2	~180
Cusseque		51	16		78	17	8	1	44	8	~237
Tundavala			18		34	7	7	1	15	4	~102
Share of taxa per BBB type (total: 118)						24	19	4	60	11	
Share of taxa with tree relatives per BBB type (total: 49)						12	2	1	33	1	
Share of taxa without tree relatives per BBB type (total: 69)						12	17	3	27	10	

Abbreviations: Bic, Bicuar; Cus, Cusseque; Li, lignotuber; RC, root crown; Ro, bud-bearing root; Tun, Tundavala; WR, woody rhizome; Xy, xylopodium.



**FIGURE 1** Number of geoxyle taxa per BBB type and plant family, and the proportional biogeographic origin of each family per BBB type. Only plant families with at least four geoxyle taxa are shown, the remaining families are summarized in Figure S1, and a general summary is provided in Table S4

links to the Eastern coast (EC) and Central African tropical forest (TF) biomes. In comparison, Arid regions (AR), Cape (CP), Afromontane belt (AM) (together with 26.2%) and Madagascar (MD) (with 5.2%) contributed much less (Figure 2).

A weak biogeographic pattern is discernible among BBB types. Particularly the minor biomes of origin contributed increased proportions of lignotubers (CP) and root crowns (AR, AM, MD), compared to the main biomes (DW, EC and TF), which contributed over 50% of species with woody rhizomes. No exclusive relationships between BBB types and biogeographic origin were discernible. However, within most biomes we observed BBB occurrences that deviated from an expected even probability (asterisks in Figure 2 insert).

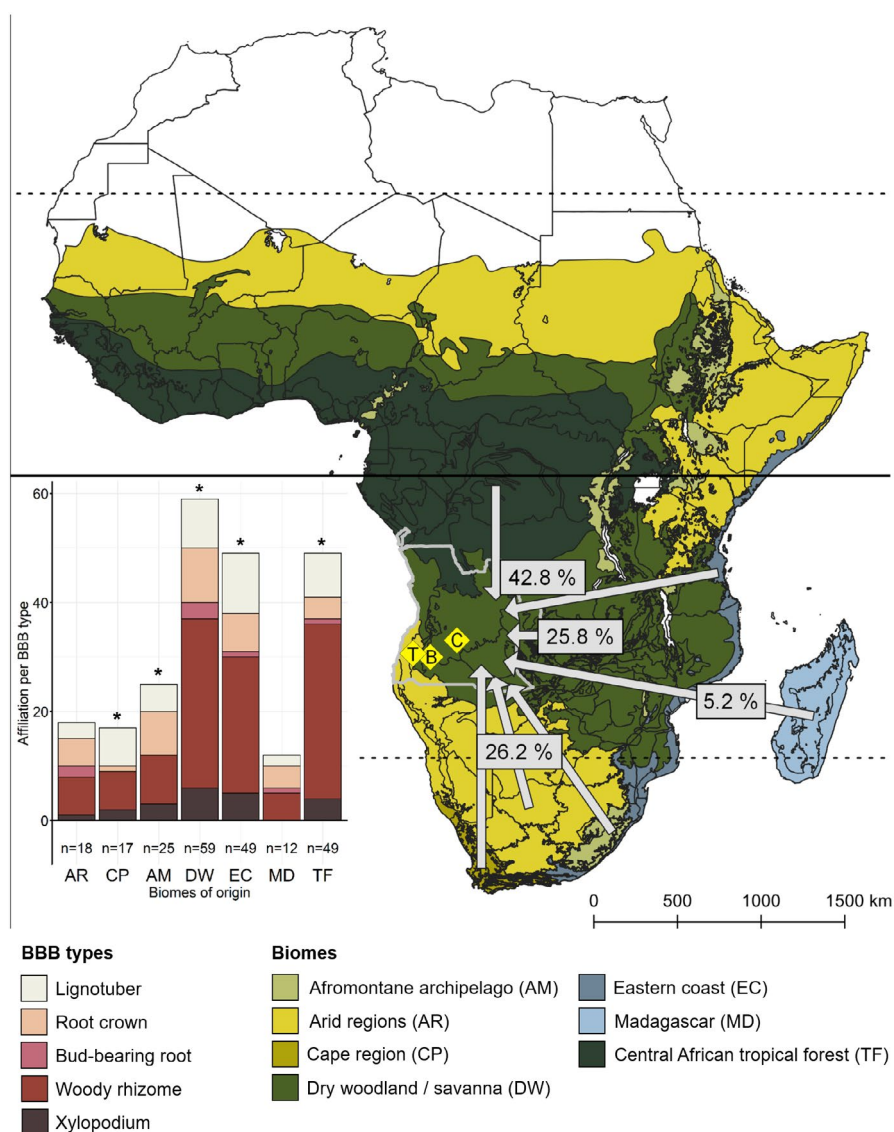
### 3.3 | Effect of environmental conditions and disturbances

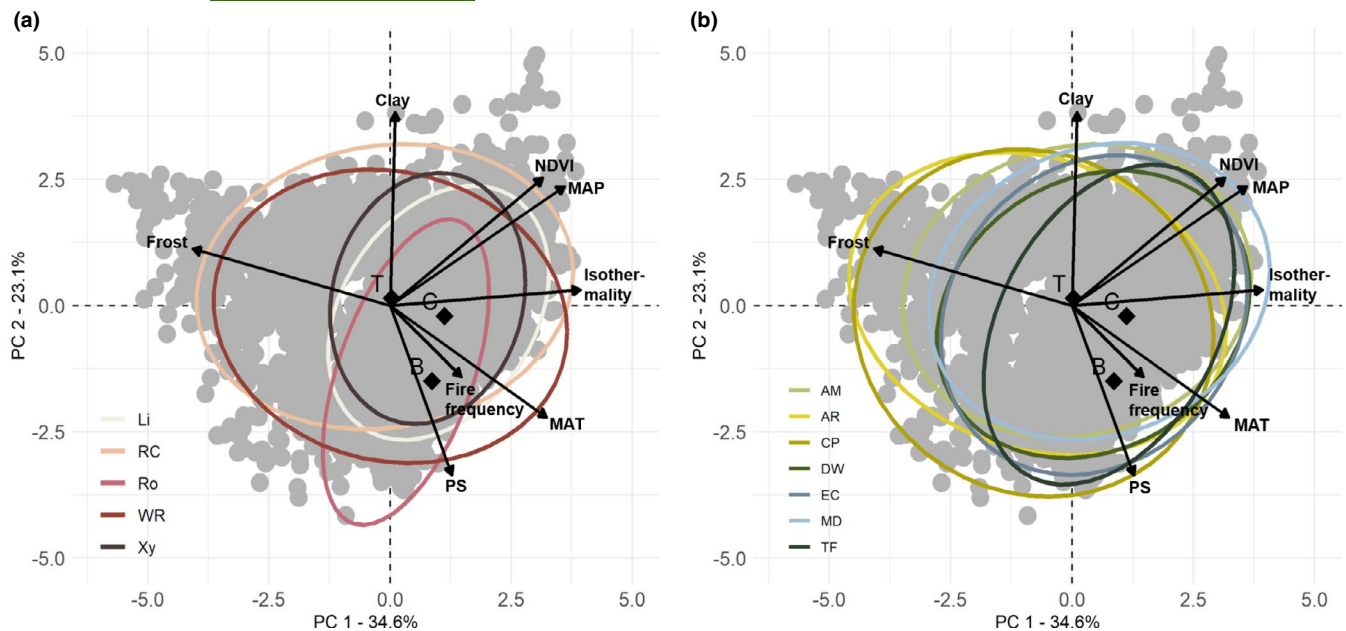
Environmental preferences of geoxyles were illustrated by a PCA, which explained 34.6% of the variance by the first and 23.1% by the

second component (Figure 3). Together with the third component, (13.0%), more than 70% of the variance in the data set was described, thereby sufficiently capturing the environmental pattern. The strongest contributing factors for the first component were annual number of frost days, isothermality and mean annual precipitation. Clay content, precipitation seasonality and NDVI contributed to the second component, whereas only fire frequency comprised the third component.

The contribution of frost to the variance in the data stands out (Figure 3). Over half (53.5%) of the 0.5° geospatial cells of Africa in our analysis indicated single frost events every 10th year or less ('frost free'), and the remaining cells range from 0.1 to over 100 annual frost events. A random spatial distribution of geoxyles would yield a similar pattern, but we did not observe this for some functional types. Whilst only 41% of lignotuber occurrences were at frost-affected sites ( $> 0.1 \text{ year}^{-1}$ ), 52% of root crown, 65% of xylopodium and 76% of woody rhizome and bud-bearing root occurrences were at frost-affected sites (Figure 4). In contrast, 30% of woody rhizome and 42% of root crown occurrences were observed at heavily frost-affected sites ( $> 20 \text{ year}^{-1}$ ), whereas all

**FIGURE 2** Sub-Saharan biogeographic origin of Angolan geoxyle species (map) and their BBB-type proportions (insert). The contributions to the Angolan species pool from surrounding biomes are shown with grey arrows and boxes. The Angolan study sites are marked in yellow (T: Tundavala; B: Bicular; C: Cusseque), and they all belong to DW. The asterisks in the insert denote biomes in which BBB type contributions are significantly uneven (Kruskal-Wallis test)





**FIGURE 3** PCA showing the environmental preferences of geoxyle species to selected parameters in the first two dimensions. In (a), points (=geoxyle observations) are grouped according to BBB type, and ellipses define 95% confidence intervals of observations for each group. In (b), points are grouped according to biomes (i.e. biogeographic origin) (see Table S6), and ellipses again define 95% confidence intervals. The diamond shapes represent the ordination of the three study sites, Bicuar (B), Cussequa (C) and Tundavala (T), in this environmental space. The selected environmental parameters are number of annual frost days (Frost), clay content in 5- to 15-cm depth (Clay), annual median NDVI (NDVI), mean annual precipitation (MAP), isothermality (diurnal:annual temperature range), annual mean temperature (MAT), fire frequency 2000–2018 and precipitation seasonality (PS). The arrows are scaled up five times to improve visibility. BBB types are lignotubers (Li), root crowns (RC), bud-bearing roots (Ro), woody rhizomes (WR) and xylopodia (Xy). The biomes are the Afromontane archipelago (AM), Arid regions (AR), Cape region (CP), Dry woodlands (DW), Eastern coast (EC) Madagascar (MD) and Tropical forests (TF)

other BBB types were not or only rarely present in such places (< 10% of occurrences).

Overall, geoxyle species overlapped in their environmental preferences but with some differentiation along the selected parameters when grouping them by their BBB type (Figure 3a, Figures S2 and S3) or by their biogeographic origin (Figure 3b, Figures S4 and S5). Whilst the two most common types, root crowns and woody rhizomes, are widely distributed in environmental space the three other types showed environmental limitation. Lignotubers, bud-bearing roots and xylopodia clearly correlated to fewer frost days than the other types, and they were associated with fire frequency along the third component. As far as the limited number of observations allow, we observed that lignotubers and xylopodia were positively associated and bud-bearing roots were rather negatively associated with fire frequency (Figure S3).

By contrast, geoxyles with an Arid (AR) or Cape region (CP) background correlated markedly with increased frost days (Figure 3b and Figures S4 and S5). Those with an Afromontane (AM), Madagascar (MD), Eastern coast (EC) or Dry woodland (DW) background correlated with higher NDVI, MAP and isothermality. Geoxyles with wet-tropical forest background spread least and were defined by increased levels of MAT, isothermality, MAP and NDVI.

To further investigate the differentiation along environmental gradients, we took a detailed look at specific preferences regarding functional types (Figure 4). Each parameter significantly differentiated

functional or biogeographic types, though to varying degrees. Precipitation seasonality, followed by clay content, mean annual precipitation and annual mean temperature, had the highest impact on BBB-type differentiation (Figure 4; Table S5). Edaphic and climatic factors, particularly those that are precipitation related, dominated functional patterns, whereas disturbances by frost and fire had less effect.

Another pattern emerged for environmental preferences regarding the biogeographic background of the geoxyles (Figure 3b, Figures S4–S6). For most of the parameters, the tropical groups, DW, TF and EC, clustered together and were segregated from the subtropical groups, AR and CP. The most influential parameters were annual mean temperature, isothermality, mean annual precipitation and annual frost occurrences. These parameters make temperature-related factors dominant for biogeographic origins, whereas, again, fire frequency played a lesser role.

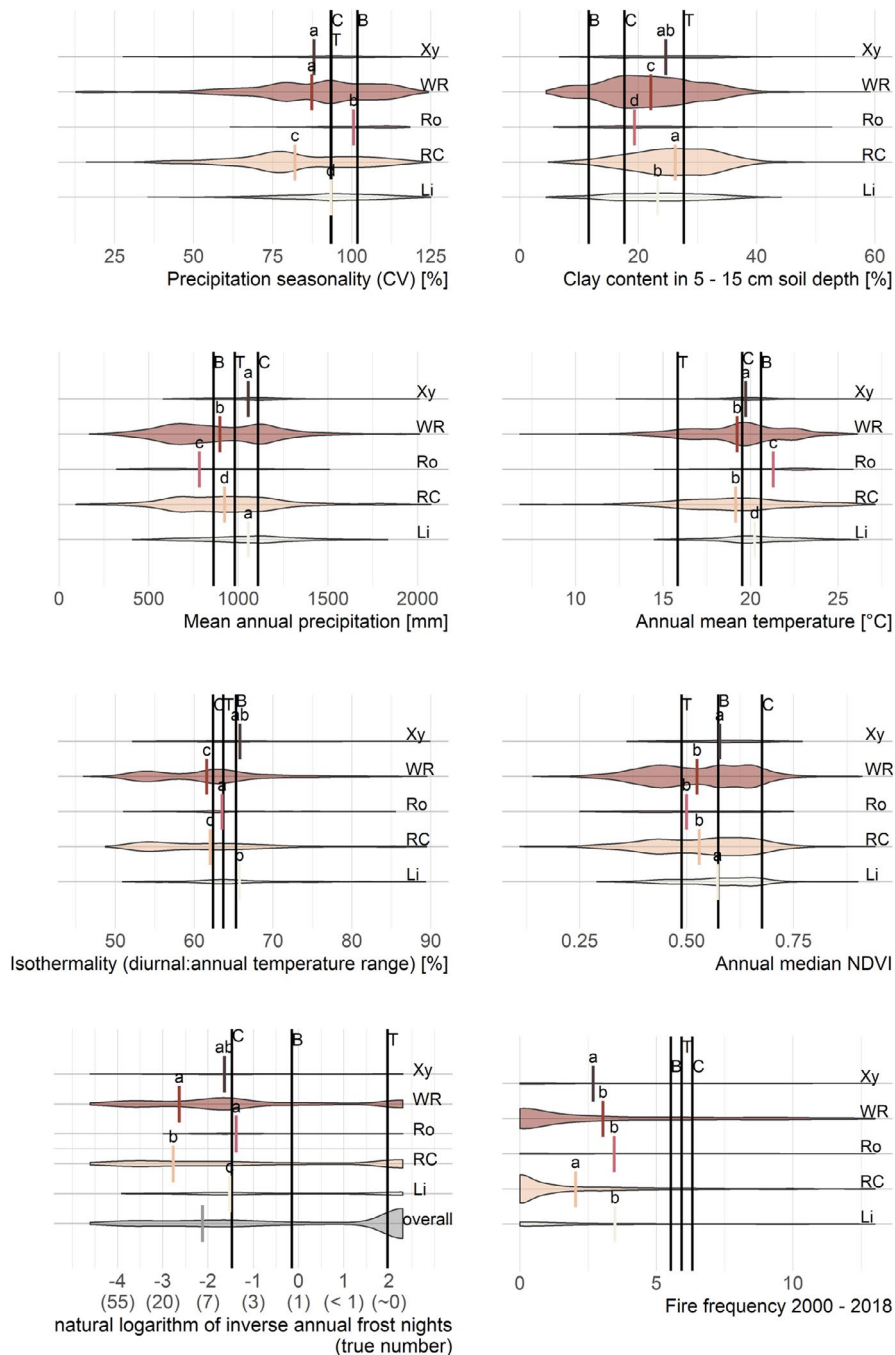
## 4 | DISCUSSION

### 4.1 | Does geoxyle species diversity enhance functional diversity?

Geoxyles contribute strongly to the resilience against disturbances like frost and fire, to biodiversity, and to the distinctiveness of tropical old-growth grasslands (Buisson et al., 2019; Veldman, Buisson,



**FIGURE 4** Selected environmental spaces occupied by geoxyles, grouped by BBB types. The violin plot represents the probability of encountering geoxyle species along a given environmental gradient: the wider the violin, the higher the number of species occurring at that level. Violin areas correspond to the respective number of data points. The coloured ticks represent the means of geoxyle species averaged for each BBB type for that environmental parameter. The order in which environmental parameters are shown reflects the strength of this parameter to separate the groups. The superscripted letters indicate the significance of differences for each parameter, tested with Welch's ANOVA and post hoc Games-Howell tests. The parameter 'frost' was strongly skewed and had to be transformed to meet the requirements of the tests. We, therefore, calculated and used the inverse frost, which means that smaller values represent higher frost frequency. To improve visibility, the axis here has a logarithmic scale, and the corresponding numbers of actual frost events are given below. The overall distribution of frost events across the studied area in Africa is given as an additional violin for comparison. The environmental conditions at our study sites (T: Tundavala; B: Bicular; C: Cusseque) have been added to visualize whether preferences and prevalent conditions at the study sites coincide. BBB types: lignotubers (Li), root crowns (RC), bud-bearing roots (Ro), woody rhizomes (WR) and xylopodia (Xy)



et al., 2015; Zaloumis & Bond, 2016). Maurin et al. (2014), e.g. listed 266 geoxyle species for southern Africa, whereas Zigelski et al. (2019) compiled 198 geoxyles for the western Zambebian phytochorion alone. We list 118 taxa with woody BBB types from just three localities across central Angola. The high species turnover rates among the localities are in a similar range to those of the Fynbos biodiversity hot spot (Kruger & Taylor, 1980) and confirm Angola as a centre of diversity for geoxyles (White, 1983).

According to Questad and Foster (2008), who studied North American fire-affected pine savannas, spatiotemporal environmental heterogeneity (e.g. caused by disturbances) combined with high functional diversity of the biota increases the number of niches

in a given ecosystem, thereby promoting species coexistence and diversity. Geoxyles are by definition species resprouting from protected BBBs (Pausas et al., 2018; White, 1976) and occupy a persistence niche in disturbance-prone ecosystems (Bond & Midgley, 2001; Clarke et al., 2013). Multiple belowground functional types indicate that different persistence strategies co-occur (e.g. rhizomes for clonal propagation and tubers for high-capacity resprouting after disturbance), which is similar to findings from the Cerrado (Pilon et al., 2021).

We observed strikingly similar spectra of BBB types between sites, despite different numbers of geoxyle species and a strong species turnover. The species pools of our sites had little overlap;

43%–65% of species were unique to any site (Table 3), which means that functional types are represented by different species at each site. In particular, our results do not support any direct effect of species diversity on functional diversity, but rather show functional redundancy of BBB types and USOs; species are to a certain degree exchangeable within their functional group (Loreau, 2000, 2004; Tilman et al., 1997).

## 4.2 | Do multiple origins promote functional and species diversity?

Species diversity follows taxonomic diversity (Enquist et al., 2002). In our study, 33 plant families contributed geoxyle taxa, whereby most genera have only one or a few geoxyle species, with only a few exceptions (e.g. *Fadogia*, nine taxa). Thus, geoxyle diversity on the Angolan Plateau is less likely to be driven by recent radiation of a few clades than by convergent evolution within many different lineages.

Conversely, several families, particularly those with a distinct biogeographic background, are dominated by a single BBB type (e.g. the wet-tropical Ochnaceae and Rubiaceae have mostly woody rhizomes, and the Cape elements Proteaceae and Santalaceae have predominantly lignotubers) (Figure 1, Figure S1). This finding implies that, despite convergent evolution, BBB types are in many cases conserved in certain biogeographic lineages. Contrastingly, globally widespread families, such as Asteraceae, Lamiaceae and Fabaceae, are environmentally less restricted (Barreda et al., 2015; Schrire et al., 2005) and exhibit broader functionality.

The diversity of BBB types in our study is linked to geoxyle taxa that did not evolve from tree species. Tree-unrelated taxa almost exclusively contributed xylopodia, root crowns and bud-bearing roots, predominant in lignifying perennial herbs (Pausas et al., 2018), to the geoxyle pool. Strikingly, two-thirds of tree-related geoxyle taxa form woody rhizomes and thus spread laterally in the grasslands, often intertwining belowground (personal observation). This belowground canopy thus mimics the canopy of woodlands and forests, from where the geoxyle species originated.

About two-thirds of geoxyles originated from Afrotropical forest and dry woodland ecosystems (Figure 2), which is consistent with previous findings (Maurin et al., 2014; Simon et al., 2009; Ziegelski et al., 2019). To a lesser degree, we also show origins from other biomes, e.g. the Cape region (Lamont et al., 2017) or the Afromontane belt (Meadows & Linder, 1993). Thus, the diverse Zambezi geoxyle flora is composed of distinct contributions from several of the surrounding biomes; only about a quarter of the species stem from this biome itself. In conclusion, our study indicates that BBB types of geoxyles did not evolve freely in situ in the Zambezi area; geoxyle lineages rather brought a predisposition towards certain BBB types based on their family and biome of origin. Environmental filters then shaped the functional groups.

## 4.3 | Do environmental factors (disturbances) determine functional types and their distribution?

Against the paleoclimatic background described in the introduction, it becomes clear that geoxyles' environmental preferences clearly reflect their biogeographic origin (Figure 3b, Figures S2 and S3). Geoxyles with an origin from wet-tropical biomes, for instance, occur at more humid, less seasonal and less frost-prone sites than geoxyles from subtropical biomes. Besides the biogeographic differentiation, we also observed a functional differentiation along climatic gradients. Frost occurrence correlates negatively with temperature and isothermality, thus reflecting a combined effect of altitude and (lower) latitude. Geoxyles with woody rhizomes and root crowns extend to higher, dryer and more subtropical regions, where they experience more frost than the fire-associated lignotubers and xylopodia. Accordingly, lignotubers in our study area are associated with more humid and productive (high NDVI) conditions, which are a proxy for proneness to fire under current fire regimes (Hoyos et al., 2017; Pettorelli et al., 2005).

Root crowns and woody rhizomes occupy a similar climatic space in the PCA, but topsoil texture, expressed by clay content (Dixon, 1991), differentiates them. Root crowns seem to prefer topsoil with higher nutrient concentrations (Wigley et al., 2019) because they are not able to spread laterally. In contrast, rhizomes propagate widely (Herben & Klimešová, 2020), compensating for lower nutrient availability at their sites with an increased spatial coverage (February et al., 2019). Less clayey and, therefore, looser soils should furthermore facilitate the advancement of rhizomes, allowing them to colonize sites that are too resource-poor for other BBB types (Herben & Klimešová, 2020; references therein).

Different functional types reflect environmental (and particularly disturbance-controlled) niche diversity. Fidelis et al. (2014) showed that for the Brazilian subtropical Campos, size and diversity of BBBs depend on the frequency of disturbances. Simultaneously, species richness decreased with declining disturbances, which is consistent with observations in grassland ecosystems globally (Fidelis et al., 2014; Peterson & Reich, 2008; Simon et al., 2009; Walker & Peet, 1984). This correlation implies that the costly formation of BBBs is beneficial only under high-disturbance regimes (Vesk & Westoby, 2004).

Since rhizomatous species are more tolerant to herbivory than non-rhizomatous species (Briske, 1996; Mack & Thompson, 1982), herbivory might have promoted the conspicuous dominance of woody rhizomes in our study area, assuming that woody rhizomes are, like fleshy rhizomes, a response to herbivory. Furthermore, rhizomes have a strong propagation advantage through clonal expansion (Herben & Klimešová, 2020; Ott et al., 2019; Pausas et al., 2018). Often in conjunction with fire, herbivory is a main driver of vegetation structure (Asner et al., 2009; Midgley et al., 2010; Staver et al., 2011; Staver & Bond, 2014), particularly in drier savanna ecosystems. We were not able to include geospatial information on herbivory in our analysis because available data sets did not meet our requirements. Regarding our study sites, the similar proportions of woody rhizomes in all sites seem to imply that decades-long absence of larger herbivores (Cusseque), the continuous presence of natural

herbivore guilds (Bicuar) and decades of cattle grazing (Tundavala) do not affect the functional spectra of geoxyles in the short term, as long as the ecosystems are kept open by other processes. However, more research in this direction is needed.

Fire frequency had the lowest effect on functional and biogeographic differentiation from all tested parameters, with a slightly higher fire frequency associated with geoxyles from tropical forests, with lignotubers and weakly with xylopodia. The latter two have evolved in fire-prone ecoregions and are pre-adapted to fire regimes (Lamont et al., 2017; Pausas et al., 2018). Geoxyles in general evolved in pre-human times and are frequently considered to be a response to fire (Lamont et al., 2017; Maurin et al., 2014). Furthermore, long-term fire experiments in Southern Africa have shown that exclusion of fire had a far greater (negative) effect on the richness of forbs (= perennial, resprouting herbs, encompassing some geoxyles) than the frequency of fire (Uys et al., 2004). However, the altogether weak and strongly varying association of geoxyles to fire frequency, suggests that as long as fire is sufficiently present, or biomass is removed otherwise (herbivores), other correlates are more important.

Undoubtedly, geoxyles depend on open habitats because they are shade-intolerant (Falster & Westoby, 2005; references therein). Even with frequent enough fires, they depend on phenologies that are asynchronous to tussock forming C4 grasses in order to not be outcompeted (Zigelski et al., 2019). In areas with low fire frequencies alternative interactions of topkill and consuming factors (i.e. frost and herbivory) appear to be plausible co-drivers of geoxyle evolution or at least community assembly, especially regarding a long evolutionary history with potentially rarer fires and stronger herbivory regimes (Hempson et al., 2017).

Having been overshadowed by fire, frost was seldom considered a serious driver of tropical grasslands. Only recently (Finckh et al., 2021) has frost been recognized as playing an important role in the emergence and/or maintenance of tropical grasslands in Africa (Botha et al., 2020; Finckh et al., 2016), India (Joshi et al., 2020) and Brazil (Brando & Durigan, 2005; Hoffmann et al., 2019), mainly by the topkill of tree saplings. Tropical frost is hard to detect because it is strongly driven by (micro)topography (Bojórquez et al., 2019); therefore, global data sets underestimate frost occurrence in tropical highlands. Even the best, but still coarse, data sets from Harris et al. (2020), with 0.5° resolution, underestimate frost occurrence 10-fold in Cusque and 40-fold in Bicuar (Table 1; Figure 4). Therefore, given the reliable occurrence of frost in the dry season, which emerged with increasing seasonality in the Pliocene (Trauth et al., 2009), we suggest that frost contributed considerably to geoxyle evolution in Afrotropical old-growth grasslands. In summary, our results indicate that environmental factors, and particularly those related to seasonality and disturbance, determine today's distribution of geoxyles with different functional types.

## 5 | CONCLUSION

Multiple biogeographic origins, which are still reflected in their current functional traits and ecological preferences, enabled

geoxyles to spread widely and become abundant in suitable habitats. Disturbances and climate seasonality are key requirements for geoxyle occurrence, whereby multiple disturbance types likely pruned out different functional responses. A long history of seasonality and disturbances drove the convergent evolution in many lineages, leading to the high geoxyle diversity in Angola and beyond. We particularly highlight the importance of frost as well as the better-studied disturbances of fire and herbivory. However, the interplay between topkill and consumption by frost, fire and herbivory is still not fully understood, especially at the evolutionary time scale that predates human presence and includes strong climatic fluctuations and considerable megafauna decline.

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## CONFLICT OF INTEREST

We do not have a conflict of interest.

## DATA AVAILABILITY STATEMENT

The data sets and R scripts used in this study are available at the Zenodo repository (<https://zenodo.org/>). You can find them here directly: <https://zenodo.org/record/5521402>, and the DOI is <https://doi.org/10.5281/zenodo.5521402>.

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#### BIOSKETCHES

**Paulina Meller** (also known as **P. Zigelski**) is working on the vegetation ecology of tropical ecosystems, particularly in Angola. Geoxyle grasslands, and a holistic understanding thereof, are her focus doctoral research. **Manfred Finckh** is interested in vegetation ecology and diversity in Angola and Morocco. **Marion Stellmes** is an expert on remote sensing imagery and analyses. **Alessandra Fidelis** is interested in (belowground) vegetation ecology in Cerrado, Brazil.

Author contributions: P.M. and M.F. designed the research and conducted fieldwork. M.S. contributed and processed environmental data and helped to deal with it in this study. A.F. contributed a holistic understanding of tropical grasslands globally and enriched the discussion. P.M. analysed the data and led the writing of the manuscript, to which all authors contributed and commented.

#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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