

Chapter 7

Suffrutex Dominated Ecosystems in Angola



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Abstract A small-scale mosaic of miombo woodlands and open, seasonally inundated grasslands is a typical aspect of the Zambebian phytochorion that extends into the eastern and central parts of Angola. The grasslands are home to so-called ‘underground trees’ or *geoxylic suffrutices*, a life form with massive underground wooden structures. Some (but not all) of the *geoxylic suffrutices* occur also in open woodland types. These iconic dwarf shrubs evolved in many plant families under similar environmental pressures, converting the Zambebian phytochorion into a unique evolutionary laboratory. In this chapter we assemble the current knowledge on distribution, diversity, ecology and evolutionary history of *geoxylic suffrutices* and suffrutex-grasslands in Angola and highlight their conservation values and challenges.

Keywords Endemism · Geoxyles · Miombo · Phytochorion · Underground forests · Vegetation

Introduction

Open grassy vegetation is a common aspect of Angolan landscapes and is a characteristic part of the Zambebian phytochorion. Grasses are the most conspicuous element of these landscapes towards the end of the rainy season, whereas at the onset of the rainy season many woody species of so called *geoxylic suffrutices* or ‘underground trees’ (Davy 1922; White 1976) dominate the aspect of the vegetation. Thus, in vast areas of central and eastern Angola, the open ‘grasslands’ are de-facto co-dominated by grasses and *geoxylic suffrutices*. Closely intertwined with miombo

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woodlands and with wetlands, suffrutex-grasslands constitute one of the main and most particular ecosystem types of Angola. According to Mayaux et al. (2004), they cover at least 70,080 km² or 5.6% of the Angolan territory (not including the small scale woodland suffrutex-grassland mosaics of the central Angolan plateau).

The geoxylic suffrutex life form is marked by proportionally massive underground woody organs, in literature often termed as *lignotuber*, *xylopodia* or *woody rhizomes*. Annual shoots sprout readily from the buds on these perennial woody organs, bearing leaves, inflorescences and fruits before they die back after the end of the rainy season. Coexistence of grasses and suffrutices is made possible by occupation of different ecological niches together with phase-delayed activity periods (i.e. main assimilation/flowering/fruitletting time) that reduces competition.

Exploration of Geoxylic Grasslands

The first authors who indicated the distribution and ecological particularity of suffrutex-grasslands in Angola were Gossweiler and Mendonça (1939), who classified them as heathland-like woodlands ('Ericilignosa'). They already noted the main differentiation between the *Cryptosepalum* spp. dominated suffrutex communities ('Anharas de Ongote') on ferralitic and psammo-ferralitic soils and the vegetation types characterised by *Parinari capensis* and the Apocynaceae *Landolphia thollonii* and *L. camptoloba* on leached sandy soils ('Chanas da Borracha'). They had also already observed the strong thermic oscillations of which at least the 'Anharas de Ongote' are subject (see below) and commented on the generative cycle of *Cryptosepalum maraviense* from flowering to fruitletting in the dry season (and thus, being inverse to the generative cycle of the C4-grasses).

Using a different mapping and classification approach, typical suffrutex-grasslands mostly on sandy soils were again mapped and described by Barbosa (1970) as 'Chanas da Borracha' (alluding to the presences of species of the genus *Landolphia*), 'Chanas da Cameia', and 'Anharas do Alto'. The *Cryptosepalum* spp. dominated 'Anharas de Ongote' on ferralitic soils are described (but not depicted on the map) as being inserted in the main miombo types of the Angolan plateau. However, he describes the typical spatial pattern, i.e. how they appear close to the headwaters of the small tributaries and then follow the watercourses in narrow or broad fringes downstream. Gossweiler and Mendonça (1939) as well as Barbosa (1970), treated these ecosystems as particular site specific plant communities closely linked to woodland ecosystems, and not as grass-dominated savannas.

White (1983), however, mapped and described only the sandy 'Chanas' as 'Kalahari and dambo-edge suffrutex grassland' in the context of the 'Zambeian edaphic grassland', but did not refer to the 'Anharas de Ongote' which constitute a key (but small scale) element of the miombo ecosystems of the Angolan Plateau. Even in his prominent suffrutex review, White (1976) focuses solely on the 'Chanas' in the range of the Zambezi Graben and neither mentions (psammo-) ferralitic

'Anharas', nor lists their dominant key species *Cryptosepalum maraviense* and *C. exfoliatum* ssp. *suffruticans* in his suffrutex list. He certainly recognises a transition zone between Zambebian and Guineo-Congolian floras that spans over central and northern Angola (where the 'Anharas' are included) (White 1983). However, he did not recognise the importance and floristic singularity of the ferralitic suffrutex-grasslands dominated by *Cryptosepalum* spp.

Suffrutex Flora and Endemism

The suffrutex life form appears in many different floristic groups and obviously evolved convergently. A similar center of geoxyle diversity has been reported from the Brazilian Cerrado. Today, 198 species from 40 families are listed for the western Zambebian phytochorion (White 1976; Maurin et al. 2014, own data), but an even higher number is expected as floristic exploration of the region is still poor and new species might be found (see Goyder and Gonçalves 2019). In some cases suffrutices are considered a dwarf variety or subspecies of a closely related tree species (e.g. *Gymnosoria senegalensis* var. *stuhlmanniana*, *Syzygium guineense* ssp. *huillense*) and hence classified as such and not as one species, although the genetic relatedness between tree and dwarf form is rarely investigated. On the other hand, not all dwarf forms are obligate suffrutices; some can facultatively outgrow the dwarf state if protected from environmental stressors (White 1976), for instance *Oldfieldia dactylophylla* or *Syzygium guineense* ssp. *macrocarpum* (Zigelski et al. 2018).

Within the suffrutex communities of the Zambebian phytochorion, the Rubiaceae have the highest number of described taxa (46), followed by Anacardiaceae (22) and Lamiaceae (14). Table 7.1 lists all families with known geoxylic suffrutex taxa occurring in Angola and gives examples of common geoxyles for each family. Furthermore, Fig. 7.1 shows some examples and aspects of suffrutex species given in Table 7.1. The unique Zambebian geoxylic flora with a high number of endemic species (Brenan 1978; White 1983; Frost 1996) is a consequence of challenging environmental conditions, as illustrated further below. According to Figueiredo and Smith's catalogue of Angolan plants (2008) and our list of suffrutices (Table 7.1), 121 of the 198 suffrutex species occurring in the Zambebian phytochorion are known from Angola (61%). Of these 121 species 12 are endemic to Angola (10%).

Environmental Conditions of Suffrutex-Grasslands Through the Year

The substrate strongly influences the species composition of the suffrutex-grasslands. In Angola geoxylic suffrutices occur on (a) well-drained arenosols which are found as seasonally flooded savannas in the Zambezi Graben of the

Table 7.1 List of plant families with geoxylic suffrutices in the Zambezan phytochorion

Plant family	N°	Species common in Angola	Angolan endemics
Rubiaceae	46	<i>Pygmaeothamnus zeyheri</i> (Sond.) Robyns, <i>Pachystigma pygmaeum</i> (Schltr.) Robyns	2, e.g. <i>Leptactina prostrata</i>
Anacardiaceae	22	<i>Lannea edulis</i> (Sond.) Engl., <i>Rhus arenaria</i> Engl.	3, e.g. <i>Lannea gossweileri</i>
Lamiaceae	14	<i>Clerodendrum ternatum</i> Schinz, <i>Vitex madiensis</i> ssp. <i>milanjensis</i> (Britten) F.White	
Fabaceae-Papilionioideae	13	<i>Erythrina baumii</i> Harms, <i>Abrus melanospermum</i> ssp. <i>suffruticosus</i> Hassk.	3, e.g. <i>Adenodolichos mendesii</i>
Proteaceae	11	<i>Protea micans</i> ssp. <i>trichophylla</i> (Engl. & Gilg) Chisumpa & Brummitt	1, <i>Protea paludosa</i> (Hiern) Engl.
Ochnaceae	9	<i>Ochna arenaria</i> De Wild. & T. Durand, <i>Ochna manikensis</i> De Wild.	
Passifloraceae	7	<i>Paropsia brazzaeana</i> Baill.	
Fabaceae-Detarioideae	6	<i>Cryptosepalum maraviense</i> Oliv., <i>C. exfoliatum</i> ssp. <i>suffruticans</i> (P.A.Duvign.)	
Apocynaceae	5	<i>Chamaeclitandra henriquesiana</i> (Hallier f.) Pichon	1, <i>Landolphia gossweileri</i>
Ebenaceae	5	<i>Diospyros chamaethamnus</i> Mildbr, <i>Euclea crispa</i> (Thunb.) Gürke	
Celastraceae	4	<i>Gymnosporia senegalensis</i> var. <i>stuhlmanniana</i> Loes.	
Dichapetalaceae	4	<i>Dichapetalum cymosum</i> (Hook.) Engl.	
Fabaceae-Caesalpinioideae	4	<i>Entada arenaria</i> Schinz	
Myrtaceae	4	<i>Syzygium guineense</i> ssp. <i>huillense</i> , (Hiern) F. White <i>Eugenia malangensis</i> (O.Hoffm.) Nied.	
Tiliaceae	4	<i>Grewia herbaceae</i> Hiern	
Combretaceae	3	<i>Combretum platypetalum</i> Welw. ex M. A. Lawson	2, e.g. <i>Combretum argyrotrichum</i>
Euphorbiaceae	3	<i>Sclerocroton oblongifolius</i> (Müll.Arg.) Kruijt & Roebers	
Loganiaceae	3	<i>Strychnos gossweileri</i> Exell	
Annonaceae	2	<i>Annona stenophylla</i> ssp. <i>nana</i> (Exell) N. Robson	
Apiaceae	2	<i>Steganotaenia hockii</i> (C. Norman) C. Norman	
Chrysobalanaceae	2	<i>Parinari capensis</i> Harv., <i>Magnistipula sapinii</i> De Wild.	
Meliaceae	2	<i>Trichilia quadrivalvis</i> C.DC.	
Moraceae	2	<i>Ficus pygmaea</i> Welw. ex Hiern	
Myricaceae	2	<i>Morella serrata</i> (Lam.) Killick	
Phyllanthaceae	2	<i>Phyllanthus welwitschianus</i> Müll.Arg.	
Ranunculaceae	2	<i>Clematis villosa</i> DC.	

(continued)

Table 7.1 (continued)

Plant family	N°	Species common in Angola	Angolan endemics
Achariaceae	1	<i>Caloncoba suffruticosa</i> (Milne-Redh.) Exell & Sleumer	
Anisophyllaceae	1	<i>Anisophyllea quangensis</i> Engl. ex Henriq.	
Clusiaceae	1	<i>Garcinia buchneri</i> Engl.	
Dilleniaceae	1	<i>Tetracera masuiana</i> De Wild. & T. Durand	
Fabaceae-Caesalpinioideae	1	<i>Bauhinia mendoncae</i> Torre & Hillc.	
Hypericaceae	1	<i>Psorosperum mechowii</i> Engl.	
Ixonanthaceae	1	<i>Phyllocosmus lemaireanus</i> (De Wild. & T. Durand) T. Durand & H. Durand	
Lecythidaceae	1	<i>Napoleonaea gossweileri</i> Baker f.	
Linaceae	1	<i>Hugonia gossweileri</i> Baker f. & Exell	
Malpighiaceae	1	<i>Sphedamnocarpus angolensis</i> (A. Juss.) Planch. ex Oliv.	
Malvaceae	1	<i>Hibiscus rhodanthus</i> Gürke	
Melastomaceae	1	<i>Heterotis canescens</i> (E. Mey. ex Graham) Jacq.-Fél.	
Picrodendraceae	1	<i>Oldfieldia dactylophylla</i> (Welw. ex Oliv.) J.Léonard	
Rhamnaceae	1	<i>Ziziphus zeyheriana</i> Sond.	
Urticaceae	1	<i>Pouzolzia parasitica</i> (Forssk.) Schweinf.	

N°: overall number of Suffrutex species in the Zambezi phytocorion; examples of species occurring in Angola are given for each family. Compilation of families and species according to White (1976), Maurin et al. (2014) and own data

Moxíco province or as sandy alluvial deposits on fossil river terraces along the valleys of the southern slopes of the Angolan plateau (Fig. 7.2a); (b) on psammo-ferralitic plinthisols as they frequently occur on the Bie Plateau in central Angola. The suffrutex-grasslands on ferralitic soils mostly occur on mid- and foot-slopes and are embedded within a matrix of miombo woodland (Fig. 7.2b).

Environmental conditions in suffrutex-grasslands change dramatically throughout the year. The most perceived stresses are man-made fires in the dry season (May–October) which are mostly deployed to induce resprouting for livestock fodder or to facilitate hunting (Hall 1984). Depending on fire intensity, which in turn depends mostly on fuel load, ambient temperature and wind (Govender et al. 2006), such fires can completely burn unprotected aboveground biomass.

Another abiotic stress occurring mostly in the early dry season (June–August) is nocturnal frost, peaking immediately before sunrise. At this time of year masses of cold dry air from southern latitudes intrude into south-central Africa (Tyson and Preston-Whyte 2000). As depressions accumulate confluent cold air, the undulating topography of the Angolan highlands facilitates frequent radiation frost especially in valleys (Revermann and Finckh 2013; Finckh et al. 2016). Up to 44 frost events per dry season (with a minimum temperature of -7.5 °C) were recorded by Finckh et al. (2016), with a temperature span of up to 40 degrees within 12 h. Most woody

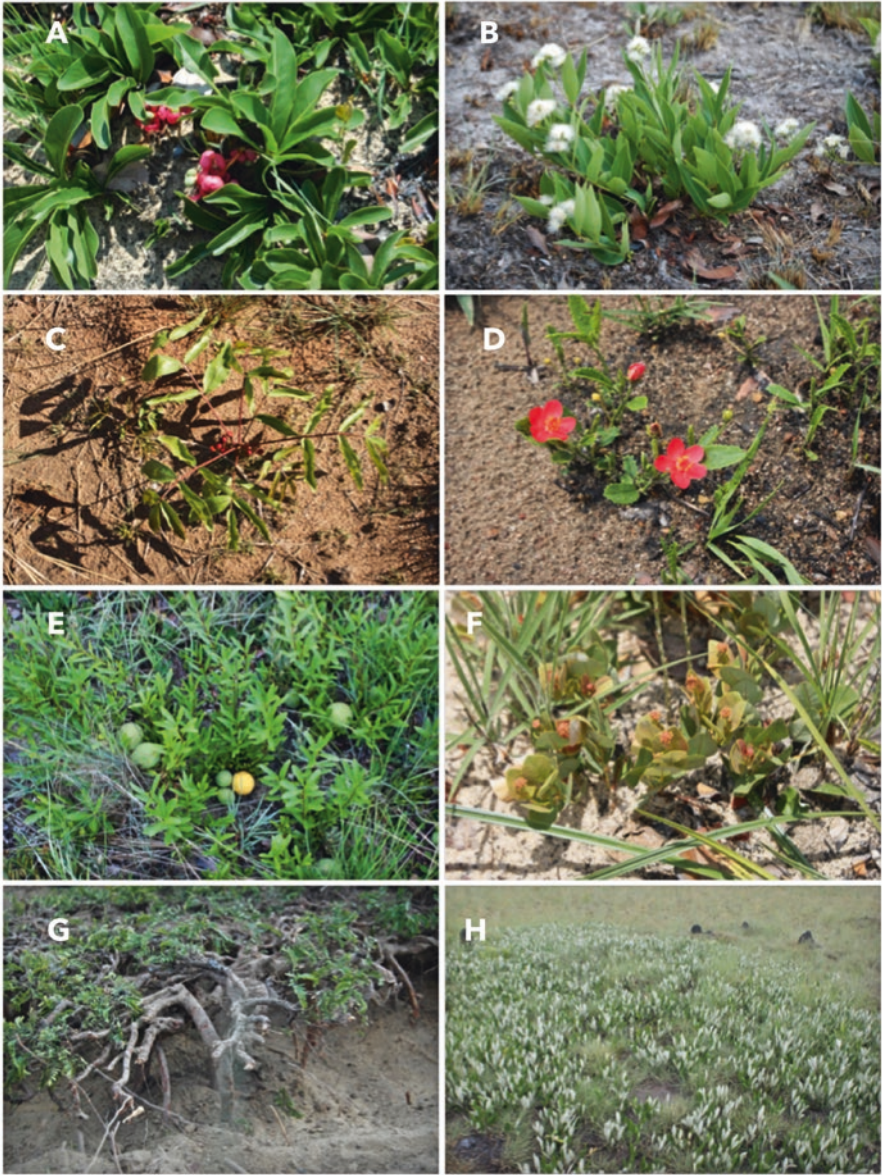


Fig. 7.1 Common Angolan suffrutex species. (a) *Ochna arenaria* (Ochnaceae), fruiting and growing on sandy sediments of the Bie Plateau. (b) *Syzygium guineense* ssp. *huillense* (Myrtaceae) flowering in the dry season and growing on sandy soils of the Bie Plateau. (c) *Lannea edulis* (Anacardiaceae), bearing edible fruits, growing on Kalahari sands in southeast Angola. (d) *Hibiscus rodanthus* (Malvaceae), growing on Kalahari sands in southeast Angola and flowering in the rainy season. (e) *Landolphia gossweileri* (Apocynaceae), typical element of the ‘Chanas da Borracha’, growing on sandy soils of the Bie Plateau and bearing edible fruits. (f) *Phyllanthus welwitschianus* (Phyllanthaceae), growing on sandy soils of the Bie Plateau and flowering in the rainy season. (g) *Cryptosepalum exfoliatum* ssp. *suffruticans* (Fabaceae – Detarioideae) with excavated rootstocks, typical element of the ‘Anharas de Ongote’, growing on psammoferrallitic soils of the Bie Plateau. (h) *Parinari capensis* (Chrysobalanaceae), typical element of the ‘Chanas da Borracha’, growing on slightly elevated termite mounds in flooded savannas of the Cameia National Park, Moxico Province

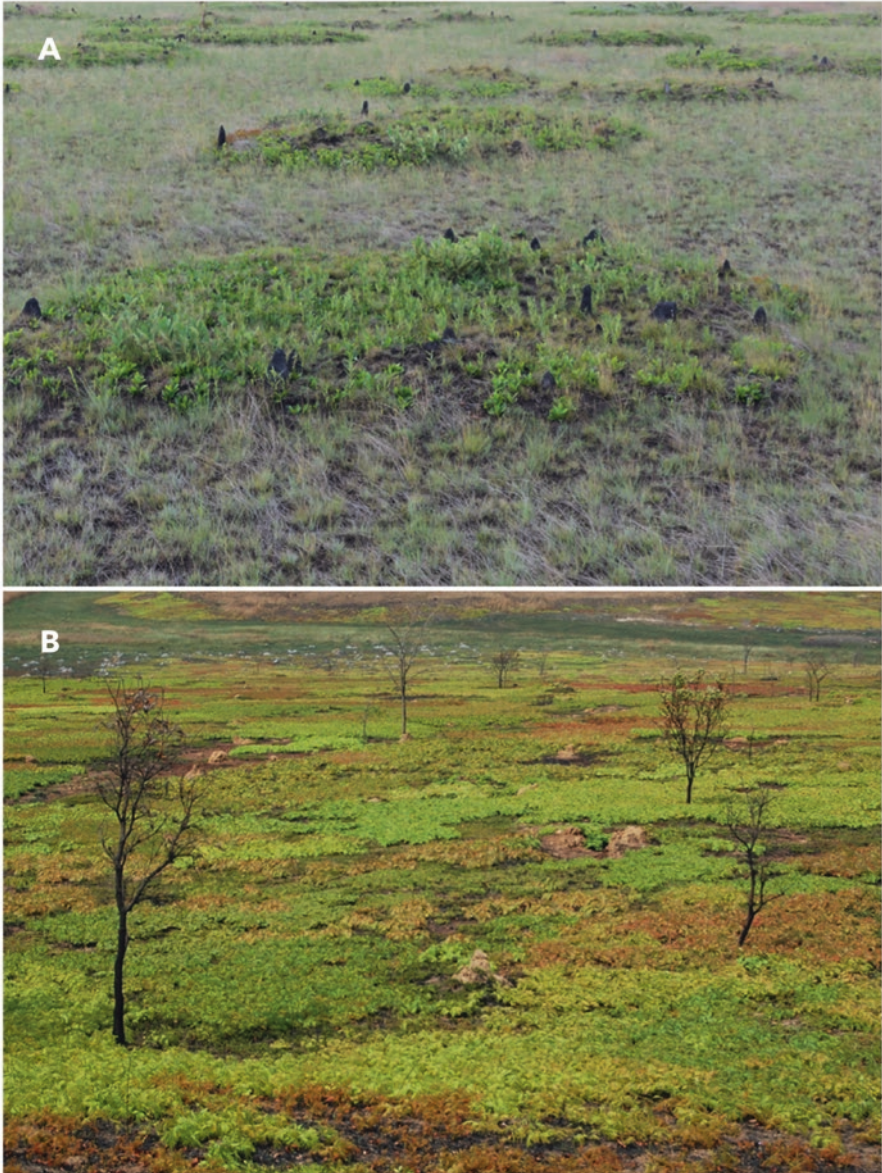


Fig. 7.2 Typical geolytic suffrutex grasslands of Angola. **(a)** ‘Chanas da Cameia’ in the Cameia National Park, Moxíco Province, during dry season in June. The slightly elevated termite mounds provide habitat for several geoxyle species that avoid the low-lying areas that are waterlogged from January to May. **(b)** ‘Anharas de Ongote’ in the Sovi Valley on the southern slopes of the Bie Plateau, in August. The mid- and footslopes are dominated by suffrutex-grassland with the characteristic reddish and green patches of the fresh leaves of *Cryptosepalum maraviense*, whereas the wetlands in the drainage lines are covered mostly by Cyperaceae (background, in dark green)

species from tropical background (including geoxylic suffrutices) are sensitive to frost, their leaves wilt or their shoots die-off entirely.

The geoxylic suffrutex species seem to be triggered by the destruction of their shoots by frost and/or fire, as they readily resprout after these disturbances and in most cases already start flowering in the dry season. The suffrutices therefore have often already finished their generative cycle when the grasses start to cover them.

The suffrutex-grasslands of the sandy plains in eastern Angola are furthermore subject to seasonal flooding in the late rainy and early dry season (January–May), leading, for example, in the Cameia National Park to standing water up to 0.5 m deep. Whereas grass species dominate the sites which are inundated for several months, suffrutex species seem to avoid fully waterlogged sites and grow patchily on slightly elevated termite mounds (Fig. 7.2a) or other well drained sites.

The dominant grass species seem to profit from inundation. Their tufts develop massively in the middle of the rainy season and they flower and bear fruits throughout the flooding season (own observations).

Knowledge Gaps on the Evolution of the Geoxylic Suffrutices and the Formation of Suffrutex-Grasslands

A common observation within suffrutex ecosystems is the resemblance (Meerts 2017) and assumed close relatedness of suffrutex species to tree species that occur in forests and woodlands. The indigenous people (e.g. the Chokwe in eastern Angola) in many cases recognise the similarity and relatedness and use similar local names for such pairs, for instance Muhaua and Mupaua for the tree and suffrutex forms of *Syzygium guineense* Willd. DC. The striking fact that the suffrutex life form was developed by several plant families independently and at roughly the same time (Maurin et al. 2014) indicates a common driver that triggered its convergent evolution.

Grassy biomes emerged in Africa in the late Miocene approximately 10 mya (Cerling et al. 1997; Keeley and Rundel 2005; Herbert et al. 2016). This period is characterised by global climatic fluctuations which led to cooler, drier conditions, to a drop of atmospheric CO₂ concentrations and particularly to pronounced precipitation seasonality (i.e. wet and dry seasons) in southern Africa (Pagani et al. 1999). As a consequence, humid tropical forests retreated to more favorable sites further north and were replaced by more open dry and seasonal tropical forest ecosystems like the miombo (Bonnefille 2011). In parts where miombo landscapes prevail today, canopies were disrupted and allowed the establishment of open ecosystems embedded in woodland matrices. These open ecosystems were then rapidly occupied by light-demanding C₄-grasses and the evolving geoxylic suffrutices.

It is still an open discussion why open suffrutex-grasslands are able to persist within the woodlands (or vice versa). It is however likely that rainfall seasonality and the above described abiotic stresses that characterise the suffrutex-grasslands

play a major role in their establishment and maintenance (Sankaran et al. 2005; Staver et al. 2011).

Savanna ecologists tend to see fire as the main driver for grassland formation. On the one hand frequent fires prevent tree establishment if saplings cannot outgrow the reach of the flames and are destroyed therein. For woodlands in eastern South Africa, a fire free time period of at least 5 years is necessary for many tree species to escape the ‘fire trap’ (Sankaran et al. 2004; Gignoux et al. 2009). This time window, allowing for successful reestablishment of trees, is rarely achieved in Angolan grasslands, at least nowadays (Schneibel et al. 2013; Stellmes et al. 2013). C4-savanna grasses, however, respond positively to periodic burning and resprout within weeks (Bond and Keeley 2005), thus being able to colonise seasonally burnt sites.

Forest ecologists, on the other hand, attribute the frequent short duration frost events in the dry season for preventing tree recruitment in the open areas (Finckh et al. 2016). As the list of suffrutices (Table 7.1) shows, mainly (but not exclusively) tropical families or genera evolved suffrutex life forms. Frost is deleterious to most tropical tree taxa, as they have not developed physiological adaptations to this ‘un-tropical’ stress factor, thus showing little or no frost tolerance (Sakai and Larcher 2012). As the suffrutex-grasslands are typically situated in particularly frost prone sites (depressions), tree taxa that are not adapted to frost are being filtered out of such environments.

In any case, a promising strategy to cope with seasonally returning thermic stress (by frost or fire) is to protect sensitive organs (buds) by hiding them underground. Tree species relocated their woody biomass and regenerative buds belowground at the expense of growth height and were thus able to cope with frost and fire prone sites (White 1976; Maurin et al. 2014; Finckh et al. 2016). Even shallow soil depths of less than 10 cm are sufficient to alleviate thermic stresses (Revermann and Finckh 2013). The high number of tropical genera and families that contribute to the suffrutex flora show how successful this strategy is for frost sensitive and fire susceptible taxa, in order to survive the adverse conditions of the open grasslands.

Concomitantly other evolutionary advantages of the geoxylic life form have been discussed, for instance poor edaphic conditions, as favoured by White (1976). He considered the low nutrient status of the leached and locally seasonal waterlogged soils on Kalahari sands as a likely cause for the lack of regular trees and the suffrutication of them as means of compensation. However, trees as well as suffrutices often grow on the same or similarly poor soils, with comparable physical and chemical properties (Gröngröft et al. 2013); forests and grasslands are not separated by edaphic boundaries but follow topographic rather than edaphic logics.

The waterlogging argument on the other hand would imply that the woody underground organs show adaptations to inundation, for instance aerenchymatic tissue or adventitious roots (Parolin 2008). Anatomical analyses of the rootstocks of four common suffrutex species however did not provide any support for aerenchymatic tissue nor other adaptations to inundation (Sanguino 2015). Moreover, in seasonally flooded savannas suffrutices avoid inundated sites. This is even the case for

Syzygium guineense ssp. *huillense*, a suffrutex closely related to a tree species that grows along and in rivers and floodplains (Coates Palgrave 2002; Meerts and Hasson 2016).

To summarise, so far the main environmental driver for the astonishing radiation of geoxylic suffrutices has not been conclusively identified. The emergence of the suffrutex grassland at the end of the Pliocene and the peak of radiation at the beginning of the Pleistocene is clearly related to climatic seasonality and pronounced dry seasons. Dry seasons, however, did not only provide the necessary dry fuel for fire but also provided the atmospheric conditions for nocturnal frost events – the seasonality argument, thus, does not tip the balance toward fire or frost.

Conservation Value and Conservation Challenges

Various studies recognise the high floristic singularity of the Zambebian phytochorion and suffrutex-grasslands with its unique life forms contribute prominently to its high number of endemic species (Clayton and Cope 1980; White 1983). The high degree of suffrutex-grassland endemics within the Zambebian phytochorion as well as within Angola is a consequence of a unique setting of environmental drivers like nutrient poor soils, frequent frosts and fires or precipitation seasonality in a small-scale heterogeneous landscape (Linder 2001). Thus, the Zambebian phytochorion can be seen as an evolutionary laboratory that promoted the evolution of many specialised plant species, e.g. suffrutices, orchids and grasses.

Suffrutex-grasslands are sometimes misunderstood as ‘degraded forests’, overlooking their naturalness. Through this misconception they are listed as sites for reforestation in order to recover presumably lost forests and to sequester atmospheric CO₂ (Parr et al. 2014). However, the well-intentioned act of reforestation would in fact destroy biodiverse natural ecosystems (Bond 2016). A lack of understanding, however, frustrates the development of appropriate conservation measures for the suffrutex grasslands today and in the future. The rebuilding process in Angola also has risks, happening at a rapid pace and shaping the landscape to human demands with limited consideration for sustainable management (Pröpper et al. 2015). Flooded savannas in the Moxíco Province for instance are targeted for large-scale agro-industrial development (ANGOP 2017). Not even National Parks offer adequate protection to ecosystems in this area, as the first rice schemes emerged during 2016 within the limits of Cameia National Park (own observation). Deficiencies in communication and cooperation between different ministries and governance levels aggravate such problems.

Outlook

Many questions still remain to be answered around the enigmatic life form of the geoxylic suffrutices. In order to efficiently safeguard suffrutex-grasslands, we need to understand the evolutionary drivers and evolutionary processes shaping these ecosystems. For instance, a thorough understanding of the evolutionary drivers and the response of suffrutices to them would help to assess how current environmental conditions affect the Zambebian ecosystems and how landscape shaping processes work. Moreover, investigations about genetic patterns of suffrutices and close tree-relatives would give insight to speciation processes, means of propagation (clonal or sexual) and evolutionary history. Also, ecophysiological or morphological measurements would contribute another perspective from which to assess how suffrutices react to environmental stresses and change processes. All these facets are currently the subjects of incipient research.

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