Diversity, ecology and origin of geoxylic plants in the Western Zambezian Floristic Region

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Paulina Meller (ex Paulina Zigelski)

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i

The following evaluators recommended the admission of the dissertation:

Prof. Dr. Norbert Jürgens

Prof. Dr. Udo Schickhoff

Prof. Dr. Caroline Lehmann

Members of the examination commission:

Prof. Dr. Norbert Jürgens

Prof. Dr. Jörg Ganzhorn

Prof. Dr. Kai Jensen

Jun.-Prof. Dr. Philipp Porada

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- **Zigelski, P.**, Gomes, A., & Finckh, M. (2019). Suffrutex dominated ecosystems in Angola. In *Biodiversity of Angola* (pp. 109-121). Springer, Cham.

- **Meller P.**, Lages, F., Finckh, M., Gomes, A., Goyder, D. (2022). High diversity and endemism of geoxylic plants in Angolan highlands: more research and conservation measures are needed. In: Mendelsohn, J., Vaz Pinto, P. (eds). *The highlands of Angola and Namibia: a hotspot of endemism.* Ongava Research Centre, Namibia.

- **Meller, P.**, Stellmes, M., Fidelis, A. & Finckh, M. (2021). Correlates of geoxyles diversity in Afrotropical grasslands. *Journal of Biogeography*, 00, 1– 14. https://doi.org/10.1111/jbi.14305

- **Meller, P.**, Frazão, R., Lages, F., Jürgens, N. & Finckh, M. (submitted 2021). Tipping the scales: How fire controls the balance among functional groups in Angolan grasslands. *Journal of Range and Forage Science*. https://doi.org/10.2989/10220119.2021.2012822

- Finckh, M., Wendefeuer, J. and **Meller, P.** (2021), Frost-driven lower treelines in Angola and their implications for tropical forest–grassland mosaics. Journal of Vegetation Science. Accepted Author Manuscript e13084. https://doi.org/10.1111/jvs.13084

- **Zigelski, P.**, Rudolph, B., Oldeland, J., Lages, F., Jürgens, N., & Finckh, M. (2019). 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

- Gomes, A. L., Revermann, R., **Meller, P.**, Gonçalves, F. M., Aidar, M. P., Lages, F., & Finckh, M. (2021). Functional traits and symbiotic associations of geoxyles and trees explain the dominance of detarioid legumes in miombo ecosystems. *New Phytologist*, *230*(2), 510-520. https://doi.org/10.1111/nph.17168

All figures, tables and supporting information have been renumbered in a consecutive manner to increase the readability and consistency throughout the thesis. Furthermore, all individual bibliographies from the respective chapters have been combined to an overall bibliography, containing every reference. All supporting information is given at the end of the thesis. Kind permission was granted to reprint chapter V from JBI, chapter VI from AJRFS, chapter VII from JVS, chapter VIII from Elsevier, and chapter IX from NP/Wiley. All other articles were published open access. Taxonomic misidentification of two species in chapter III has been corrected in this reprint.

Contents

Summary

Worldwide, tropical grassy biomes are increasingly recognized as old-growth, biodiverse and important ecosystems. They occur in areas which climatically could support forests, but seasonality, herbivory, edaphic conditions and/or occurrence of frost or fire limit tree growth and promote open, C4 grass-dominated ecosystems instead. Geoxylic plants make out a huge part of this species richness, and thereby contribute greatly to the functioning and resilience of these disturbance-prone biomes. A geoxyle, also known as suffrutex, geoxylic suffrutex, or underground tree, is characterized by low growth height, weak annual shoots, and a disproportionally high belowground woody biomass in the form of storage organs, bud banks, rhizomes and roots.

Because geoxyles are easily overlooked as long as they are not excavated, knowledge about them is still very fragmentary or simplistic. The dominant narrative today is that they evolved from trees since the late Miocene in response to emerging C4 grasslands and concomittent fires. This view however explains the geoxylic life form only insufficiently, because not all geoxyles have tree relatives, and other evolutionary drivers are just as likely. A better understanding of this life form and its diversity, origin and functioning is urgently needed in order to predict how it will react to land use changes and intensifications, which are happening right now in many geoxyle inhabited tropical grassy biomes. Management policies need to be derived from such knowledge, in order to ensure that functioning and resilience of tropical grassy biomes, and thereby sustenance for a large part of the human population, will not be compromised.

The Zambezian Floristic Region (ZFR) in south-central Africa is a diversity hotspot of geoxyles, but why this is so is not known, until now. The ZFR is therefore the ideal study region. This work provides a comprehensive understanding of this life form, and integrates new knowledge on its diversity distribution, ecology and evolution. In **chapter I** I give an overview on what is known on the geoxylic life form so far. I show where geoxyles occur and which environmental factors are known to be associated with them, and why. Furthermore in this chapter, I compile the arguments and discussions that concern the geoxyles' origin and ecology. Based on this previous knowledge and the gaps in between, I phrase four objectives which I address in this thesis: (1) How diverse are geoxyles and where do they occur? (2) What is the biogeographical origin of geoxyles? (3) Which environmental factors have driven the evolution of the geoxylic life form? (4) Which ecological, genetic, and functional differentiations went along during geoxyle evolution?

Before answering these objectives in detail, I give an overview of the study region, the ZFR, in **chapter II**. I give detailed information on biotic and abiotic factors that might affect geoxyles, in particular on climatic, geological and edaphic, anthropogenic, and fire and herbivory conditions. Providing the reader with this knowledge, I address the first objective on diversity and distribution of geoxyles in the **chapters III, IV** and **V. Chapter III** is a general review on geoxyle grasslands in Angola and Zambia (the western ZFR). I give a brief summary on historical explorations of geoxyle grasslands in Angola, and that their uniqueness has been recognized early on. Furthermore, I compile a preliminary list of geoxyle species from Angola and Zambia, and discuss their ecology

and evolution. **Chapter IV** focusses in detail on the diversity and endemism of geoxyles in Angolan highlands. I show that the outstanding geoxyle diversity there is a response to specifc environmental conditions, particularly soil heterogeneity and frost occurrence, resulting from the higher altitude. Increasing land use change and intensification, i.e. by ploughing geoxyle grassland with tractors, pose a threat on the integrity of the landscape, because such efficient ploughing destroys geoxyles and thereby the resilience and functioning of the grassland. In **chapter V** I show selected diversity and distribution patterns across all of Africa south of the equator, thereby also addressing the biogeographical origin of geoxyles (objective 2), potential environmental drivers of the geoxylic life form (objective 3), and functional diversity of geoxyles (objective 4). This study confirms that geoxyles are a very heterogeneous group, with different belowground functional types, different biogeographical origins, and lineage-associated adaptations to different environmental conditions throughout Africa.

Subsequently, I address the third objective with environmental studies. In **chapter VI** I synthezise the findings from a fire experiment in central Angola, focussing on the effect of fire seasonality and fire exclusion on plant functional groups in geoxyle grasslands. I can show with this experiment that the timing of fire tips the balance between grasses, geoxyles, and herbs, in that each treatment favours a different functional group: geoxyles benefit from early dry season fires, herbs from late dry season fires, and fire exclusion favoured grasses. Even with fire exclusion, trees or shrubs are not able to grow, because another factor, nocturnal dry season frosts, prevent this and keep the grasslands open. In **chapter VII** I explore the role and extent of frost in the landscape further. Classifying different vegetation types (miombo woodland, ecotones, geoxyle grasslands) in a topographically pronounced landscape, and using a network of temperature loggers in such a landscape allows for predicting the microclimatic conditions. This way, I show that geoxyle grasslands are heavily affected by dry season frosts, much more than miombo woodlands. Frost and topography are therefore likely to control the layout of vegetation types in central Angola, particularly since frosts have been stronger in the past during glacial maxima.

The last objective concerning genetic, functional, and ecological differentiation, is dealt with in the following two chapters. With a case study on the (sub)species of *Syzygium guineense*, I show genetic, phenotypic and ecological differentiation between different ecotypes (**chapter VIII**). Despite great phenotypic differences, genetic exchange is still happening among ecotypes and indicate an ongoing differentiation process. In the case of *S. guineense* (sub)species, the phenotypic plasticity, and thereby enhanced adaptability to challenging environments, might be facilitated by polyploidy. Lastly, I explore functional conservatism and differentiation between congeneric tree and geoxyle species (**chapter IX**). I hereby show that many functional traits are retained by geoxyles, e.g. symbiotic associations or productivity, whereas others have changed along with the different life strategy. Most importantly, geoxyles needed to optimize photosynthesis rates in the time period of low competition (late dry season), and belowground persistence.

Synthesizing all my findings in **chapter X**, I conclude with a better understanding of the geoxylic life form in the Zambezian Floristic Region. Identifying several subcentres of diversity and endemism within the ZFR, I enumerate the diversity of geoxyles to close to 700 geoxylic species (objective 1). I show that these geoxyles are very heterogeneous, consisting of species from different biomes, plant families, and original lifeforms (objective 2). Analogously, there is not a single environmental driver that is responsible for geoxyle evolution and radiation, but several that interact with one another: fire, frost, and edaphic conditions (objective 3). Ecologically, geoxyles are strongly differentiated from close tree relatives, but they conserved several functional traits, and are genetically still in exchange (objective 4). Finally, based on these findings, I emphasize where further research is urgently needed, which particularly concerns geoxyle-animal interactions, sexual reproduction, and conservation challenges.

Zusammenfassung

Weltweit werden tropische Grasländer und Savannen zunehmend anerkannt als urwüchsige, artenreiche und wichtige Ökosysteme. Sie kommen in Gegenden vor, die aus klimatischer Sicht waldbedeckt sein könnten, aber Saisonalität, Herbivorie, Bodenbeschaffenheiten und/oder das Vorkommen von Frost oder Feuer beschränken das Baumwachstum, und schaffen stattdessen offene, C4-grasbedeckte Ökosysteme. Geoxylische Pflanzen machen einen großen Teil dieser Artenvielfalt aus und tragen deshalb sehr zum Funktionieren und zur Widerstandsfähigkeit dieser störungsbetroffenen Biome bei. Ein Geoxyle, auch bekannt als Suffrutex, geoxylischer Suffrutex oder unterirdischer Baum, ist durch seine geringe Wuchshöhe, kurzlebige, annuelle Sprosse, und eine überproportional große unterirdische, holzige Biomasse gekennzeichnet, die aus Speicherorganen, Knospenreserven, Rhizomen oder Wurzeln gebildet wird.

Das Wissen über Geoxyle ist immer noch sehr lückig und einfach, da sie leicht übersehen werden solange sie nicht ausgegraben werden. Die Hauptansicht heute ist, dass Geoxyle sich seit dem späten Miozän aus Bäumen entwickelt haben, als Antwort auf die aufkommenden C4-Grasländer und die damit einhergehenden Feuer. Diese Ansicht aber erklärt die geoxylische Lebensform nur unzureichend, da nicht alle Geoxyle nahe Baumverwandte haben, und andere evolutionären Triebkräfte genauso plausibel sind. Ein besseres Verständnis dieser Lebensform und ihrer Vielfalt, Herkunft und Funktionsweise ist aber dringend nötig um vorhersagen zu können, wie sich Landnutzungsveränderung und –intensivierung auf sie auswirken wird, die zur Zeit in vielen tropischen Graslandbiomen stattfinden, in denen Geoxyle vorkommen. Management-Empfehlungen müssen aus fundiertem Wissen abgeleitet werden um sicherzugehen, dass Funktionsweise und Widerstandsfähigkeit der tropischen Graslandbiome nicht beeinträchtigt werden, da das den Lebensunterhalt eines großen Teils der menschlichen Bevölkerung gefährden könnte.

Die Zambezische Floristische Region (ZFR) im südlich-zentralen Afrika ist ein Schwerpunkt der geoxylen Artenvielfalt, aber warum das so ist, ist bisher nicht bekannt. Die ZFR is daher ein ideales Untersuchungsgebiet. Diese Doktorarbeit bietet ein umfassendes Verständnis dieser Lebensform, und integriert neues und altes Wissen über ihre Vielfalt, Verbreitung, Ökologie und Entstehung. In **Kapitel I** gebe ich einen Überblick über den bisherigen Wissensstand der geoxylischen Lebensform. Ich zeige, wo Geoxyle vorkommen und welche Umweltbedingungen bekannterweise mit ihnen assoziiert sind, und warum. Weiterhin fasse ich in diesem Kapitel alle Argumente und Diskussion über ihre Herkunft und Ökologie zusammen. Basierend auf diesem bisherigen Wissen und den Lücken darin, formuliere ich vier Forschungsfragen in dieser Arbeit: (1) Wie vielfältig sind Geoxyle und wo kommen sie vor? (2) Was ist der biogeographische Ursprung von Geoxylen? (3) Welche Umweltfaktoren haben die Evolution der geoxylischen Lebensform vorangetreiben? (4) Welche ökologischen, genetischen und funktionellen Unterschiede gingen mit dieser Entwicklung einher?

Bevor ich diese Fragen umfassend beantworte, gebe ich einen Überblick über das Untersuchungsgebiet, die ZFR (**Kapitel II**). Ich geben detaillierte Informationen über biotische und

4

abiotische Faktoren, die Geoxyle irgendwie beeinflussen können, dies sind insbesondere klimatische, geologische und bodenbezogene, menschliche, feuer- und herbivoriebezogene Einflüsse. Nachdem ich den Leser mit diesem Grundwissen ausstatte, adressiere ich die erste Forschungsfrage über die Vielfalt und Verbreitung von Geoxylen in den **Kapiteln III, IV** und **V**. Kapitel III bietet einen generellen Überblick über geoxylische Grasländer in Angola und Zambia (die wetsliche ZFR). Ich gebe eine kurze Zusammenfassung über die historische Erforschung von geoxylischen Grasländern in Angola, die schon früh die Einzigartigkeit dieser Ökosysteme erkannt hat. Weiterhin stelle ich eine vorläufige Liste von geoxylischen Arten in Angola und Zambia zusammen und diskutiere ihre Ökologie und Evolution. **Kapitel IV** handelt umfassend von der Vielfalt und dem Endemismus von Geoxylen in angolanischen Hochländern. Ich zeige, dass die bemerkenswerte Geoxylen-Vielfalt dort durch spezifische Umweltbedingungen verursacht wird, insbesondere durch die Vielfalt von Bodentypen und das Vorkommen von Frost, ein Resultat der höheren Lagen. Zunehmender Landnutzungswandel und –intensivierung, vor allem das Traktorpflügen von geoxylischen Grasländern, stellen ein Gefahr für die Integrität der Landschaft dar, da derart effizientes Pflügen Geoxyle zerstört und damit die Funktionsweise und Widerstandsfähigkeit des Graslands. In **Kapitel V** zeige ich bestimmte Muster der Vielfalt und Verbreitung über ganz Afrika südlich des Äquators, und adressiere damit den biogeographischen Ursprung der geoxylischen Lebensform (Frage 2), die potentiellen Umweltfaktoren, die die geoxylische Lebensform hervorgebracht haben (Frage 3), und die funktionelle Vielfalt von geoxylischen Arten (Frage 4). Diese Studie bestätigt, dass Geoxyle eine sehr heterogene Gruppe formen, mit unterschiedlichen unterirdischen, funktionellen Typen, unterschiedlichen biogeographischen Ursprüngen, und abstammungsbedingten Anpassungen an unterschiedliche Umweltbedingungen in Afrika.

Anschließend adressiere ich mit Umweltstudien die dritte Forschungsfrage. In **Kapitel VI** fasse ich die Ergebnisse eines Feuerexperiments in Zentralangola zusammen, das den Effekt von Feuersaisonalität und Feuerausschluss auf funktionelle Pflanzengruppen in geoxylischen Grasländern untersucht hat. Ich kann mit diesem Experiment zeigen, dass der Zeitpunkt des Feuers die Balance zwischen Gräsern, Geoxylen und Kräutern beeinflusst, da jeder Brandzeitpunkt eine andere funktionelle Gruppe günstig beeinflusst: Geoxyle profitieren von einem Feuer früh in der Trockenzeit, Kräuter in der späten Trockenzeit und Gräser profitieren vom Feuerausschluss. Bäume und Sträucher waren sogar unter Feuerausschluss nicht in der Lage zu wachsen, da ein anderer Faktor, nächtlicher Frost in der Trockenzeit, dies verhindert, und die Grasländer offen hält. In **Kapitel VII** untersuche ich die Rolle und das Ausmaß von Frost in der Landschaft im Detail. Indem ich die unterschiedlichen Vegetationstypen (Miombo-Waldland, Übergangsbereiche, geoxylische Grasländer) innerhalb einer topographisch stark ausgeprägten Landschaft kartiere, und mit einem Netzwerk von Temperatursensoren verbinde, bin ich in der Lage die mikroklilmatischen Bedingungen in so einer Landschaft vorherzusagen. Dabei kann ich zeigen, dass geoxylische Grasländer stark von Frostnächten in der Trockenzeit betroffen sind, viel mehr als die Miombo

Waldländer. Daher kontrollieren Frost und Topographie wahrscheinlich die Verteilung der Vegetationstypen in der Landschaft in Zentralangola, insbesondere da in der Vergangenheit, während der glazialen Maxima, Fröste noch viel stärker gewesen sind.

Die letzte Forschungsfrage über die genetischen, funktionelle und ökologischen Differenzierung während der Geoxyle-Entwicklung wird in den nächsten beiden Kapiteln behandelt. Mit einer Fallstudie über die (Unter-)Arten von *Syzygium guineense* kann ich die genetische, phänotypische und ökologische Differenzierung zwischen den (Unter-)Arten zeigen (**Kapitel VIII**). Trotz großer äußerlicher Unterschiede gibt es immer noch einen Genaustausch zwischen den (Unter-)Arten, was eine anhaltende Ausweinanderentwicklung anzeigt. Diese phänotypische Plastizität, und die dadurch erhöhte Anpassungsfähigkeit an herausfordernde Umweltfaktoren, mag im Falle der (Unter-)Arten von *S. guineense* durch Polyploidie ermöglicht sein. Zuletzt erforsche ich die Beibehaltung und/oder Differenzierung von funktionellen Eigenschaften in nahe verwandten Baum-Geoxyle-Partnern (**Kapitel IX**). Dabei zeige ich, dass viele funktionelle Eigenschaften in Geoxylen erhalten geblieben sind, zum Beispiel die symbiotischen Beziehungen oder die Produktivität, während andere wegen einer geänderten Lebensstrategie abgewandelt wurden. Am wichtigsten dabei war für Geoxyle die Optimierung der Photosyntheserate während der Zeiten, in denen wenig Konkurrenz herrscht (späte Trockenzeit), und die unterirdische Persistenz.

Indem ich alle meine Ergebnisse in **Kapitel X** zusammenstelle, schließe ich diese Arbeit mit einem besseren Verständnis der geoxylischen Lebensform in der Zambezischen Floristischen Region ab. Ich habe mehrere Vielfalt- und Endemismus-Schwerpunkte innerhalb der ZFR identifiziert, und kann den Reichtum von Geoxylen auf knapp 700 Arten beziffern (Forschungsfrage 1). Ich zeige, dass diese Geoxylen sehr heterogen sind, da sie Arten aus unterschiedlichen Biomen, Pflanzenfamilien und ursprünglichen Lebensfromen umfassen (Forschungsfrage 2). Entsprechend git es nicht einen einzelnen Umweltfaktor, der für die Evolution und Verbreitung von Geoxylen verantwortlich ist, sondern mehrere, die miteinander interagieren: Feuer, Frost und Bodenbeschaffenheiten (Forschungsfrage 3). Geoxyle sind ökologisch gesehen sehr anders als ihre nahen Baumverwandten, aber sie haben mehrere funktionelle Eigenschaften behalten tauschen sich auf genetischer Ebene immer noch aus (Forschungsfrage 4). Zuletzt betone ich, basierend auf diesen Ergebnissen, wohin die zukünftige Geoxyle-Forschung gehen sollte, wobei insbesondere die Interaktion mit Tieren, die sexuelle Fortpflanzung und der Schutz von Geoxyles wichtig sind.

Resumo

A nível mundial, os biomas herbáceos tropicais são cada vez mais reconhecidos como sendo de crescimento primário, sendo biodiversificados e considerados ecossistemas importantes. Ocorrem em áreas que, em termos climáticos, poderiam suportar florestas, mas cujas sazonalidades, condições de herbivoria, edáficas e/ou a ocorrência de geadas ou queimadas, limitam o crescimento das árvores e promovem ecossistemas abertos e dominados por gramíneas C4. As plantas geoxílicas constituem uma enorme parte desta riqueza de espécies, contribuindo assim grandemente para o funcionamento e a resiliência destes biomas propensos a perturbações. Um geoxílico, também conhecido como suffrutex, geoxylic suffrutex, ou árvore subterrânea, é caracterizado por pouco crescimento em altura, rebentos anuais fracos, e uma biomassa lenhosa subterrânea desproporcionalmente elevada sob a forma de órgãos de armazenamento, reservatórios de botões, rizomas e raízes.

Uma vez que as plantas geoxílicas passam facilmente despercebidas, desde que não sejam escavadas, o conhecimento sobre elas é ainda muito fragmentário ou simplista. A teoria dominante hoje em dia é que elas evoluíram das árvores desde o antigo Mioceno em resposta a prados C4 emergentes e a incêndios concomitantes. Esta visão, contudo, explica a forma de vida geoxílica de maneira insuficiente, uma vez que nem todas as plantas geoxílicas têm parentesco com árvores, e existem outros fatores evolutivos igualmente prováveis. Uma melhor compreensão desta forma de vida e da sua diversidade, origem e funcionamento é imprescindível para prever como irá reagir às mudanças e à intensificação do uso do solo, que estão a ocorrer actualmente em muitos biomas geoxílicos habitados por gramíneas tropicais. As políticas de gestão precisam de se basear neste conhecimento, a fim de assegurar que o funcionamento e a resiliência dos biomas herbáceos tropicais, bem como o sustento de uma grande parte da população humana, não serão comprometidos.

A Região Florística Zambeziaca (ZFR) na África Centro-Sul é um hotspot de diversidade de plantas geoxílicas, mas o motivo pelo qual tal acontece, não é conhecido, até ao momento. A ZFR é, portanto, a região ideal para o estudo. Este trabalho proporciona uma compreensão abrangente desta forma de vida, e integra novos conhecimentos sobre a sua distribuição de diversidade, ecologia e evolução. No **capítulo I** dou uma visão geral acerca do que se sabe até agora sobre a forma de vida geoxílica. Mostro onde ocorrem plantas geoxílicas e quais os factores ambientais que se sabe estarem associados a elas, e porquê. Além disso, neste capítulo, compilo os argumentos e discussões que dizem respeito à origem e ecologia das geoxílicas. Com base neste conhecimento anterior e nas lacunas existentes entre eles, enunciei quatro objectivos que abordei nesta tese: (1) Quão diversas são as geoxílicas e onde ocorrem? (2) Qual é a origem biogeográfica das geoxílicas? (3) Que factores ambientais têm impulsionado a evolução da forma de vida geoxílica? (4) Que diferenciações ecológicas, genéticas e funcionais se verificaram durante a evolução das geoxílicas?

Antes de responder a estes objectivos em pormenor, dou uma visão geral da região de estudo, o ZFR, no **capítulo II**, bem como informações detalhadas sobre factores bióticos e abióticos que podem afectar as geoxílicas, em particular sobre condições climáticas, geológicas e edáficas, antropogénicas, de fogo e de herbivoria. Proporcionando ao leitor este conhecimento, abordo o primeiro objectivo sobre diversidade e distribuição de geoxílicas nos **capítulos III, IV e V**. O **capítulo III** é uma revisão geral sobre os prados de plantas geoxílicas em Angola e na Zâmbia (o ZFR ocidental). Faço um breve resumo sobre as explorações históricas de prados geoxílicos em Angola, e cuja singularidade foi reconhecida desde o início. Além disso, compilo uma lista preliminar de espécies geoxílicas de Angola e da Zâmbia, e apresento a sua ecologia e evolução. O **capítulo IV** foca em detalhe a diversidade e endemismo das geoxílicas nas terras altas de Angola. Demonstro que a extraordinária diversidade de geoxílicas é uma resposta às condições ambientais das espécies, particularmente a heterogeneidade do solo e a ocorrência de geadas, resultantes da altitude mais elevada. A crescente mudança e intensificação do uso do solo, ou seja, a lavoura de prados geoxílicos com tractores, representa uma ameaça à integridade da paisagem, uma vez que destrói as geoxílicas e, consequentemente, a resiliência e o funcionamento dos prados. No **capítulo VI**, mostrou a diversidade e padrões de distribuição seleccionados em toda a África a sul do equador, abordando assim também a origem biogeográfica das geoxilicas (objectivo 2), potenciais factores ambientais da forma de vida geoxílica (objectivo 3), e diversidade funcional das geoxílicas (objectivo 4). Este estudo confirma que as geoxílicas são um grupo muito heterogéneo, com diferentes tipos funcionais abaixo do solo, diferentes origens biogeográficas, e adaptações associadas à linhagem a diferentes condições ambientais em toda a África.

Posteriormente, abordei o terceiro objectivo com estudos ambientais. No **capítulo VI** sintetizo os resultados de uma experiência de queimada no centro de Angola, focando o efeito da sazonalidade do fogo e da exclusão do fogo em grupos funcionais de plantas em prados geoxílicos. Posso concluir com esta experiência que o tempo de fogo favorece o equilíbrio entre gramíneas, geoxílicas e ervas, na medida em que cada tratamento favorece um grupo funcional diferente: as geoxílicas beneficiam de queimadas no início da estação seca, as ervas de queimadas no final da estação seca, e a exclusão de queimadas favorece as gramíneas. Mesmo com a exclusão do fogo, as árvores ou arbustos não conseguem crescer, porque outro factor, as geadas noturnas da estação seca, impedem-no e mantêm os prados abertos. No capítulo VII exploro melhor o papel e a extensão das geadas na paisagem. A classificação de diferentes tipos de vegetação (floresta de miombo, ecótones, prados geológicos) numa região topograficamente pronunciada, e a utilização de uma rede de sensores de temperatura nessa mesma região, permite prever as condições microclimáticas. Desta forma, mostro que os prados geoxílicos são fortemente afectados pelas geadas da estação seca, muito mais do que as florestas de miombo. A geada e a topografia são, portanto, susceptíveis de controlar a distribuição dos tipos de vegetação no centro de Angola, particularmente desde que as geadas foram mais fortes, no passado, durante o último Período Glacial.

O último objectivo relativo à diferenciação genética, funcional e ecológica, é tratado nos dois capítulos seguintes. Com um estudo de caso sobre as (sub)espécies de *Syzygium guineense*, mostro a diferenciação genética, fenotípica e ecológica entre os diferentes ecótipos (**capítulo VIII**). Apesar das grandes diferenças fenotípicas, o intercâmbio genético ainda está a acontecer entre ecótipos e indica um processo contínuo de diferenciação. No caso da (sub)espécie *S. guineense*, a plasticidade fenotípica, e consequentemente uma maior adaptabilidade a ambientes difíceis, pode ser facilitada pela poliploidia. Finalmente, exploro o conservadorismo funcional e a diferenciação entre espécies de árvores congéneres e espécies geoxílicas (**capítulo IX**). Mostro que muitas características funcionais são retidas pelas geoxílicas, tais como associações simbióticas ou produtividade, enquanto outras se modificaram de acordo com uma estratégia de vida diferente. Mais importante ainda, as geoxílicas precisaram de optimizar as taxas de fotossíntese no período de baixa competição (final da estação seca) e persistência abaixo do solo.

Sintetizando todas as minhas descobertas no **capítulo X**, termino com uma maior compreensão sobre a forma de vida geoxílica na Região Florística Zambeziaca. Identificando vários subcentros de diversidade e endemismo dentro da ZFR, enumero a diversidade de geoxílicas para cerca de 700 espécies (objectivo 1). Mostro que estas geoxílicas são muito heterogéneas, consistindo em espécies de diferentes biomas, famílias de plantas e formas de vida originais (objectivo 2). Analogamente, não existe um único factor ambiental responsável pela evolução e radiação, mas sim vários que interagem entre si: fogo, geada e condições edáficas (objectivo 3). Ecologicamente, as geoxílicas são fortemente diferenciadas dos seus parentes próximos, as árvores, mas conservam vários traços funcionais, e ainda estão em intercâmbio genético (objectivo 4). Finalmente, com base nestas descobertas, destaco onde é urgente a necessidade de mais investigação, no que diz respeito particularmente às interacções entre as plantas geoxílicas e animais, reprodução sexual e desafios de conservação.

-I-
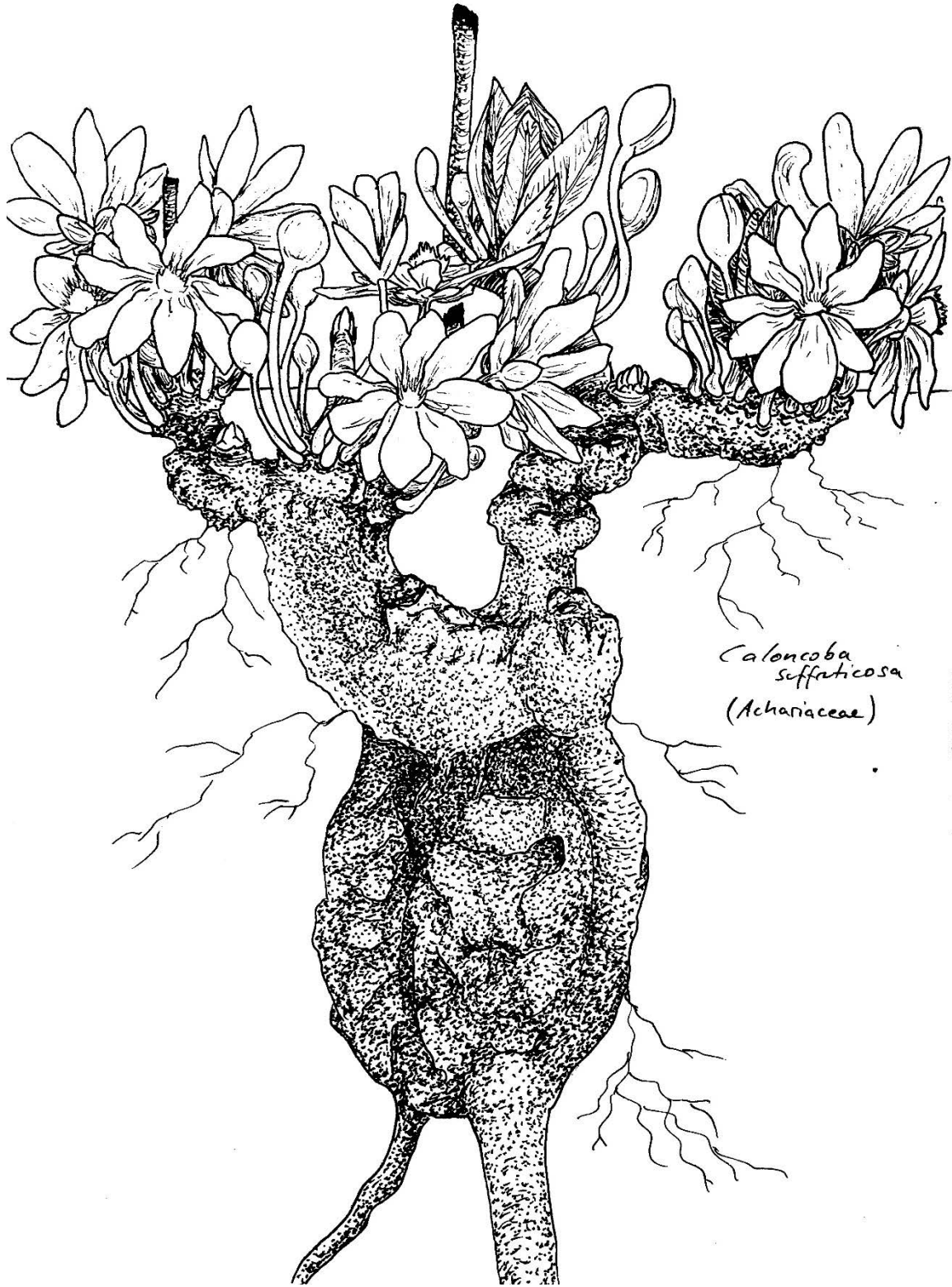
Caloncoba
suffruticosa
(Achariaceae)

General introduction

We tend to overlook what is not directly visible or accessible to us. This way, terrestrial ecosystems have been studied far longer and better than marine ones (Di Marco *et al.*, 2017; Tydecks *et al.*, 2018), but the same is true for the aboveground parts of terrestrial ecosystems in comparison to their belowground parts (Ottaviani *et al.*, 2020). Yet research in recent years has increasingly uncovered how important that belowground part is (Smith *et al.*, 2015). For instance, soils store substantial amounts of biomass and carbon in the form of plant roots, stems and storage organs. The ratio of aboveground to belowground plant biomass differs between biomes, tropical forests for instance have the highest aboveground ratio, whereas tropical grasslands and savannas have strikingly high belowground ratios (Ottaviani *et al.*, 2020). The little known belowground part of African grasslands will be the centre of this thesis.

Tropical grasslands and savannas are characterized by a continuous layer of C4 grasses with variable tree cover of 0% – 60%, occurring in regions with a seasonal climate, i.e. pronounced wet and dry seasons (Scholes & Archer, 1997). These grassy biomes constitute about 20% of the worlds land cover and provide crucial services such as forage and alimentation, belowground carbon storage, or erosion control (Veldman *et al.*, 2015; Lehmann & Parr, 2016; Schmidt *et al.*, 2019; Zhao *et al.*, 2020). As of 2020, around 1.4 billion people, a substantial part of the world human population (ca 18%), live in grassy biomes and rely on their functionality for subsistence (percentage derived from Doxsey-Whitfield *et al.*, 2015; Fedele *et al.*, 2021).

In addition to grasses and trees, tropical grassy biomes are also composed by persistent, resprouting non-graminoids like herbs, geophytes, or geoxylic plant species. These plant species in the ground layer constitute a huge part of the biomes' biodiversity (Siebert & Dreber, 2019). Furthermore, their resprouting ability makes tropical grassy biomes resilient to recurrent disturbances such as fire (Buisson *et al.*, 2019), thereby enabling continuous provision of the above listed contributions to people. Tropical grassy biomes are increasingly recognized to be old-growth, biodiverse, and important biomes (Veldman *et al.*, 2015), which evolved as response to seasonal climate, topography, fire and herbivory (Bond & Keeley, 2005; Sankaran *et al.*, 2008; Staver & Bond, 2014; Herbert *et al.*, 2016). An important, but not undisputed narrative today is that within a specific precipitation range, tropical forested and grassy biomes represent alternative stable states, and realisation of one biome or the other is determined by disturbance regimes and fire in particular (Staver *et al.*, 2011; Archibald *et al.*, 2019).

How did these open grassy systems arise in the tropics, where precipitation would allow forests to prevail? About 6 – 8 million years ago, the climate changed, and wet-tropical forests globally gave way to expanding C4 grasslands and savannas. With their C4 photosynthetic pathway, grasses were at an advantage in coping with declining CO_2 air concentrations (Cerling *et al.*, 1997), and with cooler, more arid and seasonal climate (Herbert *et al.*, 2016). This caused global environmental changes at the Miocene/Pliocene boundary. In the tropics, these changes allowed for wildfires and for nocturnal frosts to occur in the dry season, thereby facilitating the spread of

disturbance-prone grasslands (Osborne, 2008). Many plant species evolved in response to these changed environmental conditions, and developed functional traits for surviving recurrent frosts and fires. One such response strategy is the geoxylic life form.

Plants with this life form are known under several terms like geofrutices ("earth-shrubs"), geoxyles ("earth-woods"), suffrutices ("sub-shrubs"), geoxylic suffrutices ("sub-shrubs with earth-wood"), functional herbs or underground trees (White, 1976; Maurin *et al.*, 2014). Some, like Uys *et al.* (2004), treat them as forbs, which in the ground layer encompass "all broad-leafed plants, in contrast to the narrow-leaf graminoids" (Küchler, 1949), and some as dwarf- or subshrubs (Ratter *et al.*, 1997; Durigan *et al.*, 2020). The terms are often vague and used inconsistently, all trying to catch some of the characteristics of these plants. For consistency in the following thesis, I will mostly use the term "geoxyle" (except in chapter III where I also use "suffrutex"). I define a plant occurring in grassy biomes as geoxyle, if it has an obligate low growth habit (< 2 m) and is able to flower and bear fruits in this state. This distinguishes them from trees which can also get trapped in a facultative dwarf state by recurrent top-kill (Trollope, 1982; Hoffmann *et al.*, 2009). A geoxyle has to have a woody base, and most of its woody biomass belowground. It has to be perennial and being able to resprout from belowground woody storage organs and bud banks when aboveground biomass has been killed or removed.

Geoxyles are known from several tropical grassy biomes, most notably Zambezian and - to a much lesser degree - Sudanian floristic regions, Cape region, Pondoland and Highveld in Africa, and the Cerrado in Brazil (White, 1976; Ratter *et al.*, 1997; Pennington & Hughes, 2014). **Fig. 1.1** depicts the global extent of tropical grassy biomes to date, and in which of these occurrence of geoxylic plants has been reported. Beside the diversity hotspots in South-central Africa and Brazil, some geoxyles also occur in Northern Australia, Venezuela and Florida.
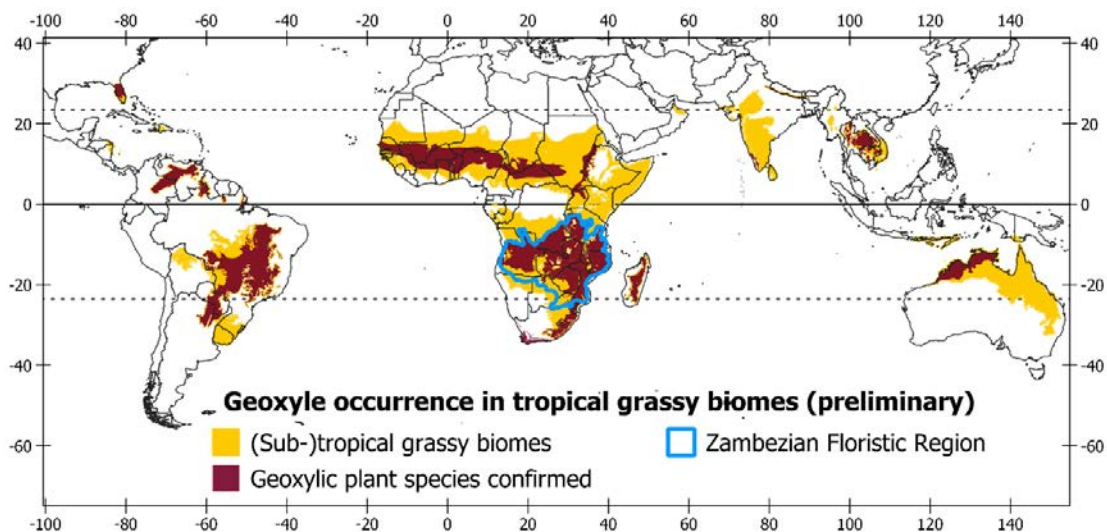
Figure 1.1: Preliminary map on global distribution of (sub)tropical grassy biomes and geoxyles therein. The dashed lines indicate the tropics (23.5° north and south), and the solid line the equator. The extent of (sub)tropical grassy biomes shown here is based on Murphy *et al.* (2016) and personal communication with international grassland and savanna experts on Twitter. The same goes for occurrences of geoxyles within those grassy biomes. My study area, the Zambezian Floristic Region, is highlighted. Plotted with QGIS 3.10.14.

A first essay about South African geoxyles was published around 100 years ago by Burtt Davy (1922), followed by White (1976) who coined the term underground tree. He noted that the Zambezian floristic region is particularly abundant and rich in geoxyle species, downright forming underground forests, and that many of them are closely related to tree species from aboveground forests, from which they presumably evolved. This was much later verified by Maurin *et al*. (2014), who showed that African congeneric tree-geoxyle pairs diverged mostly within the last 2 million years (maximum 15 mya), which falls exactly into a period of strong environmental change with spreading of grassy biomes (Trauth *et al.*, 2009; Herbert *et al.*, 2016). However, limiting geoxyles to only species with close tree relatives, as it has been done in literally all previous studies (e.g. Gomes *et al.*, 2019; Lamont *et al.*, 2017; Maurin *et al.*, 2014; Meerts, 2017), neglects an existential part of the diversity and ecology of grassy biomes. I will hence use a broader concept of geoxyles in my thesis (see above). By including all species that evolved these morphological and functional features, regardless of their relatives, I address some of the many knowledge gaps that still exist about the geoxyles' diversity, ecology and evolution in Africa.

The true extent of "geoxylicity" in afrotropical grassy biomes has not been fully recognized so far, due to different concepts of this life form (tree relative or not?) and only recent systematic, belowground research. An increased effort is necessary to do so, because the geoxylic life form is not detectable without excavating at least parts of the plant. Yet African geoxyles new to science are described again and again in publications, e.g. Hind and Goyder (2014), Dessein *et al.* (2003) or Vollesen (1981). Most studies either focussed on the genetic (Maurin *et al.*, 2014), morphological (Meerts, 2017) or functional difference (Gomes *et al.*, 2019) between congeneric tree-geoxyle pairs, on their longevity (Chidumayo, 2019; Dayaram *et al.*, 2020), or, subsumed under "forbs" or "shrubs", on how they are affected by fire or herbivory (Uys *et al.*, 2004; Bombo *et al.*, 2021). However, despite concentrated publication efforts in the last two decades, and important reviews early on (Burtt Davy, 1922; White, 1976), many basic questions are still not answered, and simplistic narratives remain unchallenged. For instance, it is not known how many geoxyle species exist, and why South-central Africa in particular is so diverse in geoxyles. Moreover, factors governing their overlap and distribution in this area have not been identified, although this would be crucial to predict how geoxyles will be affected by future climate and land use change. The dominant explanation for geoxyle evolution is fire, but detailed studies showing how geoxyles respond to fire are missing. Alternative or additional environmental drivers like frost are increasingly debated (Finckh *et al.*, 2016), but little investigated and thus dismissed by researchers favouring the fire theory (Davies *et al.*, 2016a; Lamont *et al.*, 2017). Yet since both environmental factors are common in Afrotropical grasslands, a comprehensive approach is needed to elucidate the effects of these and further environmental drivers on the ground layer. Some aspects of congeneric trees and geoxyles have been studied, but many remain open, for example whether geoxyles differentiated not only morphologically, but also functionally from sympatric trees, by adapting different physiological strategies or changing symbiotic associations. Particularly in South-central

Africa do ectomycorrhizal symbionts enable their tree hosts to thrive despite the nutrient poor soils (Corrales *et al.,* 2018), but what about closely related geoxyles? And although it has been ascertained that many geoxyles evolved from tree species, nothing is known about possible evolutionary and genetic pathways that led to this development, i.e. what enabled tree species to become geoxylic.

Objectives and chapter outline

In the following chapters, I want to provide a better understanding of the geoxylic life form and how it is adapted to its ecosystem. I do so by addressing the above stated knowledge gaps with the following four objectives:

(1) How diverse are geoxyles and where do they occur?

(2) What is the biogeographical origin of geoxyles?

(3) Which environmental factors have driven the evolution of the geoxylic life form?

(4) Which ecological, genetic, and functional differentiations went along during geoxyle evolution?

Beforehand, I will give an overview of my general study region, the Zambezian Floristic Region (**chapter II**). The first objective, addressing the geoxyles' diversity and distribution patterns, will be discussed and answered thoroughly in **chapters III, IV,** and **V. Chapter V** also deals with the origin of geoxyles, thereby answering the second objective, and with environmental drivers of the geoxylic life form, thereby contributing to the third objective. **Chapters VI** and **VII** also delve into the third objective. The fourth objective, concerning genetic, functional, and ecological differentiation, is dealt with in **chapters VIII** and **IX**. Lastly, **chapter X** provides a synthesis of all findings and an overall discussion.

-II-

Dolichos dongalita
(Fabaceae)
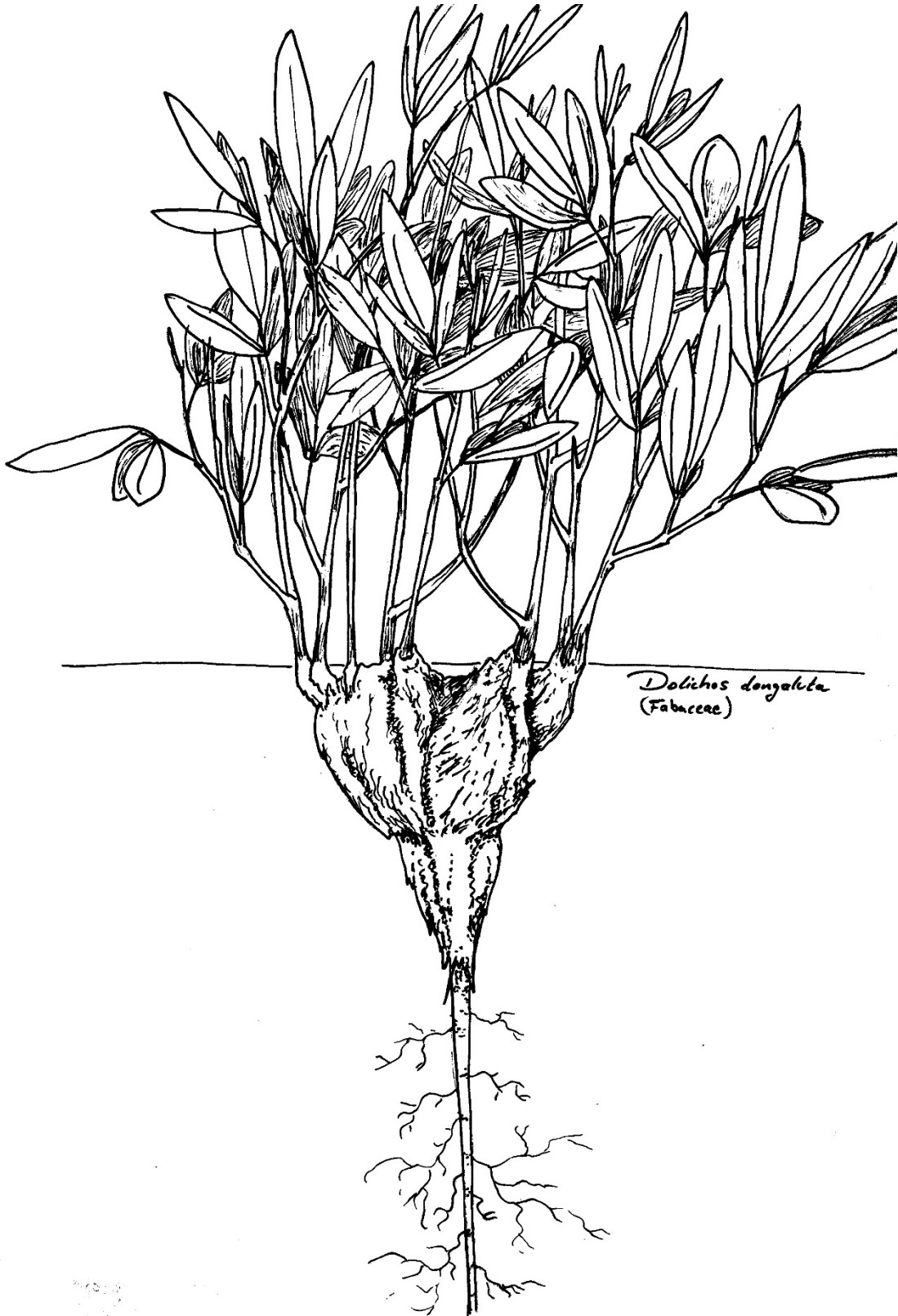
Study region

General

Geoxyles occur in a range of suitable habitats in the tropics around the world. Their probably best studied hotspot of diversity and distribution is the Zambezian phytochorion, or Zambezian Floristic Region (ZFR) in South-central Africa (White, 1976, 1983a, 1993). Being the focal study area of my thesis, I will here give an overarching overview on the environmental conditions in this area, before providing more local site descriptions in the respective chapters. The ZFR occupies large parts of Angola, D.R. Congo, Malawi, Mozambique, Tanzania, Zambia and Zimbabwe, and reaches the more humid, northern regions of Namibia, Botswana and South Africa (**Fig. 2.1**). It covers ca 4.2 mio km² in total and hosts the largest and most diverse share of species of all Afrotropical realms (MacKinnon & MacKinnon, 1986), approximately 8500 plant species of which 54% are endemic to the region (White, 1983). By 2020, the region is also settled by ca 180 million people, with a very uneven population density (**Fig. 2.2**). Urban areas and their surrounding are inhabited most densely, whereas rural areas, particularly in the western and north-eastern part, are scarcely populated. The people of the ZFR depend highly on natural resources, up to 80% extract these resources for income, housing, energy, water and/or alimentation (Fedele *et al.,* 2021).
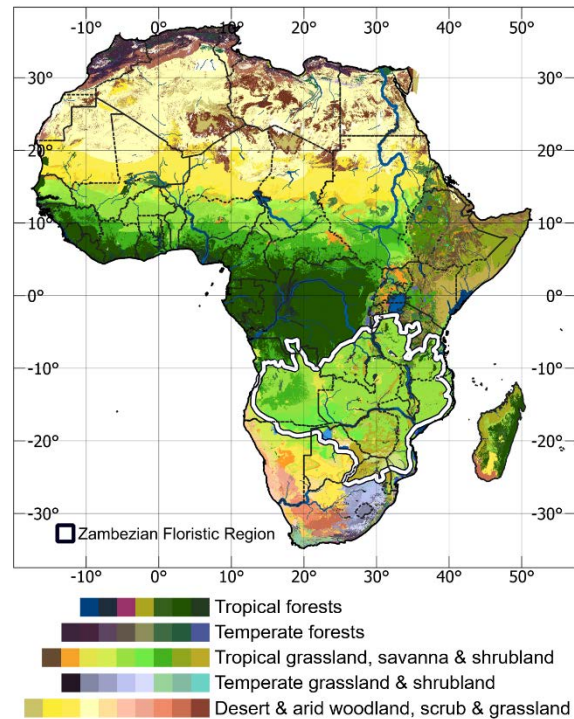
Figure 2.1 Vegetation macro groups of Africa based on Sayre et al. (2013), with the extent of the Zambezian Floristic Region. Plotted with QGIS 3.10.14
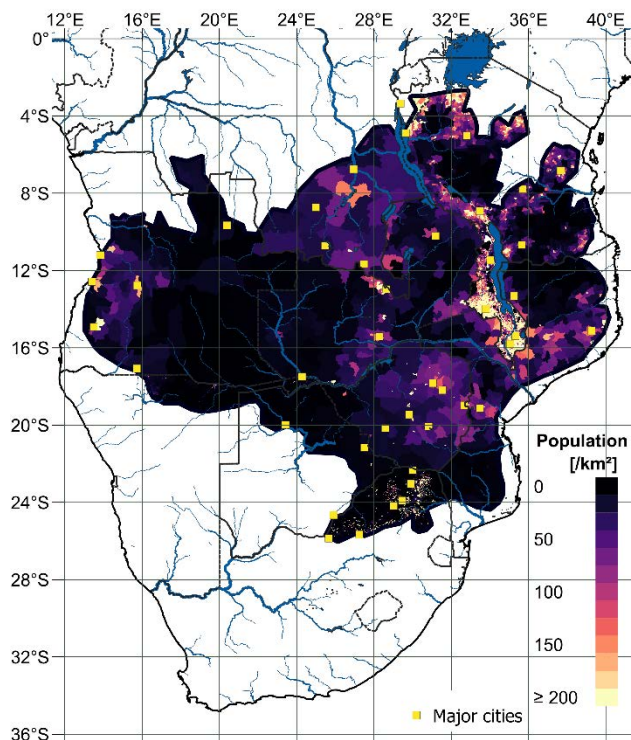
Figure 2.2 Human population density per km² across the Zambezian Floristic Region in 2020, with indication of major urban areas. The overall population in the area accounts to ca 180 mio people. Population data derived from GPWv4 (2021) and plotted with QGIS v3.10.14.

Climate

The ZFR is characterized by a seasonal climate with a pronounced summer rainy season of 5 – 6 months (November to March), and a pronounced winter dry season of 4 – 5 months (May - September), with transitions in April and October, respectively. There is a precipitation gradient from the south-west (maximum 600 mm/y) to the north-east (maximum ≥1500 mm/y), but the biodiverse core of the ZFR thrives at 1000 – 1200 mm/y (**Fig. 2.3**). Mean annual temperature ranges from 12°C to 27°C, whereby the lower average temperatures occur at higher elevations (**Fig. 2.4**). The average temperature however masks the strong seasonal and daily amplitudes of temperature. While the rainy season is warm (> 20°C), with less temperature variation throughout the day, the first half of the dry season is characterized by hot days (> 30°C) and cold nights, with rare to frequent nocturnal frost events, depending on the topography and tree cover (Finckh *et al.*, 2021). Nocturnal temperatures below 0°C are particularly frequent in open grasslands further inland (no oceanic influence), at higher elevations, and in valleys and depressions where the cold air can pool (Willan, 1957) (**Fig. 2.5**). Towards the end of the dry season, nocturnal temperatures rise and it is the hottest period of the year, with both day and night temperatures above 20°C.

Fire regime and herbivory

Anthropogenic fires are very frequent in the ZFR, ca 67% of the area burned at least
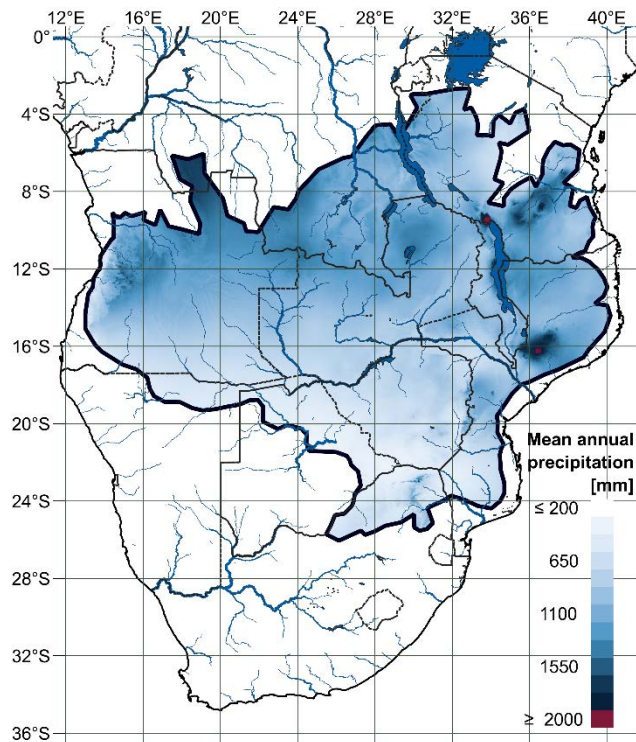
Figure 2.3 Mean annual precipitation across the Zambezian Floristic Region. Precipitation data derived from WorldClim2 (Fick and Hijmans, 2017) and plotted with QGIS v3.10.14.
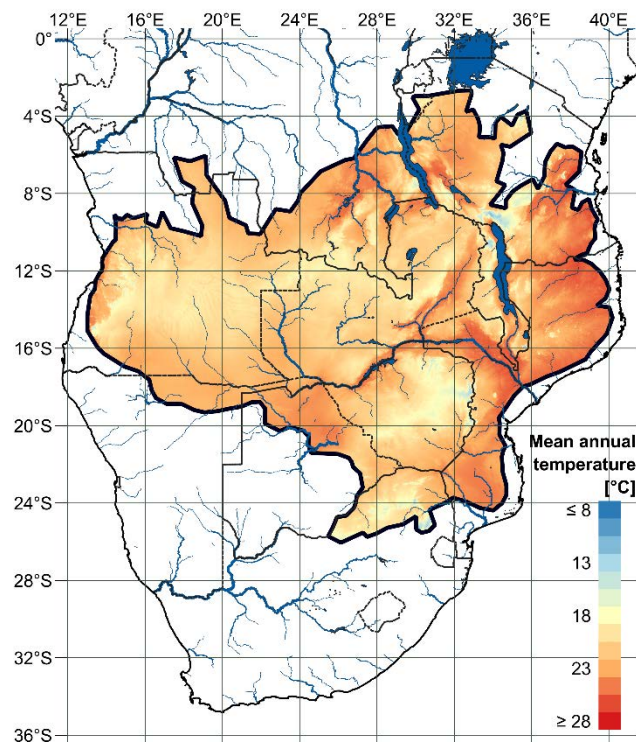
Figure 2.4 Mean annual temperature across the Zambezian Floristic Region. Temperature data derived from WorldClim2 (Fick and Hijmans, 2017) and plotted with QGIS v3.10.14.

19

once over the last 19 years (2000 – 2018) (**Fig. 2.6**). Mostly, fires return once per decade (55% of the area), whereby ca 35% of the area experiences fires at least every 4 years, and 1.2% even every year. Particularly grasslands are burned annually (personal observation). People use fires for different purposes, hence fires are also ignited in different seasons. Early in the dry season (June, July), the surroundings of villages are burned for better overview and security, and grasslands are burned to facilitate hunting. Later on at the end of the dry season (September/October), crop fields are prepared in woodlands using slash-and-burn practices, and grasslands in the southern regions are burned to promote grass regrowth for livestock fodder. Since the vegetation is much drier then than at the start of the dry season, these fires often escape and can affect the woodlands severely. Natural fires caused by lightning strikes may happen, but very rarely and certainly do not define or control the current fire regime.

Impact of wild (mega)herbivores and of livestock is heterogeneous throughout the region. Elephants for instance potentially occur in the whole region, but play a major role for vegetation structure rather in drier parts and larger protected areas of the ZFR, e.g. Zimbabwe (Mapaure & Campbell, 2002). Some areas are reported to host low densities of wild herbivores, like the Bié Plateau in Angola (Huntley *et al.*, 2019), whereas others like the Liuwa Plains National Park in Zambia (Creel *et al.*, 2017) are teeming with wildlife, which nowadays
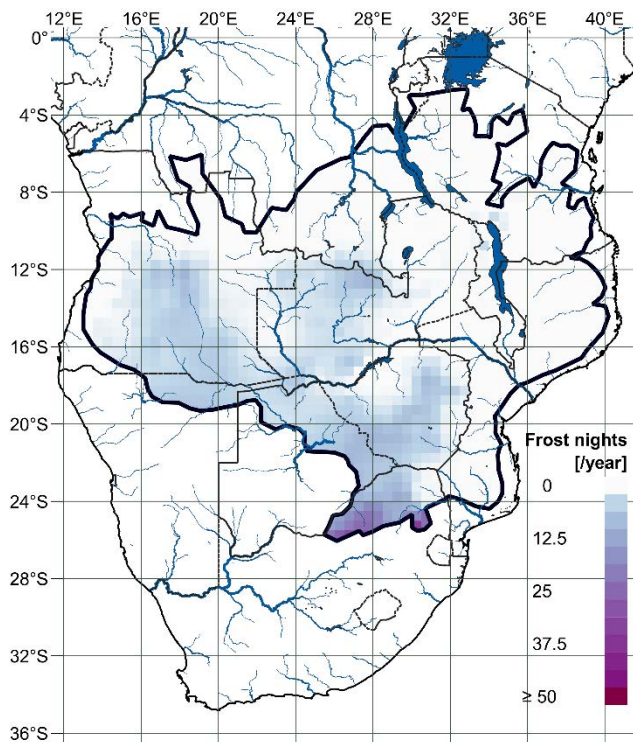
Figure 2.5 Frost nights per year across the Zambezian Floristic Region. Annual average calculated upon the number of frost events from 1969 - 2019. Frost data derived from CRU TS v4.04 (Harris et al.. 2020) and plotted with QGIS v3.10.14.
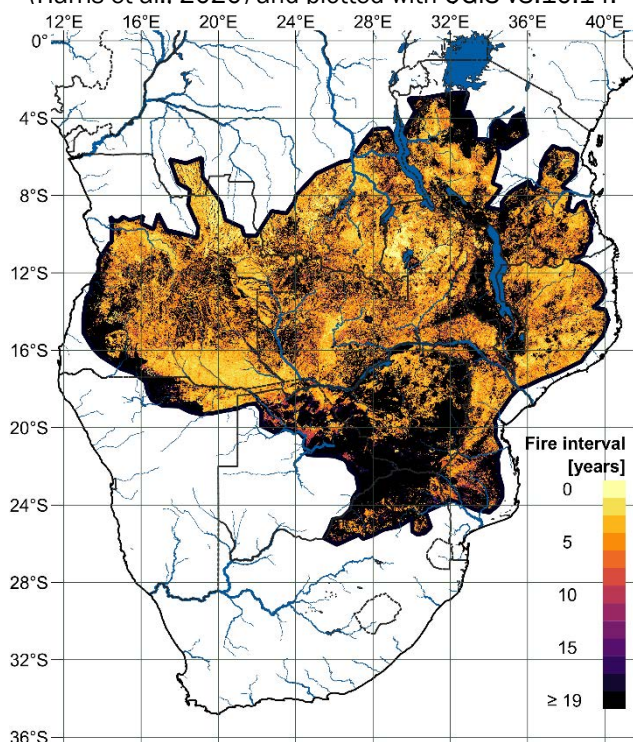
Figure 2.6 Interval between two fires in years across the Zambezian Floristic Region. The observation period is 2000 – 2018, the maximum interval is thus 19 years. Data derived from Burned Area Product MCD64A1 collection 6 (Giglio *et al.*, 2015), processed according to Stellmes *et al.* (2013a), and plotted with QGIS v3.10.14.

is also an aspect of land and conservation management. A far greater impact on vegetation is presented in parts of the ZFR by domestic livestock, including transformations of woodlands or grasslands to rangeland (Nduwamungu *et al.*, 2008), or unsustainable stocking densities threatening the provision of important ecosystem services (Ruvuga *et al.*, 2019).

Elevation, lithography and soils

The ZFR is situated on the Central African plateau, mostly between 800 m and 1500 m altitude (**Fig. 2.7**). However, it reaches elevations above 2000 m along its western border, the Angolan Escarpment, and up to 3000 m in the north-east, which is part of the Rift valley system. It also extends towards the coastal plains in the east, descending down to 200 m. Except for the parts situated at higher elevations (≥ 1800 m), which can be rugged, or Inselbergs, the landscapes are more or less undulating over large areas and interwoven with drainage lines. The high elevation sites of the ZFR are based on hard, durable substrates (**Fig. 2.8**): by plutonic or metamorphic bedrock in its western part, and by volcanic or plutonic bedrock in the eastern part. The central, lower lying part is dominated by softer sedimentary substrates, as are the courses of major rivers (Zambezi) and the eastern coastal plains. The soils overlying the sedimentary substrates (**Fig. 2.9**) are majorly Ferralsols, which cover about one third of the area in the northern ZFR (haplic: 31.8%; acric:
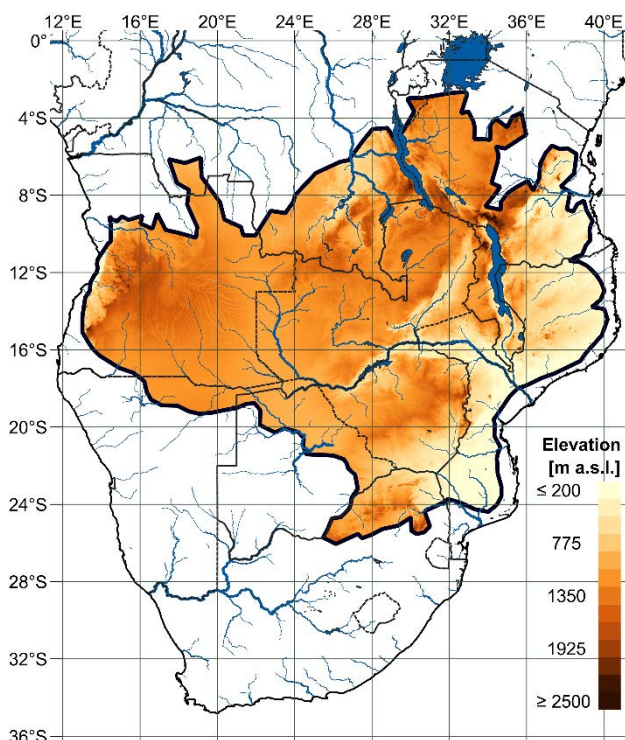
Figure 2.7 Elevation across the Zambezian Floristic Region. Data derived from the Digital Elevation Model CGIAR CSI SRTM (Jarvis et al., 2008) and plotted with QGIS v3.10.14.
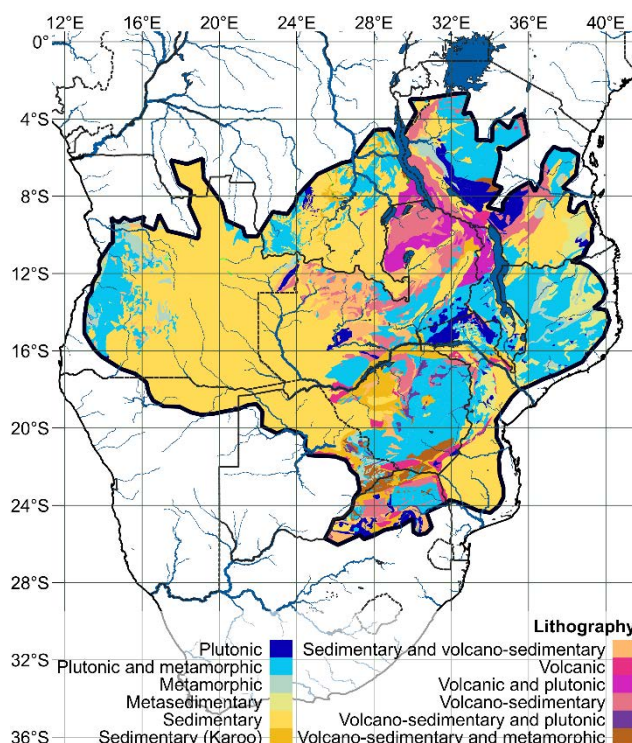
Figure 2.8 Lithography across the Zambezian Floristic Region. Data derived from the Carte géologique de l'Afrique (BRGM, 2016) and plotted with QGIS v3.10.14.

5.4%), and Arenosols (ferralic: 10.6%; haplic: 8.3%), which are very pronounced in the western part of the ZFR, where they are part of the Kalahari Sand Sea (Thomas & Shaw, 1993). The more heterogeneous and more diverse substrates in the eastern part of the ZFR are intermingled and form a complex mosaic that reflects the geologically active zone of the Rift valley system (McConnell, 1972). The overlying soils are similarily heterogeneous, but dominated by Lixisols (19.5% of the ZFR) and Luvisols (9.4% of the ZFR). Further minor soiltypes are present in the area as well, e.g. Podzols in the Barotse Plains in Western Zambia. Most soil types in the ZFR are nutrient poor, acidic and low in exchangeable bases and organic matter (Cole, 1963; Timberlake & Chidumayo, 2011).

Vegetation types

Natural vegetation within the ZFR is controlled by precipitation, soil substrates and hydrology, and by disturbances including fire, frost and herbivory. However, human population density and subsequent land use practices and their intensity, like charcoal production, shifting cultivation, commercial farming, mining, or urbanisation alter natural vegetation patterns increasingly (Wallenfang *et al.*, 2015; Catarino *et al.*, 2020; Wilson & Scholes, 2020; Malunga *et al.*, 2021). Climate change is adding to this increasingly, too (Jinga & Ashley, 2019; Jinga & Palagi, 2020). Until now, miombo woodlands cover most of the area (areas of higher tree cover in **Fig. 2.10**), also owing
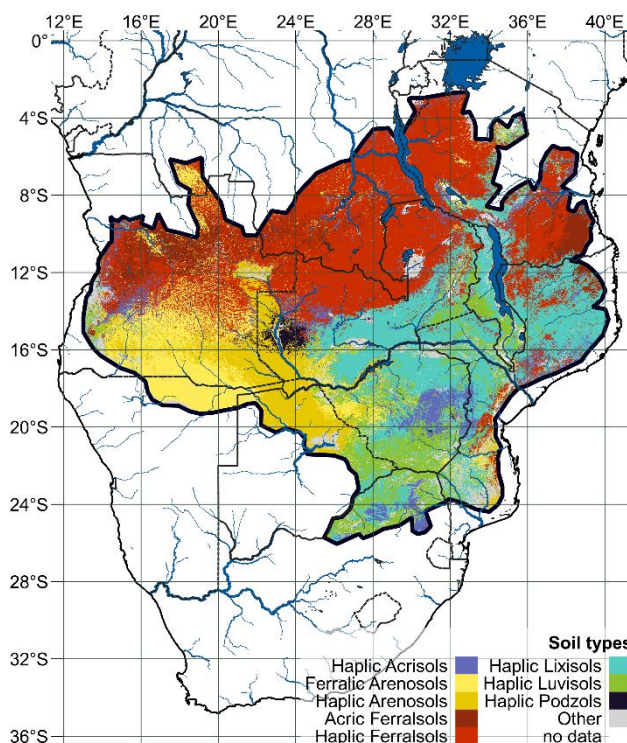
Figure 2.9 Soil types across the Zambezian Floristic Region. Data derived from the World Reference Base (WRB) Soil classification as included in SoilGrids250m (Hengl *et al.*, 2017a) and plotted with QGIS v3.10.14.
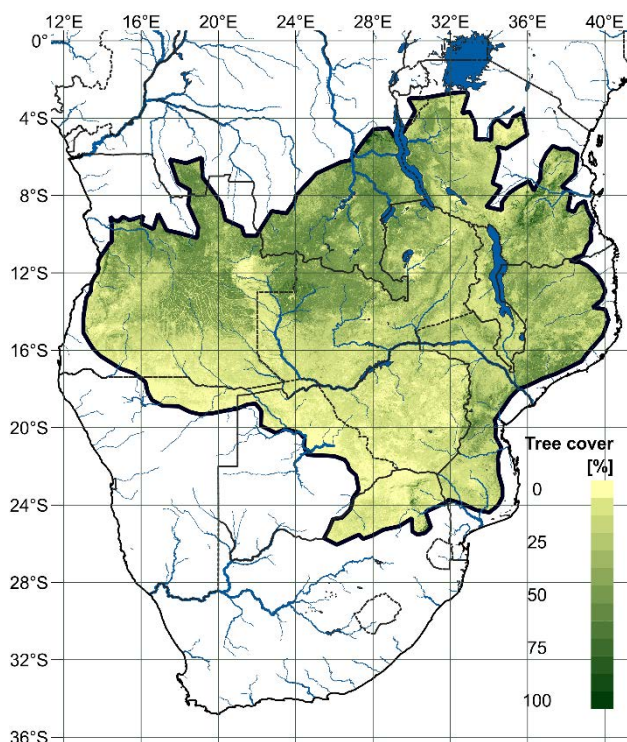
Figure 2.10 Tree canopy cover (canopy closure of vegetation ≥ 5 m height) across the Zambezian Floristic Region in 2000. Data derived from the Global Forest Extent based on Landsat (Hansen et al., 2013) and plotted with QGIS v3.10.14.

22

the main part of the ZFR the name "Miombo ecoregion". These woodlands are dominated by Fabaceae tree species, particularly of the subfamily Detarioideae. They are characterized by trees of the genera *Brachystegia*, *Julbernardia,* and *Isoberlinia*. In fact, "miombo" is the name for *Brachystegia* trees in local languages. The conspicuous dominance and abundance of these trees is attributed to their ectomycorrhizal associations, which are strong assets in the nutrient-poor soils of the ZFR (see above). Areas with less than 1000 mm precipitation per year are regarded as dry miombo, they are found in the south and east of the ZFR, whereas wet miombo (precipitation > 1000 mm/y) is richer, more biodiverse and occurs in the north-west (see **Fig. 2.3**). The western, less humid areas of the ZFR (600 – 800 mm/y) are covered by *Baikiaea* woodlands, and further to the south and east, where precipitation is even less (400 – 800 mm/y), mopane and mixed woodlands are dominant. The most humid and most elevated parts of the ZFR, along the Rift Valley system in the east, are covered by evergreen montane forests and forest-grassland mosaics. Evergreen dry forests dominated by *Cryptosepalum* trees occur in the upper Zambezi, Kubango and Kuito catchments, and riparian forests are common along watercourses.

Areas of higher tree cover are interspersed with open grasslands, ecotones, or wetlands, often forming small-scale mosaic landscapes. The more open areas are home to a high diversity of plants, and among them geoxyles. Different sets of drivers promote these open landscapes, even though the dominant narrative is that ancient fire regimes, which are anthropogenic either way, are the primary cause (Bond & Keeley, 2005). Alternative causes for open grassland can be when soils are waterlogged (so called dambos) or seasonally flooded (Fynn *et al.*, 2015; Zigelski *et al.*, 2018) which occur throughout the ZFR, and allow for small-scale coexistence of various plant functional groups. For instance, (semi-)aquatic plants (*Eleocharis* spp., *Eriocaulon* spp.) and nutrient specialists (*Utricularia* spp., *Drosera* spp.) occur in the deepest, inundated zones, transitioning to drier slopes characterized by C4 grasses (e.g. *Andropogon eucomus*), geophytic herbs (*Hypoxis* spp., *Gladiolus* spp.), and geoxyles (e.g. S*yzygium guineense* subsp. *huillense*).

The Copperbelt in northwest Zambia and Katanga area in southern DR Congo contain grasslands caused by and adapted to high content of (toxic) metals in the soil, particularly copper and cobalt (Brooks et al., 1985). Many plant species, of which some are geoxyles, occur there and are specifically adapted to the metal-rich soil conditions, being endemic to the region. These specialists are often recognizable by their species names, e.g. *Acalypha cupricula*, *Crotalaria cobalticola*, *Ocimum metallorum*).

Other geographically restricted and endemism-rich grasslands occur in highland areas. Afromontane grasslands occur above an upper treeline, for instance along the Angolan escarpment in the west (exemplary endemic species: *Stomatanthes tundavalaensis*) (Hind & Goyder, 2014), or on plateaus in the eastern part of the ZFR (Nyika plateau, *Plecthranthus acaulis*) (Burrows & Willis, 2005). However, in highland areas on the central Angolan plateau, grasslands also occur below a lower treeline, on slopes and in valleys that are subject to frequent frosts (Finckh *et al.*, 2016).

The different types of grassland in South-central Africa, their distinct geoxyle communities, and environmental drivers will be illustrated and discussed in the following chapters.
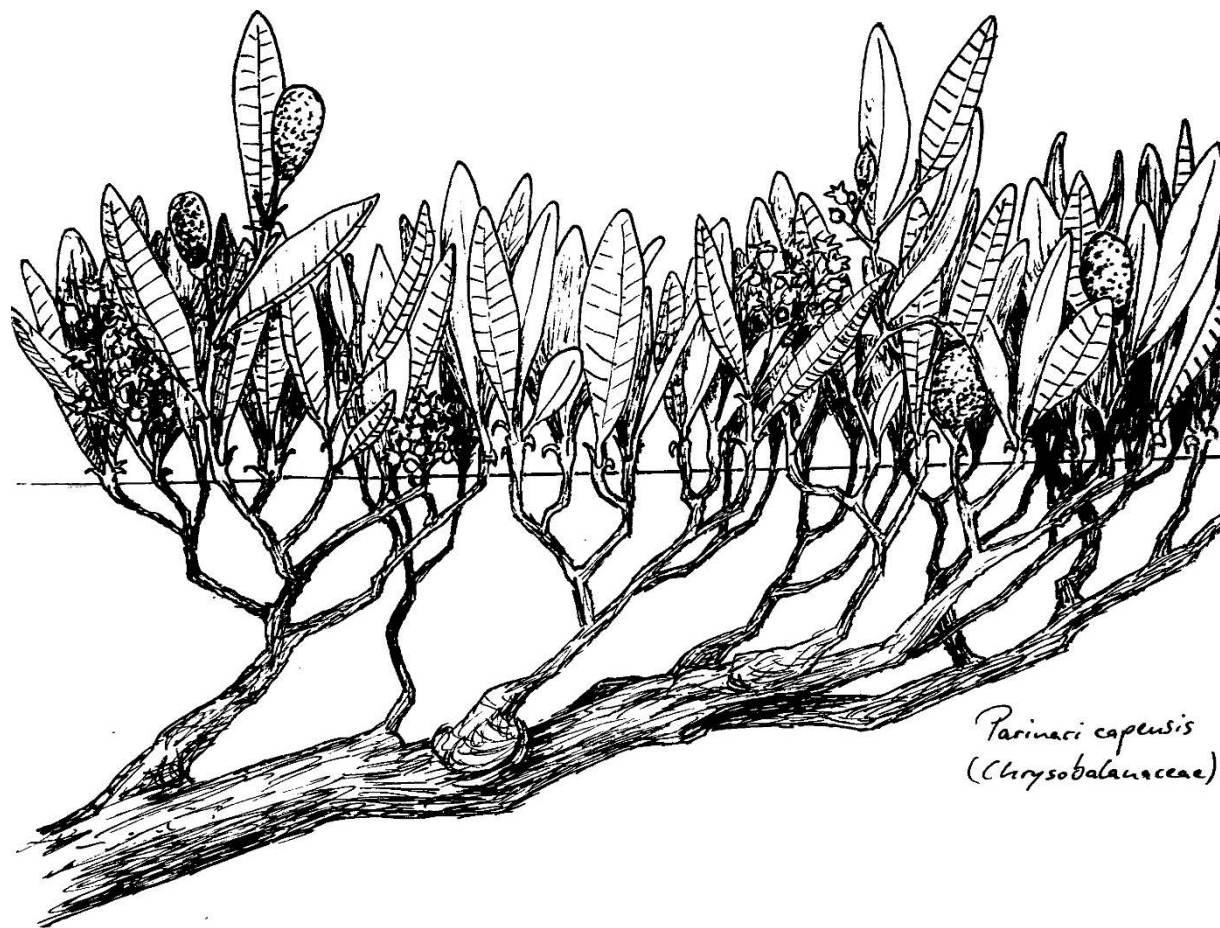
Parinari capensis
(Chrysobalanaceae)

Suffrutex dominated ecosystems in Angola

Paulina Zigelski, Amândio Gomes & Manfred Finckh

Abstract

A small-scale mosaic of miombo woodlands and open, seasonally inundated grasslands is a typical aspect of the Zambezian 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 Zambezian 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 Zambezian 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' (Burtt 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 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/fruiting 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 psammoferralitic 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 fruiting 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 (1983a), however, mapped and described only the sandy 'Chanas' as 'Kalahari and dambo-edge suffrutex grassland' in the context of the 'Zambezian 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 *Brachystegia russelliae* or *Cryptosepalum maraviense* in his suffrutex list. He certainly recognises a transition zone between Zambezian and Guineo-Congolian floras that spans over central and northern Angola (where the 'Anharas' are included) (White, 1983a). However, he did not recognise the importance and floristic singularity of the ferralitic suffrutex-grasslands dominated by *Brachystegia* or *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 Zambezian 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 & Gonçalves, 2019). In some cases suffrutices are considered a dwarf variety or subspecies of a closely related tree species (e.g. *Gymnosporia 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 Zambezian phytochorion, the Rubiaceae have the highest number of described taxa (46), followed by Anacardiaceae (22) and Lamiaceae (14). **Tab. 3.1** lists all families with known geoxylic suffrutex taxa occurring in Angola and gives examples of common geoxyles for each family. Furthermore, **Fig. 3.1** shows some examples and aspects of suffrutex species given in **Tab. 3.1**. The unique Zambezian geoxylic flora with a high number of endemic species (Brenan, 1978; White, 1983a; 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 (**Tab. 3.1**), 121 of the 198 suffrutex species occurring in the Zambezian phytochorion are known from Angola (61%). Of these 121 species 12 are endemic to Angola (10%).

Table 3.1 List of plant families with geoxylic suffrutices in the Zambezian phytochorion Plant family N° Species common in Angola Angolan endemics

Plant family	N°	Species common in Angola	Angolan endemics
Rubiaceae	46	*Pygmaeothamnus zeyheri* (Sond.) Robyns, *Pachystigma pygmaeum* (Schltr.) Robyns	2, e.g. *Leptactina prostrata*
Anacardiaceae	22	*Lannea edulis* (Sond.) Engl., *Rhus arenaria* Engl.	3, e.g. *Lannea gossweileri*
Lamiaceae	14	*Clerodendrum ternatum* Schinz, *Vitex madiensis* ssp. *milanjensis* (Britten) F.White	
Fabaceae-Papilionioideae	13	*Erythrina baumii* Harms, *Abrus melanospermum* ssp. *suffruticosus* Hassk.	3, e.g. *Adenodolichos mendesii*
Proteaceae	11	*Protea micans* ssp. *trichophylla* (Engl. & Gilg) Chisumpa & Brummitt,	1, *Protea paludosa* (Hiern) Engl.
Ochnaceae	9	*Ochna arenaria* De Wild. & T.Durand, *Ochna manikensis* De Wild.	
Passifloraceae	7	*Paropsia brazzaeana* Baill.	
Fabaceae-Detarioideae	6	*Brachystegia russelliae* I.M.Johnst., *Cryptosepalum* sp. nov.	
Apocynaceae	5	*Chamaeclitandra henriquesiana* (Hallier f.) Pichon	1, *Landolphia gossweileri*
Ebenaceae	5	*Diospyros chamaethamnus* Mildbr, *Euclea crispa* (Thunb.) Gürke	
Celastraceae	4	*Gymnosporia senegalensis* var. *stuhlmanniana* Loes.	
Dichapetalaceae	4	*Dichapetalum cymosum* (Hook.) Engl.	
Fabaceae-Caesalpinioideae	4	*Entada arenaria* Schinz	
Myrtaceae	4	*Syzygium guineense* ssp. *huillense* , (Hiern) F.White *Eugenia malangensis* (O.Hoffm.) Nied.	
Tiliaceae	4	*Grewia herbaceae* Hiern	
Combretaceae	3	*Combretum platypetalum* Welw. ex M.A.Lawson	2, e.g. *Combretum argyrotrichum*
Euphorbiaceae	3	*Sclerocroton oblongifolius* (Müll.Arg.) Kruijt & Roebers	
Loganiaceae	3	*Strychnos gossweileri* Exell	
Annonaceae	2	*Annona stenophylla* ssp. *nana* (Exell) N.Robson	
Apiaceae	2	*Steganotaenia hockii* (C. Norman) C. Norman	
Chrysobalanaceae	2	*Parinari capensis* Harv., *Magnistipula sapinii* De Wild.	
Meliaceae	2	*Trichilia quadrivalvis* C.DC.	
Moraceae	2	*Ficus pygmaea* Welw. ex Hiern	
Myricaceae	2	*Morella serrata* (Lam.) Killick	
Phyllanthaceae	2	*Phyllanthus welwitschianus* Müll.Arg.	
Ranunculaceae	2	*Clematis villosa* DC.	
Achariaceae	1	*Caloncoba suffruticosa* (Milne-Redh.) Exell & Sleumer	
Anisophyllaceae	1	*Anisophyllea quangensis* Engl. ex Henriq.	
Clusiaceae	1	*Garcinia buchneri* Engl.	
Dilleniaceae	1	*Tetracera masuiana* De Wild. & T.Durand	
Fabaceae-Cercioideae	1	*Bauhinia mendoncae* Torre & Hillc.	
Hypericaceae	1	*Psorosperum mechowii* Engl.	
Ixonanthaceae	1	*Phyllocosmus lemaireanus* (De Wild. & T.Durand) T.Durand & H.Durand	
Lecythidaceae	1	*Napoleonaea gossweileri* Baker f.	
Linaceae	1	*Hugonia gossweileri* Baker f. & Exell	
Malpighiaceae	1	*Sphedamnocarpus angolensis* (A.Juss.) Planch. ex Oliv.	
Malvaceae	1	*Hibiscus rhodanthus* Gürke	
Melastomaceae	1	*Heterotis canescens* (E. Mey. ex Graham) Jacq.-Fél.	
Picrodendraceae	1	*Oldfieldia dactylophylla* (Welw. ex Oliv.) J.Léonard	
Rhamnaceae	1	*Ziziphus zeyheriana* Sond.	
Urticaceae	1	*Pouzolzia parasitica* (Forssk.) Schweinf.	

Figure 3.1 Common Angolan suffrutex species. (a) *Ochna arenaria* (Ochnaceae), fruiting and growing on sandy sediments of the Bíe Plateau. (b) *Syzygium guineense* subsp. *huillense* (Myrtaceae) flowering in the dry season and growing on sandy soils of the Bíe 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 Bíe Plateau and bearing edible fruits. (f) *Phyllanthus welwitschianus* (Phyllanthaceae), growing on sandy soils of the Bíe Plateau and flowering in the rainy season. (g) *Cryptosepalum* sp. nov. (Fabaceae – Detarioideae) with excavated rootstocks, typical element of the 'Anharas de Ongote', growing on psammoferralitic soils of the Bíe 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

Figure 3.2 Typical geoxylic 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 Bíe Plateau, in August. The mid- and footslopes are dominated by suffrutex-grassland with the characteristic reddish and green patches of the fresh leaves of *Brachystegia russelliae* whereas the wetlands in the drainage lines are covered mostly by Cyperaceae (background, in dark green).

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 Moxíco province or as sandy alluvial deposits on fossil river terraces along the valleys of the southern slopes of the Angolan plateau (**Fig. 3.2a**); (b) on psammo-ferralitic plinthisols as they frequently occur on the Bíe 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. 3.2b**).

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 & Preston-Whyte, 2000). As depressions accumulate confluent cold air, the undulating topography of the Angolan highlands facilitates frequent radiation frost especially in valleys (Revermann & 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 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. 3.2a**) 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 & 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 & 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.*, 2013b). C4-savanna grasses, however, respond positively to periodic burning and resprout within weeks (Bond & 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 (**Tab. 3.1**) 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 & 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 & 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* subsp. *huillense*, a suffrutex closely related to a tree species that grows along and in rivers and floodplains (Coates Palgrave, 2002; Meerts & 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 Zambezian phytochorion and suffrutex-grasslands with its unique life forms contribute prominently to its high number of endemic species (Clayton & Cope, 1980; White, 1983). The high degree of suffrutex-grassland endemics within the Zambezian 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 Zambezian 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 sequestrate atmospheric CO_2 (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 Zambezian 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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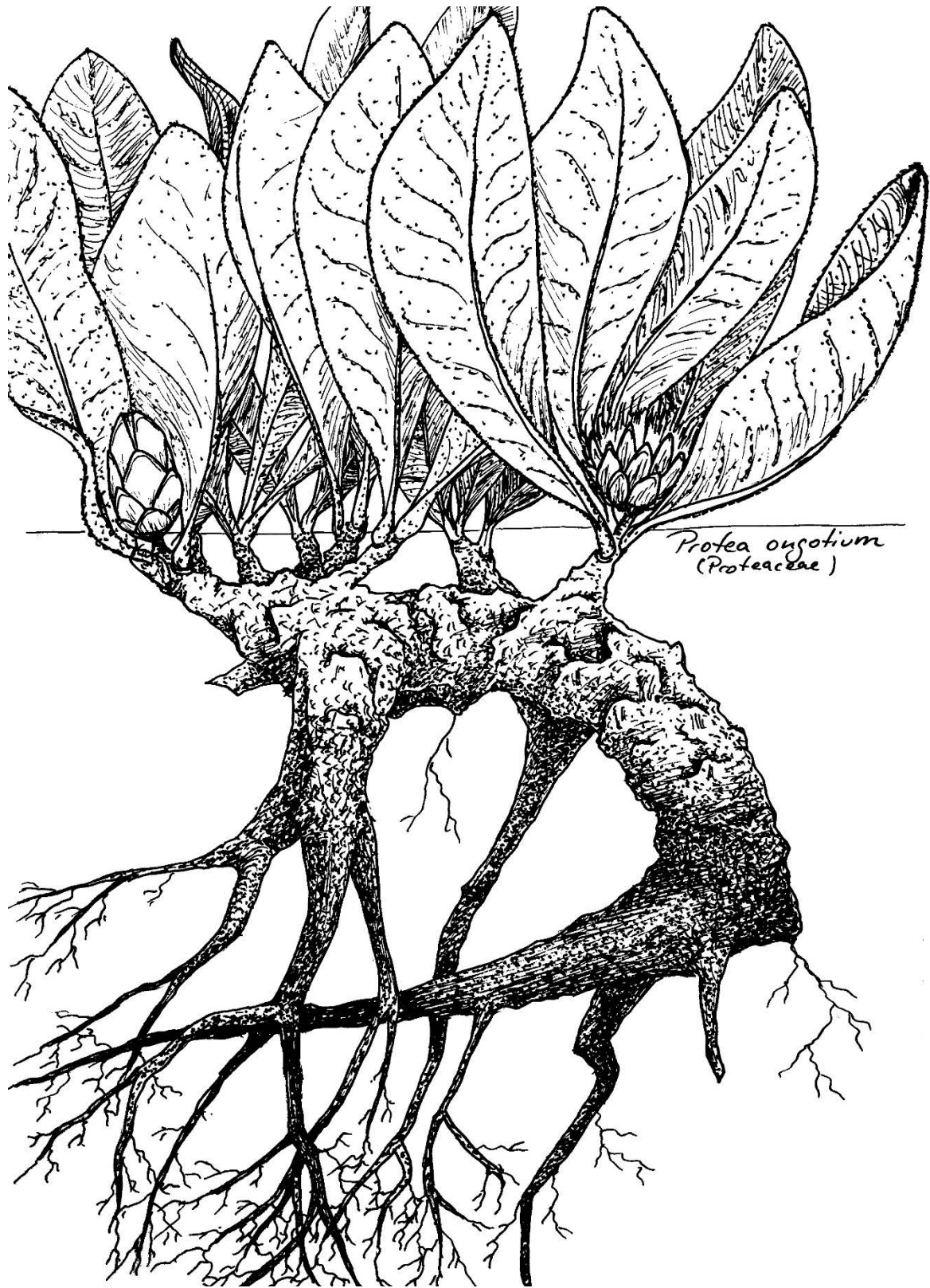
Protea ougotium
(Proteaceae)

High diversity and endemism of geoxylic plants in Angolan highlands: more research and conservation measures are needed

Paulina Meller, Fernanda Lages, Manfred Finckh, Amândio Gomes, David Goyder

Introduction

Geoxylic suffrutices, or geoxyles for short, are woody plants with an eccentric growth form, owing them the name "underground trees", because most woody biomass is underground (White, 1976; Maurin *et al.*, 2014; Pausas *et al.*, 2018; Zigelski *et al.*, 2019) (**Fig. 4.1**). This biomass encompasses roots, woody rhizomes, xylopodia or lignotubers and serves as an underground storage organ and bud bank, which are 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-living 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, can cover the ground densely (Meller *et al.*, 2021a), and reach impressive ages of thousands of years (Alves *et al.*, 2013; Braam Van Wyk, personal communication). Coexistence with grasses is possible because geoxyles begin to resprout and flower in the dry season, well before the grasses do. Due to this asynchronicity in assimilation periods and generative propagation, competition between geoxyles and grasses is reduced (Zigelski *et al.*, 2019). Although geoxyles tend to be overlooked in grasslands due to their lower stature, they contribute strongly to biodiversity, functionality, carbon stocks and 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 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.*, 2021b). Many geoxyles evolved from tree and shrub species (White, 1976; Maurin *et al.*, 2014), and many of them are remarkably similar to closely related tree species regarding morphological traits, 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, so that periodical aboveground disturbances and biomass removal are regarded as a key necessity for their occurrence (Fidelis *et al.*, 2014). Particularly the Cerrado (Brazil) and south-central Africa represent hot spots of diversity and endemism for geoxyles (White 1983; Maurin *et al.* 2014; Pennington and Hughes 2014). The Zambezian phytochorion (phytochorion = centre of endemism (White, 1983)) (**Fig. 4.2a**) with its mosaic of miombo woodlands and

open vegetation types, and particularly the Angolan montane forest-grassland mosaic (Olson *et al.*, 2001) provide ideal conditions for geoxyles in Angola: 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, D.R. Congo, Zimbabwe, Mozambique and Malawi are also rich in geoxyles, whereas most parts of Namibia or Botswana are too arid. Several highland areas in Africa have been reported to harbour endemic geoxyles, e.g. the Nyika Plateau in Malawi (Willis *et al.*, 2001), and the Highveld (Burtt Davy, 1922) and the Cape floristic region of South Africa (Grobler & Cowling, 2021).

According to the catalogue of Angolan plants (Figueiredo & Smith, 2008), our own compilations (Zigelski *et al.,* 2019; Meller *et al.*, 2021b), and research for this chapter, Angola is home to at least 133 different geoxyle species in the strict sense (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", one can count 229 different taxa, 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 western highlands are predominantly composed of different species and endemics than those of the Kalahari sands in the eastern, less elevated parts of Angola. In this chapter, we focus on Angola's endemic geoxyle species that are restricted to the highlands.
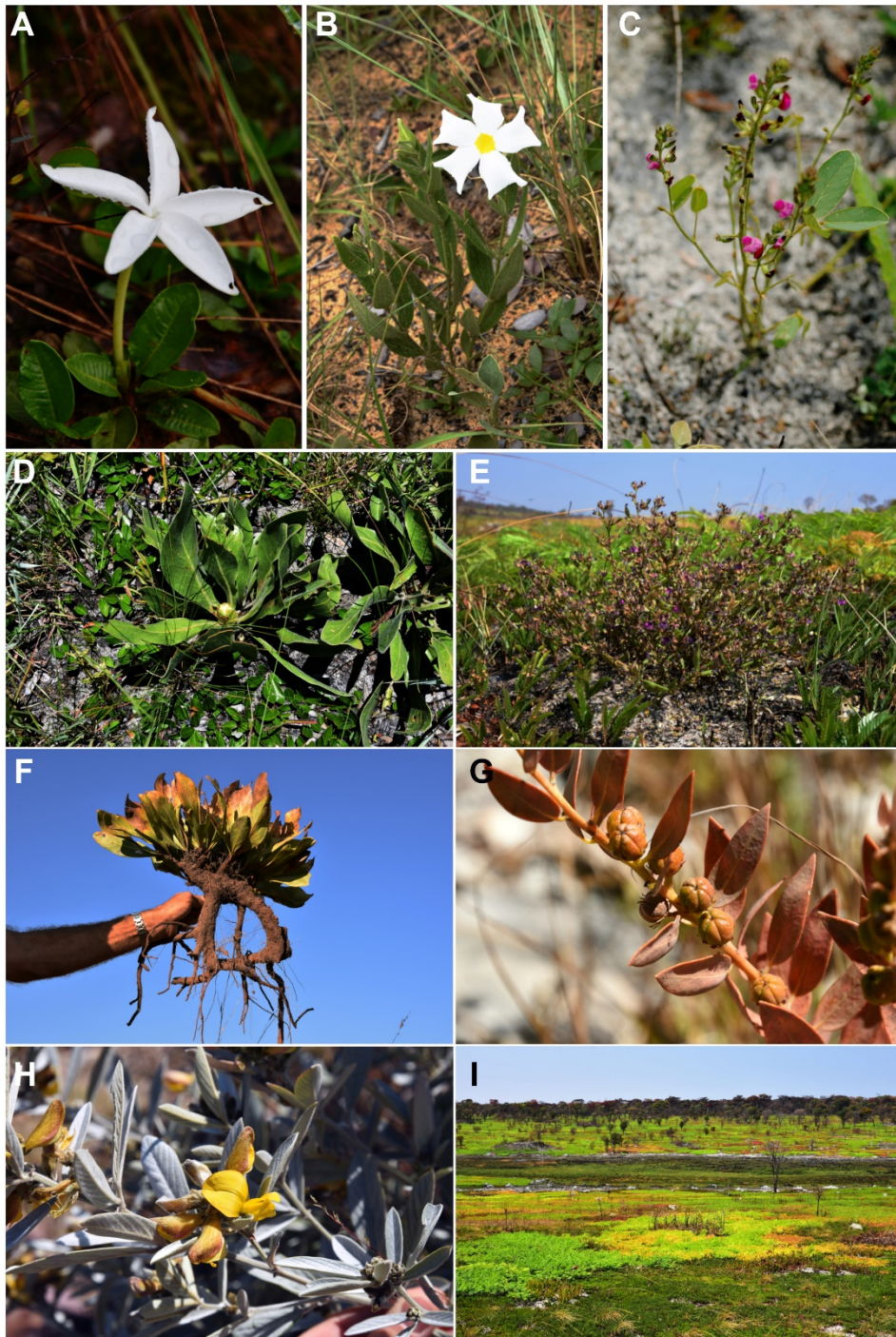
Figure 4.1 (next page): Highland endemic geoxylic plants of Angola. A) *Leptactina prostrata* (Rubiaceae). B) *Thunbergia retefolia* (Acanthaceae). C) *Adenodolichos mendesii* (Fabaceae). D) *Protea ongotium* (Proteaceae). E) *Dolichos dongaluta* (Fabaceae). F) *Protea ongotium* excavated (lignotuber). 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 plateau, end of dry season.

Materials and 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), on own ongoing vegetation surveys conducted in Bié, Huíla, Moxíco and Cuando-Cubango provinces since 2011, and on a thorough search of geoxyle literature (White, 1976; Maurin *et al.*, 2014; Revermann *et al.*, 2017; Goyder *et al.*, 2018; Zigelski *et al.*, 2019). 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 wasn't 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 ("with a woody base") and a stricter definition ("with woody underground organs and with congeneric tree relatives") and enumerated the species accordingly (**Tab. 4.1**). If geoxyle taxa also occur outside of Angola, or if they are endemic to Angola but restricted to the lowlands ($\leq$ 1200 m), they were excluded, leaving us a final list of 126 highland taxa. We retrieved georeferenced occurrence data of these taxa from the Vegetation Database of the Okavango Basin (ID AF-00-009) in the Global Index of Vegetation-Plot Databases (https://www.gvid.info), own vegetation databases from Angolan Biodiversity Observatories (http://www.sasscalobservationnet.org/), from collections stored at the herbarium LUBA in Lubango, Angola, and from GBIF (doi.org/10.15468/dl.43fwmf) (GBIF, 2021). For the two latter we manually added georeferences to entries with precise enough locality descriptions. This way we yielded 1630 entries.

Geoxyle species endemic to the highlands

The result is shown in **Fig. 4.2**, with particular hotspots for highland geoxyles on the escarpment near Lubango, and on the Bié and Huambo plateaus. Although the elevated plateau of (south-)eastern Angola is also particularly rich in geoxyles (Goyder *et al.*, 2018; Zigelski *et al.*, 2018, 2019), its species pool differs from the species occurring in the highlands of central and western Angola, because the highland geoxyles do not extend (much) into the eastern areas (**Fig. 4.2b**). This observation is in accordance with the findings of Linder (2001), who identified two centres of species endemism and diversity in Angola, one extending from central Angola towards the east across Katanga and Zambia, the other on the Huíla plateau.

Meller *et al.* (2021b) have shown that multiple biogeographic origins and environmental heterogeneity promote geoxyle diversity in Angola. 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). Towards the west, altitudes increase, the topography becomes much more rugged, and weathered plinthosols and shallow substrates on unweathered bedrock predominate (Huntley, 2019). (South-)eastern Angola on the other hand is characterized by gently undulating landscapes covered by deep and nutrient poor deposits of Kalahari sand that extend further to the east (Zambia) and south (Namibia, Botswana). Rainfall and its seasonality varies little along the east - west gradient, comprising minimum ~ 800 mm/y for highland specific geoxyles to occur (**Fig. 4.2c**); for grasslands, this implies that fuel loads (cured grasses) are sufficiently abundant throughout, and sufficiently fire prone and fire affected (Govender *et al.*, 2006; Archibald *et al.*, 2010).

However, the exposure to other aboveground disturbances differs along the gradient. The higher lying areas of the Bié, Huíla and Huambo plateaus are prone to localized frequent frosts (up to 40 per year) in the dry season, 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, and particularly in the Pleistocene, the climate in Angola had been even cooler and more arid, which likely entailed increased nocturnal frost events and severity (Demenocal, 1995; Herbert *et al.*, 2016). Strikingly, the highest areas along the western escarpment receive very little frost and then only in enclosed valleys (SASSCAL WeatherNet; personal observations PM, MF), probably due to the mild oceanic influence.

Several ecological theories may help to explain the high number of highland endemic geoxyle taxa in Angola, e.g. because dispersal has been limited in the past (Freestone & Inouye, 2006), because climatic conditions have been stable over a long time (Lovett & Friis, 1996), and/or because soils in highlands are more heterogeneous on the 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. As a result, we observe a considerably higher number of geoxyle taxa endemic to the Angolan highlands (strict sense: 22, broad sense: 50) than of lowland endemic geoxyles (strict sense: 13, broad sense: 25). One has to bear in mind, however, 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 do Lopollo near Lubango) and expedition routes.
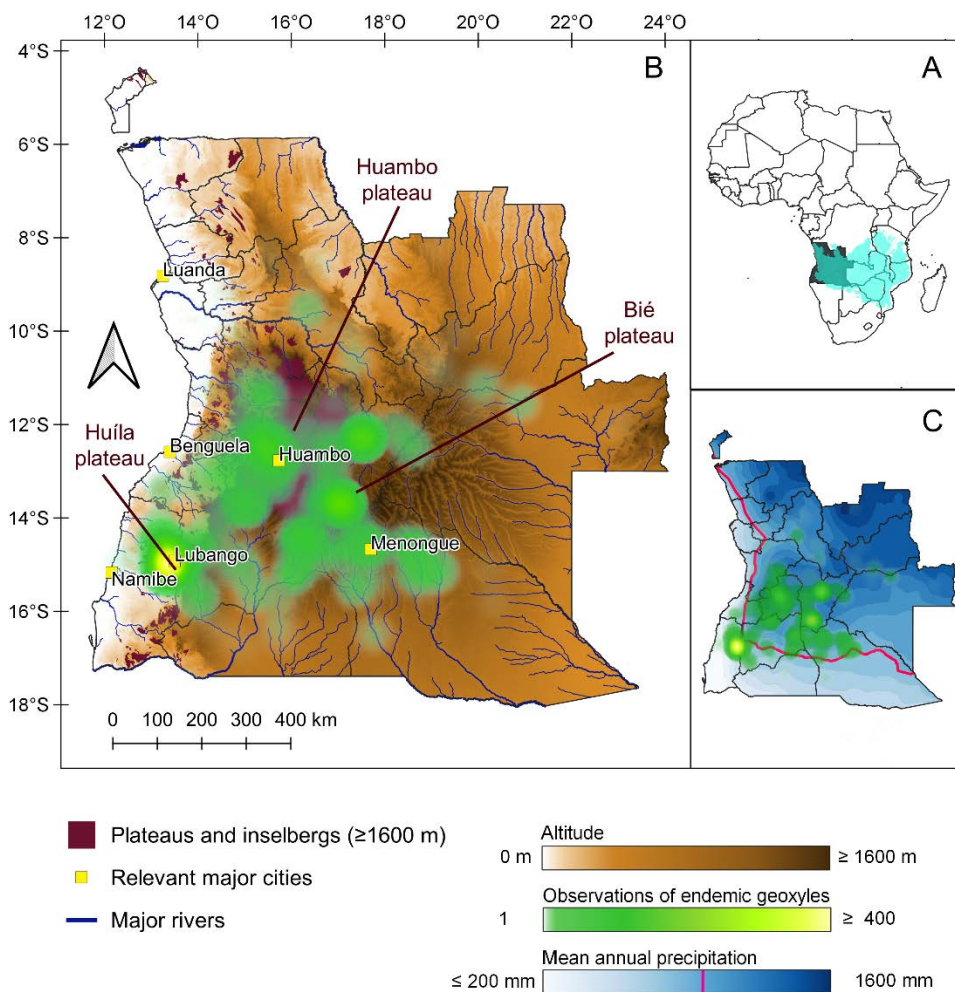
Figure 4.2: Distribution of 126 geoxylic taxa endemic to Angola, occurring in highlands. A) Location of Angola (shaded) and of the Zambezian centre of endemism (phytochorion) (cyan). B) Angola in detail, showing topography with highlighted highlands, and the density of collections and observations of endemic geoxyle taxa. C) Distribution of mean annual precipitation across Angola, overlaid with the same geoxyle density as in B), and showing that highland specific geoxyles do not generally occur where precipitation falls below 800 mm/y (pink line).

Table 4.1: Number of geoxyle taxa endemic to the Angolan highlands (columns 2 and 3) and endemic to Angola but also occurring at lower altitudes (columns 4 and 5). As species descriptions are often vague and insufficient with regard to belowground parts, we compiled the table with increasingly strict definitions of geoxyles. I) taxa with "a woody base" can be termed geoxyles in the broad sense, this group may also include perennial herbs. II) taxa with woody underground storage organs (USO) have a woody base and extended belowground woody structures. III) taxa with tree relatives have a woody base, USOs and congeneric tree relatives; these are geoxyles in the strict sense. We compiled these numbers for Angolan endemic taxa that have been observed only in highlands (≥ 1500 m), and for those that also occur in lower areas.

	Restricted to highlands		Also occurring beyond	
	Number of endemic taxa	From x families	Number of endemic taxa	From x families
With a woody base	91	23	126	23
Of which with a woody USO	50	16	77	16
Of which with tree relatives	22	10	32	13

Table 4.2: Families with most geoxyle taxa. The number of highland endemic geoxyles in families with at least 5 geoxyle taxa is given. For comparison, the total number of geoxyle taxa in these families that occur in Angola (including non-endemics) is given in brackets. Some important geoxyle families don't have (enough) highland endemics and are therefore included in the group "other": Anacardiaceae (11 taxa), Apocynaceae (5 taxa), Ochnaceae (6 taxa) and Proteaceae (9 taxa).

	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)

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 will 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 likewise sufficient to buffer short thermal peaks caused by the passage of fire (Auld & Bradstock, 1996), as well as nocturnal frost pulses of several hours length (Revermann & Finckh, 2013). The soil temperature in 5-10 cm depth only deviates slightly in both cases. However, the geoxyles' location in the topsoil might not protect them from physical impacts. Historically, the Angolan Plateau always had low densities of natural meso- and mega-herbivores (Huntley *et al.*, 2019), which implies that geoxyle grasslands there were probably not heavily affected by grazing or trampling. In Cangandala National Park at the slopes of the Angolan Plateau, herds of Giant Sable antelopes (*Hypotragus niger*) have been seen grazing in geoxyle grasslands after fire, when grasses are rare in dry season (personal observation AG). However, it is yet unclear what effect modern herbivory and trampling by cattle has on geoxyles, particularly regarding land use change from natural grasslands to intensively used rangeland, or transformation of rangelands to agricultural use.

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 will not easily recuperate. Their strategy is to grow slowly, to persist and to reach high ages *(Alves et al.*, 2013; Braam Van Wyk, personal communication), whereas propagation via seeds seems only secondary and little successful, since geoxyle seedlings seem to be very rare (personal observation, PM). This means that even after an agricultural field has been abandoned, it may take a long time for geoxyles to recolonize the area, once their belowground structures are cleared from

it. To date, agriculture in more remote parts of Angola is only starting to become industrialized, 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 reclaim land pervaded by massive belowground woody structures, as seen for instance on the Bié and Huambo plateau (**Fig. 4.3**, personal observation AG, MF, PM).

Figure 4.3: Tractor-ploughed fields in geoxyle grasslands near Chitembo, Bié, appeared in July 2021. The plough is deep and strong enough to destroy the massive belowground geoxyle structures. Such fields are then planted with crops like cassava, maize, or beans.

Analogously, misguided attempts to afforest tropical grasslands in order to sequestrate 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 were left unharmed, once they are overshadowed by trees, the shade-intolerant geoxyles would rapidly become outcompeted (Zaloumis & Bond, 2016; Buisson *et al.*, 2019). Like intensified agriculture, this would destroy biodiverse, old-growth natural grasslands (Bond, 2016).

It becomes clear that geoxylic species face imminent threats in Angola due to accelerating land use change and intensification. The still insufficiently understood geoxyle diversity makes it difficult to estimate specific conservation needs, because many geoxyle species are poorly known and/or described, and 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 in the Angolan highlands, 119 taxa (94.4%) are either data deficient or not assessed. The high rate of localized endemics facing land use intensification, however, lets us expect a substantial threat to at least some of the geoxylic species, e.g. to *Barleria kacondensis* subsp *glabrescens* (EN B1ab(iii)) (Darbyshire *et al.*, 2021) or *Bolusia ervoides* ("rare species and is known from only few collections") (Van Wyk *et al.*, 2010).

1   **Table 4.3:** Endemic geoxyle taxa occurring in the Angolan highlands. Only taxa with a congeneric tree relative are listed here, a full list of endemic geoxyle taxa is provided
2   in **Table S4.1**. For orientation it is annotated whether they are strictly highland endemic, and whether they are geoxyles in a broad sense (with a woody base), or stricter
3   sense (with a woody USO). Close tree relatives from Southern-Central Africa are also provided, however, since phylogenetic studies are lacking for most geoxyle taxa, the
4   tree taxa here should be regarded as examples, not necessarily as the truly closest tree relative. Where species are restricted to particular plateaus, escarpments or
5   localities these are outlined; wider distributions within Angola are presented as an alphabetical list of provinces abbreviated as follows BE – Benguela, BI – Bié, CC –
6   Cuando-Cubango, CN – Cuanza Norte, CS – Cuanza Sul, CU – Cunene, HU – Huambo, HI – Huíla, LS – Lunda Sul, MA – Malange, MO – Moxíco, and NA – Namibe.

Taxon	Family	Distribution	Woody USO	Highland endemic	Close tree relative(s)
Baphia sp. nov.	Fabaceae	CC, BI, MO	x		*Baphia bequaertii*
Clutia benguelensis Müll.Arg.	Euphorbiaceae	BE, BI, HI, HU	x	x	*Clutia abyssinica*
Combretum argyrotrichum Welw. ex M.A.Lawson	Combretaceae	HU plateau, HI escarpment	x	x	*Combretum zeyheri*
Combretum viscosum Exell	Combretaceae	BE, BI, HI, HU	x	x	
Cryptosepalum sp. nov. aff. *maraviense*	Fabaceae	BI plateau	x	x	*Cryptosepalum exfoliatum*
Dissotis benguellensis A.Fern. & R.Fern.	Melastomataceae	HU, Serra de Moco		x	*Dissotis melleri*
Dissotis carrissoi A.Fern. & R.Fern.	Melastomataceae	CS, Huambo			
Erythrina pygmaea Torre	Fabaceae	HI plateau	x	x	*Erythrina abyssinica*
Euclea angolensis Gürke	Ebenaceae	HI plateau	x	x	*Euclea divinorum*
Euphorbia asclepiadea Milne-Redh.	Euphorbiaceae	BI plateau			*Euphorbia matabelensis*
Euphorbia parifolia N.E.Br.	Euphorbiaceae	HI escarpment, Tundavala	x	x	
Fadogia caespitosa Robyns	Rubiaceae	HI plateau	x		*Fadogia erythroploea*
Fadogia chrysantha K.Schum.	Rubiaceae	HU plateau	x	x	
Fadogia graminea Wernham	Rubiaceae	BI plateau	x		
Fadogia punctulata Robyns	Rubiaceae	HU plateau	x	x	
Fadogia stenophylla Welw. ex Hiern	Rubiaceae	HI escarpment, Lubango	x		
Gnidia fruticulosa Gilg	Thymelaeaceae	HI plateau		x	*Gnidia glauca*
Gnidia newtonii Gilg	Thymelaeaceae	HI escarpment, Humpata		x	
Gnidia rendlei Hiern	Thymelaeaceae	HI escarpment, Mumpulla		x	
Gnidia welwitschii Hiern	Thymelaeaceae	HI escarpment, Humpata		x	

Grewia suffruticosa K.Schum.	Malvaceae	HI plateau	x	x	*Grewia bicolor*
Hypericum abilianum N.Robson	Hypericaceae	HI escarpment, Humpata		x	*Hypericum roeperianum*
Julbernardia gossweileri (Baker f.) Torre & Hillc.	Fabaceae	CC, HI, HU, MA	x		*Julbernardia paniculatum*
Lannea gossweileri Exell & Mendonça	Anacardiaceae	BI plateau	x	x	*Lannea discolor*
Lannea rubra Hiern (Engl.)	Anacardiaceae	HI escarpment, Tundavala	x	x	
Leptactina prostrata K.Schum.	Rubiaceae	BI plateau, MO	x		*Leptactina platyphylla*
Ozoroa xylophylla (Engl. & Gilg) R.Fern. & A.Fern.	Anacardiaceae	BI and HI plateaus	x	x	*Ozoroa insignis*
Pavetta nana K.Schum.	Rubiaceae	HI escarpment, Tchivinguiro	x	x	*Pavetta gardeniifolia*
Phyllanthus microdendron Müll.Arg.	Phyllanthaceae	BI plateau	x	x	*Phyllanthus muellerianus*
Protea dekindtiana Engl.	Proteaceae	HI escarpment, Tchivinguiro	x	x	
Protea ongotium Beard	Proteaceae	BI and HI plateaus	x	x	
Protea paludosa subsp. *paludosa* Hiern (Engl.)	Proteaceae	BI and HI plateaus	x	x	*Protea gaguedii*
Protea poggei subsp. *haemantha* (Engl. & Gilg) Chisumpa & Brummitt	Proteaceae	BI plateau, MO	x		
Protea poggei subsp. *heliophila* Chisumpa & Brummitt	Proteaceae	HU plateau	x	x	
Psychotria moninensis (Hiern) E.M.A.Petit	Rubiaceae	CC, BE, BI, HI, HU, MA	x		*Psychotria succulenta*
Psychotria welwitschii (Hiern) Bremek.	Rubiaceae	HU, HI and NA escarpment	x	x	
Tricalysia angolensis A.Rich. ex DC.	Rubiaceae	CC, CU, BI and HI plateaus	x		*Tricalysia elliotii*
Vangueria cistifolia var. *cistifolia* (Welw. ex Hiern) Lantz	Rubiaceae	BI, HI, MA	x		*Vangueria infausta*
Vangueria fulva (Robyns) Lantz	Rubiaceae	BI and HI plateaus	x	x	
Vitex caespitosa Exell	Lamiaceae	BI, BE, HU	x	x	*Vitex ferruginea*

7

8

Knowledge gaps and research priorities

Reading to this point here, several knowledge gaps and research priorities about geoxyles already became apparent: the impact of herbivory on geoxyle grasslands cannot be assessed without sound studies, and the same is true for threats and conservation needs of individual geoxyle species and communities. The diversity, richness and multiple origin of geoxyle species makes it difficult to grasp and study them as a whole (Meller *et al.*, 2021b), 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 to similar environmental drivers.

One characteristic of geoxyle grasslands is the low agricultural potential of the soils on which they occur, and 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 CEC (< 20 cmolc/dm³) and base saturation (71% - 78%) (Gröngröft *et al.*, 2013; Gomes *et al.*, 2021). This is also evident from other co-occurring plant species that are adapted to low nutrient contents, e.g. orchids. From pristine species-rich grassland ecosystems worldwide it is known that application of N- and P-fertilizers leads to diversity losses and homogenizations in grasslands (Tilman & Downing, 1994; Harpole & Tilman, 2007). If (industrial) agriculture in Angolan geoxyle grasslands intensifies further, we worry that fertilizers might have a similar effect on geoxyle diversity, in the long term. Studies in this direction are urgently needed.

The many endemic species and often localized 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 so far, except for a study on the widely distributed and polymorphic *Syzygium guineense* complex, which includes geoxylic forms, and where gene flow happens over wide ranges between geoxyle, shrub and tree forms (Zigelski *et al.*, 2019b). But 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 then. Furthermore, demographic studies of geoxyle species are practically non-existent, with one exception (Chidumayo, 2019), making it hard to explain 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 already almost 100 years ago (1922), followed by treatises from White (1976), Maurin *et al.* (2014) and Zigelski *et al.* (2019a). These articles, however, focus mostly on ecological and evolutionary aspects and are not enough to cover and explain the complexity of the geoxylic growth form. Moreover, research on the life cycle of geoxyles would make conservation and management plans more sustainable and holistic. Pending aspects like animal-geoxyle-interactions, plant-fungi and plant-microbe mutualisms, pollination/pollinators, dispersal mechanisms, growing rates, and success rate of generative reproduction (and how to improve it) need to be addressed. To conclude, we see imminent threats of destruction and loss of

a landscape home to unique plant evolution, before we even have started to grasp and comprehend

its functioning, diversity, history, biotic interactions and contributions to people.
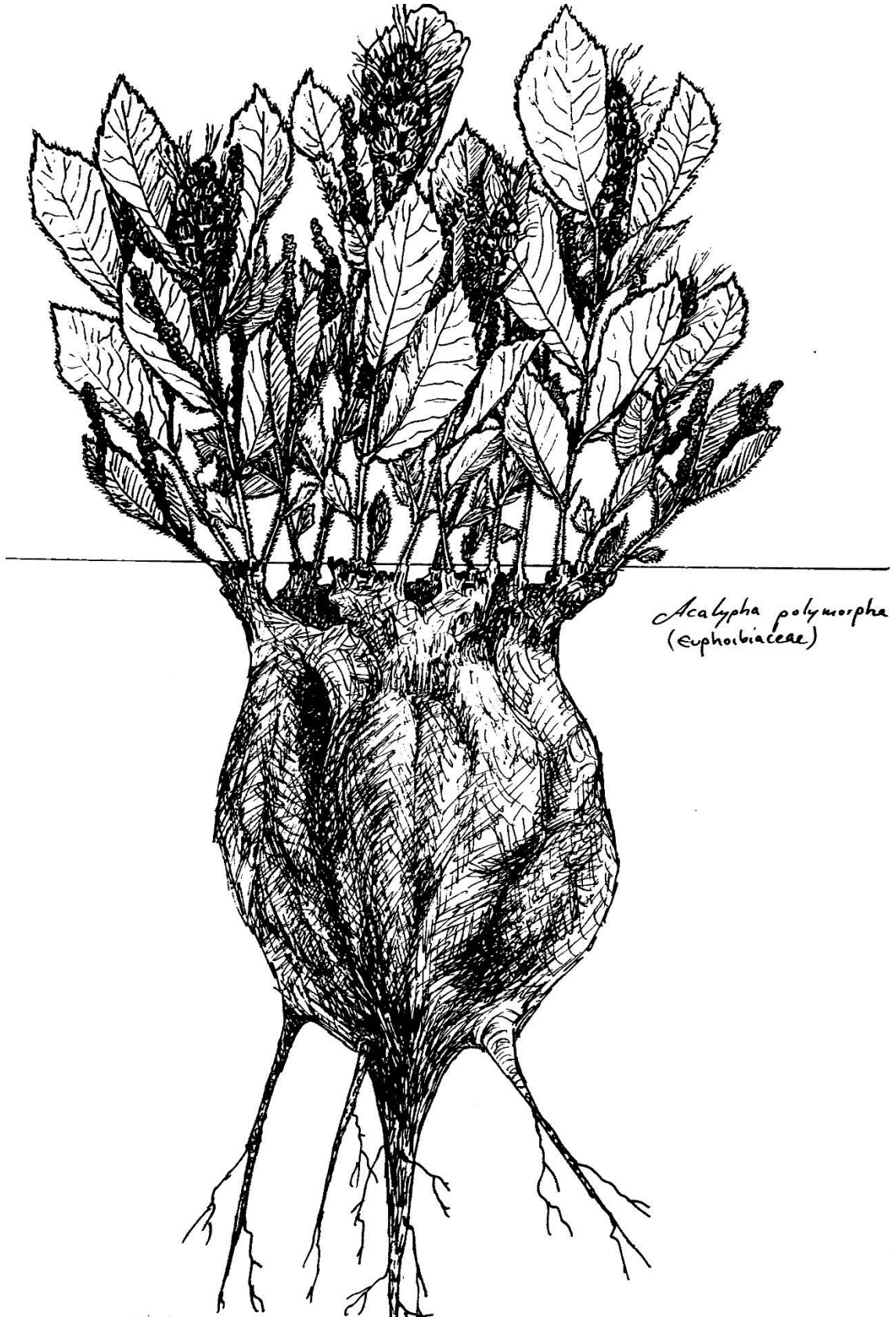
Acalypha polymorpha
(euphorbiaceae)

Correlates of geoxyle diversity in Afrotropical grasslands

Paulina Meller, Marion Stellmes, Alessandra Fidelis, Manfred Finckh

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 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 part of the Zambezian 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 analyzed 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 Zambezian 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.

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

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; Veldman *et al.*, 2015; Veldman, 2016; Pennington *et al.*, 2018). 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 (Scheiter & Higgins, 2009; García Criado *et al.*, 2020), agricultural expansion, and ecosystem-altering management like fire suppression and afforestation (Veldman *et al.*, 2015b; Abreu *et al.*, 2017; Bastin *et al.*, 2019; Buisson *et al.*, 2019).

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 (White, 1976; Maurin *et al.*, 2014; Pausas *et al.*, 2018; Zigelski *et al.*, 2019), which serve as underground storage organs (USOs) and belowground bud banks (BBBs). Both functions are essential for resprouting after disturbance (Pausas *et al.*, 2018; Ott *et al.*, 2019). 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 (Maurin *et al.*, 2014; Finckh *et al.*, 2016; Wigley *et al.*, 2019). Periodical aboveground disturbances are regarded as a key necessity for the occurrence of geoxyles; otherwise, they are easily outcompeted (Fidelis *et al.*, 2014). The impacts of herbivory, frost and fire for tropical grassland evolution and maintenance is currently hotly debated (Midgley *et al.*, 2010; Staver & Bond, 2014; Lamont *et al.*, 2017; Botha *et al.*, 2020).

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 is 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, Democratic Republic of the Congo, and Zambia that belong to the Zambezian 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). While Maurin *et al*. (2014) placed many of the geoxyle species into 'savanna lineages', other authors point to further sources of the Zambezian 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 mya), Africa has experienced major climatic changes due to global cooling, increasing seasonality and aridification (Zachos *et al.*, 2001; Trauth *et al.*, 2009; Herbert *et al.*, 2016). These changes led to fragmentation of tropical closed-canopy forests and the spread of open habitats (Cerling *et al.*, 1997; Bond & Keeley, 2005; Bonnefille, 2011). 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 mya (Maurin *et al.*, 2014; Lamont *et al*., 2017). 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 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 kya (Bird & Cali, 1998; Archibald *et al.*, 2012). Emergence of grassy biomes in Africa ca 15 mya 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 for the structural and floristic composition of geoxyle grasslands as it does in drier savanna ecosystems (Asner *et al.*, 2009; Archibald *et al.*, 2019). 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 (Appezzato-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 Zambezian phytochorion 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.

Materials and Methods

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 Bicuar National Park, Huíla province (Bicuar NP, S75); and at mid-altitudes on the Bié Plateau, Bié province (Cusseque, S74) (**Tab. 5.1**, **Fig. 5.1 f–h**). Each site represents a different ecoregion and they are all characterized by frequent disturbances of different types. At each site, a permanent 1-km² 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.

Table 5.1: 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 (Cusseque; Finckh *et al.*, 2021) and 2018 (Bicuar, Tundavala), and interviews with local people.

	Bicuar	Cusseque	Tundavala
Latitude	-15.100°	-13.705°	-14.800°
Longitude	14.836°	17.053°	13.407°
Altitude	1240 m	1550 m	2240 m
MAP	862 mm	1110 mm	980 mm
MAT	20.6 °C	19.5 °C	15.8 °C
Soil type	deep arenosols[1]	weathered ferralsols[2], alluvial arenosols[1]	shallow ferralsols[2], bedrock
Ecoregion	Zambezian 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

[1] Nutrient-poor and coarse-grained soils consisting mostly of unconsolidated sands

[2] Deeply weathered red or yellow soils of the humid tropics, high content of sesquioxides and low-activity clays

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). (**Fig. 5.1**). 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 **Tab. S5.1** which taxa have close congeneric tree relatives.
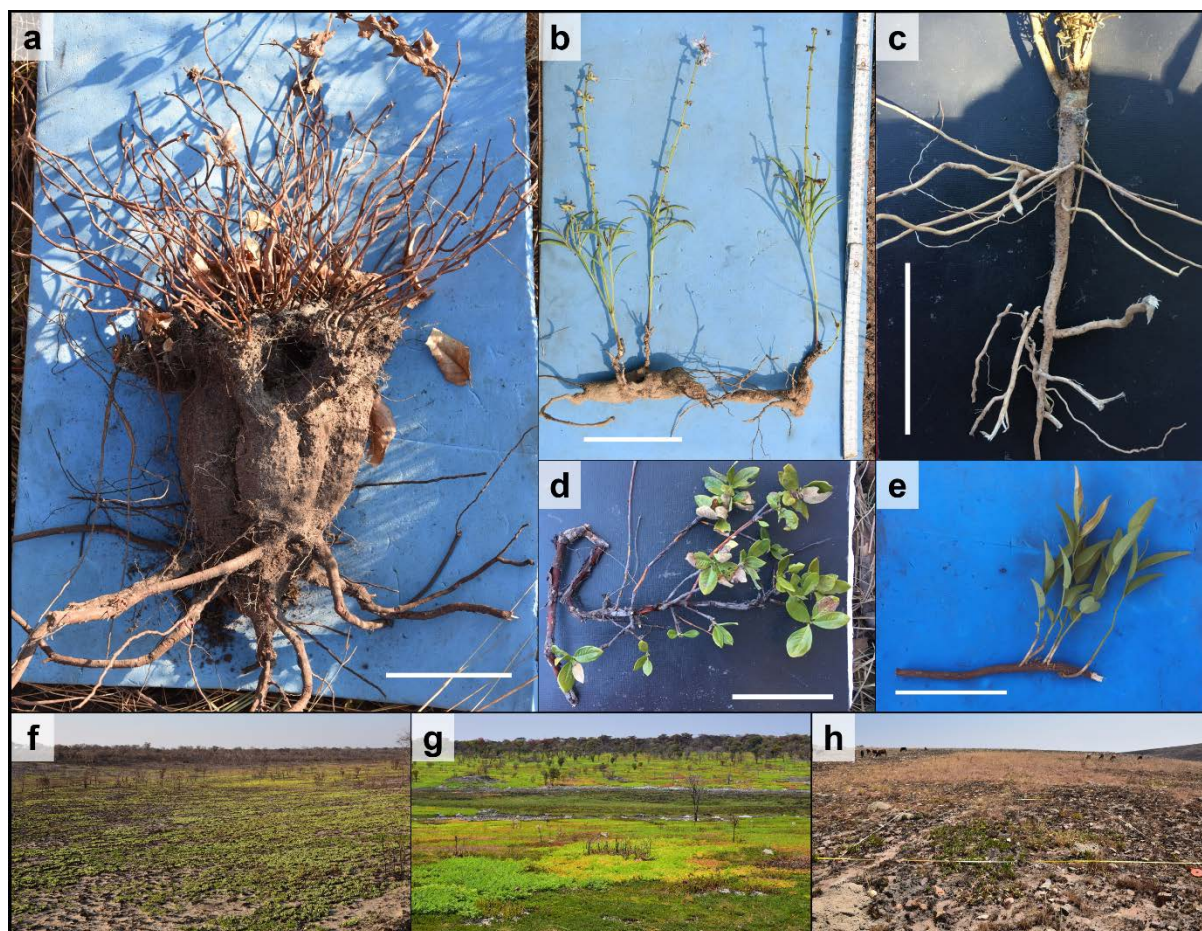
Figure 5.1: Examples of the BBB type of diversity of Angolan grasslands: a) *Acalypha polymorpha* Müll.Arg. (Euphorbiaceae) with a massive lignotuber (Li) from rocky geoxyle grasslands (Tundavala); b) *Ocimum obovatum* E.Mey. ex Benth. var. *galpinii* (Gürke) A.J.Paton (Lamiaceae) with a xylopodium (Xy), found in ferralitic geoxyle grasslands (Cusseque); c) The root crown (RC) of *Kotschya strobilantha* (Welw. ex Baker) Dewit & P.A.Duvign. (Fabaceae: Papilionoideae), common in ferralitic geoxyle grasslands (Cusseque); d) *Leptactina prostrata* K.Schum. (Rubiaceae) with woody rhizome (WR) from ferralitic geoxyle grasslands of the Angolan Plateau (Cusseque); e) bud-bearing roots (Ro) in *Ipomoea welwitschii* Vatke ex Hallier f. (Convolvulaceae) from sandy geoxyle grasslands (Bicuar NP). Bars indicate 10-cm length. The three study sites, Bicuar (f), Cusseque (g) and Tundavala (h), are shown here at the end of the dry season (September), when geoxyles resprout vigorously before the grasses resprout. Photos taken by P. Meller in 2018 (geoxyles) and September 2019 (grasslands).

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 **Tab. S5.1.**

For all identified geoxyle species at our study sites, we retrieved georeferenced locations from the Global Biodiversity Information Facility (GBIF), including synonyms (query ID https://doi.org/10.15468/dl.83zf38). The species names were checked beforehand and when 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.* (2013a).

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 v4.04 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 SoilGrids250m data provider (Hengl *et al.*, 2017a), 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 *et al.*, 2017b). 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 v4.0.3 (R Core Team, 2020) (**Tab. 5.2, Tab. S5.2**).

Table 5.2: List of selected environmental factors used in this study. The code for each bioclimatic variable is provided in parentheses.

	Variable	Code	Source
Climatic	precipitation seasonality [%] (coefficient of variation) (BIO 15)	PS	Fick & 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 *et al.*, 2017a
Disturbance	mean annual frost days 1990–2019	FROST	Harris *et al.*, 2020
	fire frequency 2000–2018	F.freq	Updated after Stellmes *et al.*, 2013a
Productivity	median NDVI 1999–2017	NDVI$_{med}$	Derived from PROBA-V data from http://www.vito-eodata.be

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 v4.0.3 (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.

Data analysis
I) Species and functional diversity measures

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

II) Ancestral background of geoxyles

Analogously, BBB-type composition and site preferences were compared per plant family using the same tests to illustrate taxonomic 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 **Tab. S5.3**. For large pantropical genera, we narrowed the focus to African diversity patterns only. We merged White's phytochoria to larger classes (as shown in **Tab. 5.3**) and use the term *biome* for these subsumed classes in this sense throughout our manuscript.

Table 5.3: Biogeographic units (biomes) used in this study and the phytochoria, according to White (1993), upon which they are based.

Biome	Code	Dominant vegetation structure	Phyto-chorion	Description
Central African tropical forests	TF	Rainforest	I	Guineo-Congolian regional centre of endemism
			X	Guinea-Congolia/Zambezia regional transition
			XI	Guinea-Congolia/Sudania regional transition
			XII	Lake Victoria regional mosaic
Afromontane belt	AM	Scrubland/ grassland	VIII	Afromontane archipelago-like region
Eastern coast	EC	Forest/ woodland/ shrubland	XIII	Zanzibar-Inhambane regional mosaic
			XV	Tongaland-Pondoland regional mosaic
Dry woodlands/ savanna	DW	Woodland/ grassland	II	Zambezian regional centre of endemism
			III	Sudanian regional centre of endemism
Arid regions	AR	Scrubland/ desert	IV	Somalia-Masai regional centre of endemism
			VI	Karoo-Namib regional centre of endemism
			XIV	Kalahari-Highveld regional transition
			XVI	Sahel regional transition
Cape region	CP	Scrubland/ grassland	V	Cape regional centre of endemism
Madagascar	MD	(Rain)forest	XIX	East Malagasy regional centre of endemism
		Woodland	XX	West Malagasy regional centre of endemism

59

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 X² 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).

III) 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 (Hampe, 2004; Araújo & Peterson, 2012) 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 analyzed the inverse of (annual frost days + 0.1).

Results

I) Species and functional diversity

In total, we observed 118 geoxyle taxa with woody BBB types from 33 plant families at the three sites, Bicuar, Cusseque and Tundavala (**Tab. S5.1**). The size of the geoxyle species pool differed greatly between sites; Cusseque had more than twice the number of taxa found in Tundavala. **Tab. 5.4** 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%).

Table 5.4: 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: Bicuar; Cus: Cusseque; Tun: Tundavala; Li: lignotuber; RC: root crown; Ro: bud-bearing root; WR: woody rhizome; Xy: xylopodium.

	Bic	Cus	Tun	At all sites	Geoxyle spp. per site	Li	RC	Ro	WR	Xy	Eudicot spp. per site
Bicuar	22	16	7		40	7	8	2	21	2	~180
Cusseque		51	16	5	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	

The species turnover among the three sites is high. Cusseque and Tundavala shared a similar number of species ($\beta_{W\ Cus\text{-}Tun}$ = 0.714) as Cusseque and Bicuar ($\beta_{W\ Cus\text{-}Bic}$ = 0.729), whereas the species pools of Bicuar and Tundavala differed more strongly ($\beta_{W\ Bic\text{-}Tun}$ = 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 (X^2 = 5.949; df = 8; p = 0.653) (**Tab. 5.4**).

II) 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 (**Tab. 5.4**). 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% in the overall, and 39.1% in the tree-unrelated geoxyle pool. 23 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 (**Fig. 5.2**). 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 (X^2 = 48.780; df = 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 (**Fig. 5.2**, **Tab. S5.4**). However, these differences were significant only with unadjusted p-values.
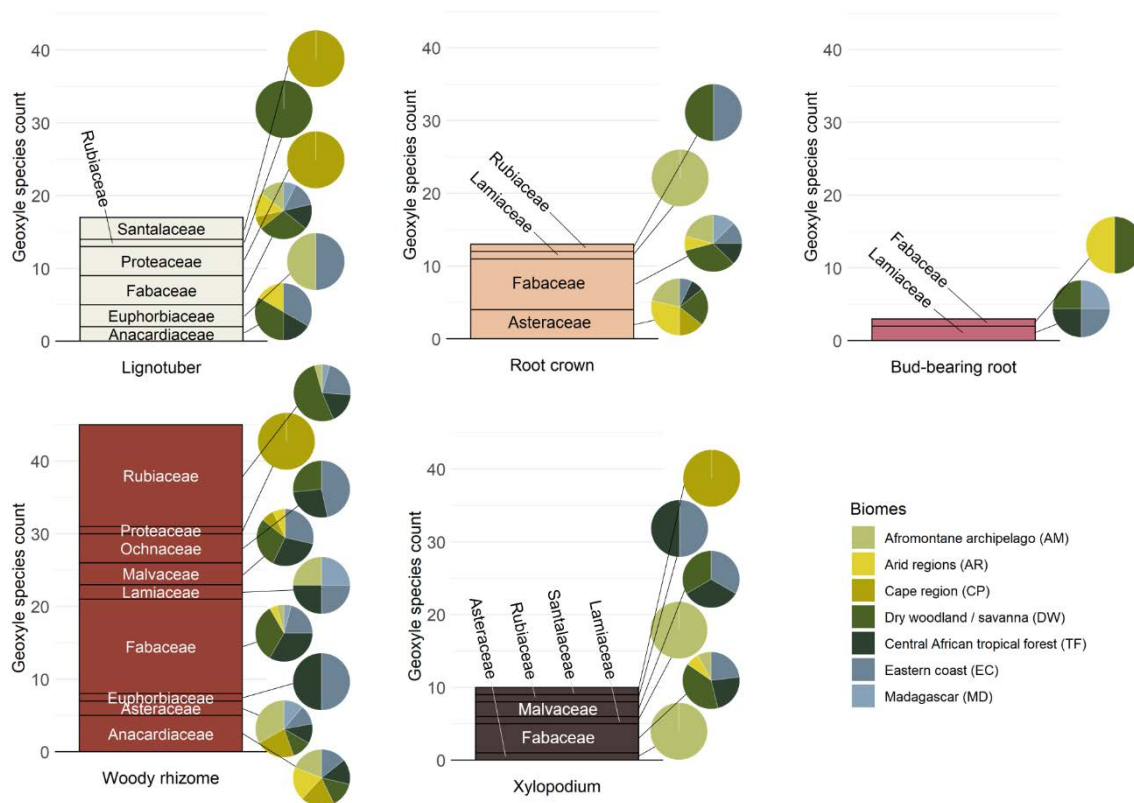
Figure 5.2: Number of geoxyle taxa per BBB type and plant family, and the proportional biogeographic origin of each family per BBB type. Only plant families with at least four geoxyle taxa are shown, the remaining families are summarized in **Figure S5.1**, and a general summary is provided in **Table S5.4**.

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 links to 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 (**Fig. 5.3**).

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 **Fig. 5.3** insert).
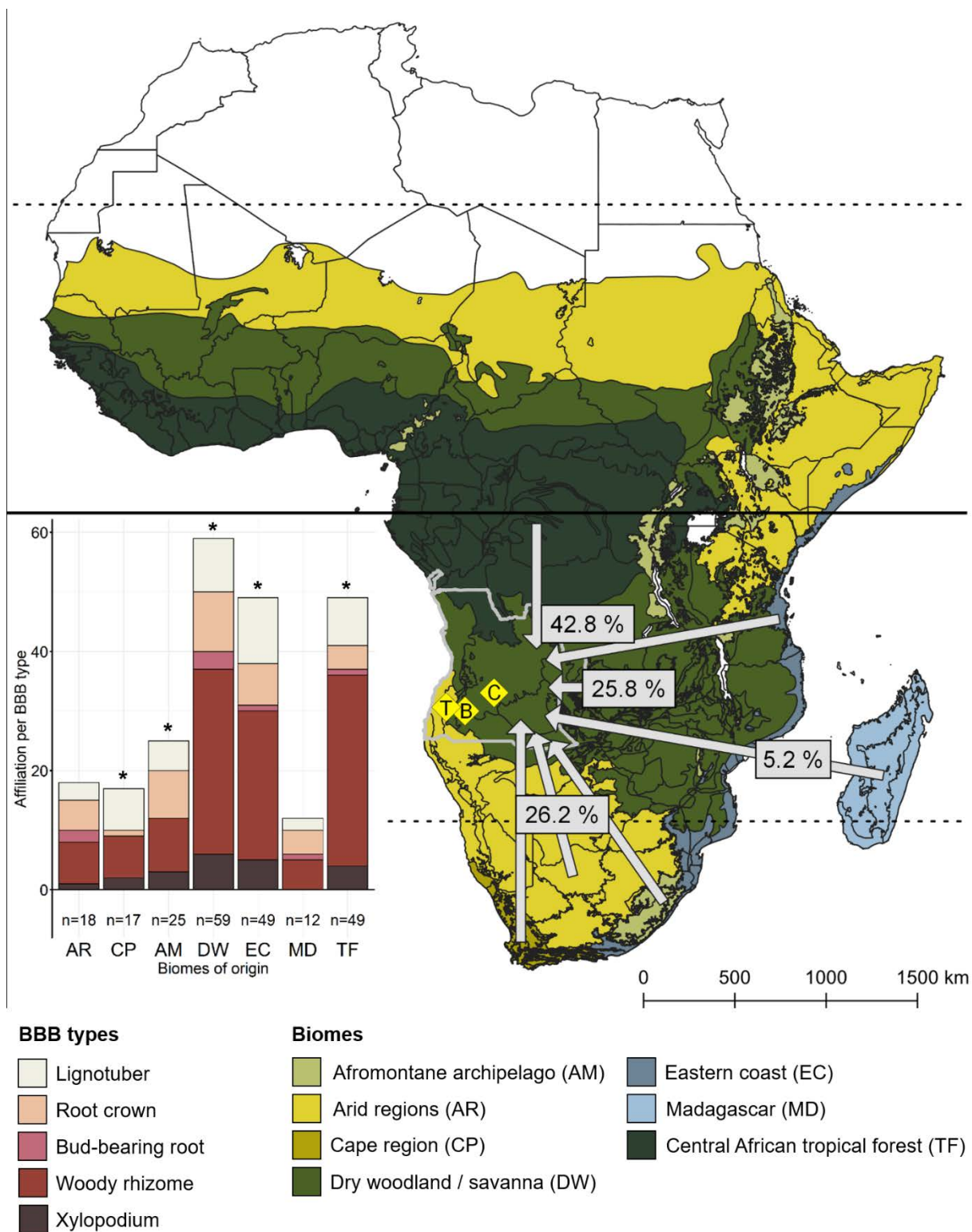
Figure 5.3: Sub-Saharan biogeographic origin of Angolan geoxyle species (map) and their BBB-type proportions (insert). The contributions to the Angolan species pool from surrounding biomes are shown with grey arrows and boxes. The Angolan study sites are marked in yellow (T: Tundavala; B: Bicuar; C: 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).

III) 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 (**Fig. 5.4**). 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 (**Fig. 5.4**). 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. While only 41% of lignotuber occurrences were at frost-affected sites (> 0.1 yr^{-1}), 52% of root crown, 65% of xylopodium, and 76% of woody rhizome and bud-bearing root occurrences were at frost-affected sites (**Fig. 5.5**). In contrast, 30% of woody rhizome and 42% of root crown occurrences were observed at heavily frost-affected sites (> 20 yr^{-1}), whereas all 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 (**Fig. 5.4a,**
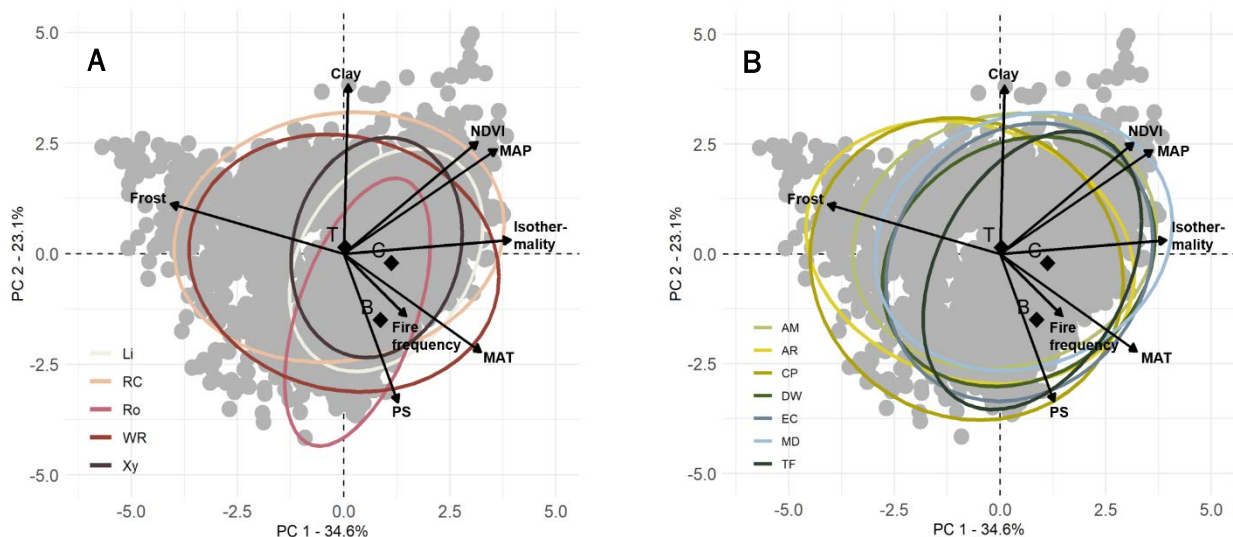
Figure 5.4: PCA showing the environmental preferences of geoxyle species to selected parameters in the first two dimensions. In a), points (= geoxyle observations) are grouped according to BBB type, and ellipses define 95% confidence intervals of observations for each group. In b), points are grouped according to biomes (i.e. biogeographic origin) (see **Tab. 5.3**), and ellipses again define 95% confidence intervals. The diamond shapes represent the ordination of the three study sites, Bicuar (B), Cusseque (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 Afromontane archipelago (AM), Arid regions (AR), Cape region (CP), Dry woodlands (DW), Eastern coast (EC) Madagascar (MD) and Tropical forests (TF).
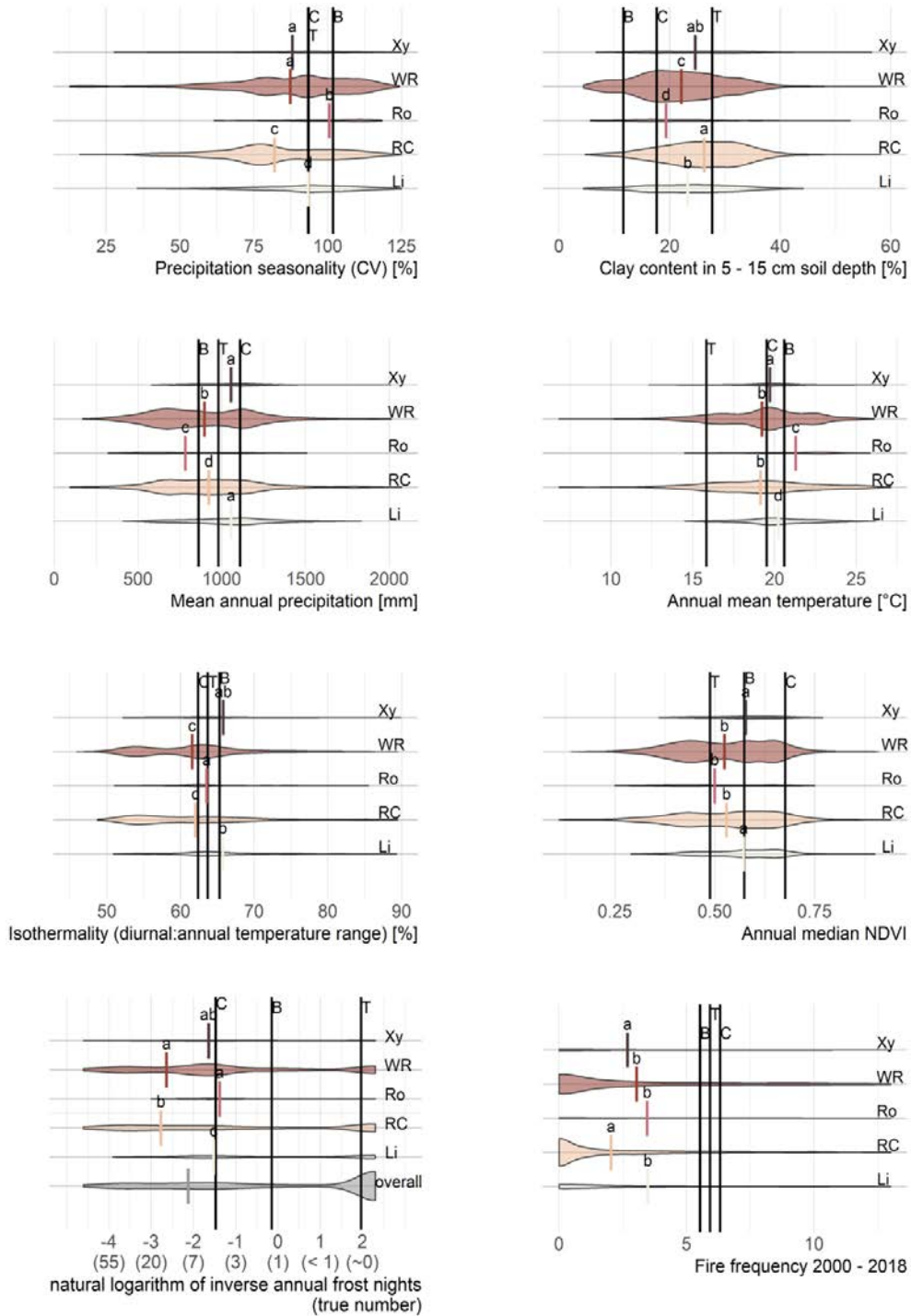
Figure 5.5: Selected environmental spaces occupied by geoxyles, grouped by BBB types. The violin plot represents the probability of encountering geoxyle species along a given environmental gradient: the wider the violin, the higher the number of species occurring at that level. Violin areas correspond 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 posthoc Games-Powell 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: Bicuar; 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).

S5.2, S5.3) or by their biogeographic origin (**Fig. 5.4b, S5.4, S5.5**). While 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 (**Fig. S5.3**).

By contrast, geoxyles with an Arid (AR) or Cape region (CP) background correlated markedly with increased frost days (**Fig. 5.4b, S5.4, S5.5**). 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 (**Fig. 5.5**). 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 (**Fig. 5.5, Tab. S5.5**). 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 biogeographic background of the geoxyles (**Fig. 5.4b, S5.4, S5.5, S5.6**). 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.

Discussion

I) 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 (Veldman *et al.*, 2015; Zaloumis & Bond, 2016; Buisson *et al.*, 2019). Maurin *et al.* (2014), for example, listed 266 geoxyle species for southern Africa, whereas Zigelski *et al.* (2019) compiled 198 geoxyles for the western Zambezian 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 (White, 1976; Pausas *et al.*, 2018) 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% to 65% of species were unique to any site (**Tab. 5.4**), 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 (Tilman *et al.*, 1997; Loreau, 2000, 2004).

II) 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) (**Fig. 5.2, S5.1**). 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 (Schrire, 2005; Barreda *et al.*, 2015) and exhibit broader functionality.

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 (**Fig. 5.3**), which is consistent with previous findings (Simon *et al.*, 2009; Maurin *et al.*, 2014; Zigelski *et al.*, 2019). To a lesser degree, we also show origins from other biomes, for example, the Cape region (Lamont *et al.*, 2017) or the Afromontane belt (Meadows & Linder, 1993). Thus, the diverse Zambezian 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 Zambezian 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.

III) 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 (**Fig. 5.4b, S5.2, S5.3**). 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 (Pettorelli *et al.*, 2005; Hoyos *et al.*, 2017).

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 (Walker & Peet, 1984; Peterson & Reich, 2008; Simon *et al.*, 2009; Fidelis *et al.*, 2014). 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 (Mack & Thompson, 1982; Briske, 1996), 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 (Pausas *et al.*, 2018; Ott *et al.*, 2019; Herben & Klimešová, 2020). 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), 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 (Maurin *et al.*, 2014; Lamont *et al.*, 2017). Furthermore, long-term fire experiments in Southern Africa have shown that exclusion of fire had a far greater (negative) effect on 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.*, 2019a). 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 (Finckh *et al.*, 2016; Botha *et al.*, 2020), 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 Cusseque and 40-fold in Bicuar (**Tab. 5.1**, **Fig. 5.5**). 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.

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 prised 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.

Acknowledgements

Data availability

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.

-VI-

Clematis
chrysocarpa
(Ranunculaceae)

Tipping the scales: How fire controls the balance among functional groups in Angolan grasslands

Paulina Meller, Raquel Frazão, Fernanda Lages, Norbert Jürgens, Manfred Finckh

Abstract

Fire plays an important role in the ecology of tropical grasslands globally. However, detailed studies comparing the response of plant functional groups to fire seasonality, and thus phenological timing, are scarce from humid Afrotropical grasslands. Such information, however, is crucial for understanding what keeps the grasslands open and for enabling evidence-based management, and conservation.

We initiated an experiment in frost- and fire-prone Angolan geoxyle grasslands in 2017, investigating the effect of different timing of fires on cover and diversity of trees, grasses, geoxyles and herbs. We installed permanent, randomized plots with fire exclusion, annual early and late dry-season burning, representing the local burning practices.

Functional plant groups reacted differently to the treatments, becoming apparent at species level and their performance metrics. After three years, grass species benefitted from late and no burning, and herbs from late burning, whereas geoxyles thrived under early burning. Tree growth was suppressed under late burning, and did not increase with fire exclusion. Species richness and diversity was higher in burnt than in unburnt plots.

Seasonal timing of fire tips the scales between geoxyles and grasses. The extraordinary plant diversity of Angolan geoxyle grasslands is a result of pyrodiversity and frost, keeping the grasslands open even in absence of fire.

Keywords: Fire ecology, geoxyles, plant diversity, pyrodiversity, frost in the tropics.

Introduction

Grasslands and savannas cover approximately a third (36%) of the African continent (Dixon *et al.*, 2014) and constitute old-growth and biodiverse ecosystems (Veldman *et al.*, 2015; Bond, 2016) Although they often occur in areas that appear climatically suitable for closed-canopy forests, recurrent disturbances caused by frost, herbivory or fire keep the tree cover low (Bond, 2008; Staver *et al.*, 2011; Murphy & Bowman, 2012; Joshi *et al.*, 2020). Instead of trees, C4 grasses dominate the vegetation structure and provide an easily combustible fuel bed in the dry season. Fires are thus very common, mostly ignited by humans for agricultural, pastoral or hunting purposes, making Afrotropical grasslands leading in global fire frequency (Andela *et al.*, 2017).

Fire experiments have been used for decades in Africa to study the effect of fire frequency and timing on vegetation (Aubréville, 1953; Trapnell, 1959; Brookman-Amissah *et al.*, 1980; Chidumayo, 1997; Savadogo *et al.*, 2008). Particularly in colonial times, several of these experiments were designed under the assumption that savannas were degraded forests, and they were intended to determine the optimal fire management for timber production (Laris & Wardell, 2006). Therefore, the focus of these experiments was on the tree layer and on tree-grass dynamics. The herbaceous (grass) layer itself became of interest only later, motivated by interests in pastoral and wildlife management. Detailed studies on the effect of fire timing on the ground layer are still sparse and stem from few sites, e.g., dry savanna in Kruger National Park (Van Wilgen *et al.*, 2007; Smith *et al.*, 2013), afromontane grasslands at Mlambonja Wilderness Area in South Africa (Uys *et al.*, 2004) and dry miombo woodlands at Marondera Grassland Research Station in Zimbabwe (Furley *et al.*, 2008). Studies from other ecoregions are lacking.

The Angolan wet miombo region is a poorly studied area regarding fire. It is characterized by a mosaic of biodiverse forests, woodlands and grasslands, and the two latter are subject to frequent anthropogenic fires. The timing of fire is controlled by humans according to their management objectives. Grasslands are burnt annually in the early to mid dry season (June–July) to facilitate hunting or clear the surroundings of villages; agricultural plots in woodlands are burnt late in the dry season (August– September) to prepare the fields for the growing season (Schneibel *et al.*, 2013; Catarino *et al.*, 2020). Other objectives (e.g., honey production) follow different seasonal logic. Particularly the later fires often escape and affect large areas, and they tend to be severe because of more and drier fuels (Govender *et al.*, 2006; Laris *et al.*, 2017; Rissi *et al.*, 2017; N'dri *et al.*, 2018).

Geoxyle grasslands are part of the miombo mosaic, but comparable ecosystems also occur in the Brazilian Cerrado (Ratter *et al.*, 1997). They are dominated by geoxyles and grasses and often include sparse trees from nearby woodlands plus a high diversity of herbs (Zigelski *et al.*, 2019). Geoxyles, also known as geoxylic suffrutices or "underground trees" (White 1976; Maurin *et al*. 2014), contribute to the diversity and resilience of old-growth tropical grasslands (Zaloumis & Bond, 2016; Buisson *et al.*, 2019). They are characterized by their massive belowground woody structures, serving as storage organs and bud banks (Pausas *et al.*, 2018). Previous studies often

treated them as forbs (perennial herbs) (Uys *et al*. 2004), or shrubs (Ratter *et al.* 1997). The codominance of grasses and geoxyles and their asynchronous phenologies, in that geoxyles flower and bear fruit before grasses start to do so, is striking (Zigelski *et al.* 2019a). Besides fire, frost has been discussed as a factor keeping the low-lying grasslands open, as it occurs reliably and frequently in the dry season in central Angola, and it topkills tree saplings in particular (Finckh *et al.*, 2016, 2021).

Pyrodiversity has been critically discussed as an important promoter of biodiversity (He *et al.*, 2019; Jones & Tingley, 2021). It describes how diverse a landscape is in terms of its fire regimes, i.e. when, where, how intense, how often, and at what scale fires affect a given landscape. The use of fire for different purposes in central Angolan landscapes thus constitutes a patch-mosaic burning, which is a base for pyrodiversity (Parr & Andersen, 2006). The extraordinary biodiversity in Angolan geoxyle grasslands has been considered to be the result of a long and continuous evolutionary history (Veldman *et al.*, 2015), heterogeneous soils (Revermann *et al.*, 2017), and, so far, mostly low-intensity land use, whereby variable timing, frequency and intensity of grassland fires (pyrodiversity) may also add to this (Jones and Tingley 2021).

Several knowledge gaps are apparent that motivate this study. Since Angolan geoxyle grasslands are poorly studied, it is not known whether the effect of seasonal timing of fire is comparable to other, better studied systems, for example in South Africa. Moreover, the effect of a pyrodiverse regime on functional groups, plant performance metrics or species diversity, has not yet been addressed in miombo landscapes. It has never been tested whether geoxyles, which had been lumped with shrubs or forbs/herbs before, also behave like shrubs or herbs. The frequency of frost also implies that fire might not be the only agent keeping the grasslands open, so that fire-exclusion studies are urgently needed. And finally, intensification and change of land use are severely affecting Angola (Archibald *et al.*, 2010; Catarino *et al.*, 2020), in addition to changed fire regimes, which in turn are expected to affect the vegetation (Archibald, 2016). Knowledge about the effects of fire management on plant diversity is therefore crucial.

To address these points, we initiated a fire experiment with early and late dry-season fire treatments and fire exclusion in an Angolan geoxyle grassland in 2017. Looking at cover, diversity and selected performance metrics of the species from the ground layer, we hypothesized that (a) the burning treatments have specific effects on the vegetation, and that functional groups of the ground layer, i.e. geoxyles, grasses and herbs, react differently to seasonal timing of fire; (b) the specific effects of the fire treatments on the functional groups are reflected in their performance metrics; and (c) burning enhances species richness and diversity.

Materials and methods

Study site

We established the fire experiment in 2017 in the geoxyle grassland ecosystem of the Cusseque area in the municipality of Chitembo, Bié Province, Angola. This site is associated with one of the SASSCAL Biodiversity Observatories installed in Angola (Cusseque, S74) (http://www.sasscalobservationnet.org) and was a core research site of the concluded Future Okavango (TFO) project, so that local environmental conditions and floristic compositions were well known. The site is in the Angolan Miombo ecoregion and is dominated by trees and geoxyles of the genera *Brachystegia* and *Cryptosepalum*. One of the dominant geoxyle species of the area was recently recognized as yet undescribed species of *Cryptosepalum* (David Goyder & Roger Polhill, personal communication), and is referred to as *Cryptosepalum* aff. *maraviense* in this article. The area is characterized by rolling landscapes with hills covered by forests and woodlands that become sparser down the slopes until they are replaced by geoxyle grasslands on the mid-slopes. In the valley bottoms are narrow, treeless peatlands that sustain small streams or rivers. The soils are composed of deeply weathered plinthosols on the hills that are nutrient poor, coarsely grained and slightly clayey (Gröngröft *et al.*, 2013).

All precipitation, around 1,100 millimetres (mm), falls within the wet season from the end of September to the end of April. The dry season lasts from May to September. The mean annual temperature is around 19.5°C (temperature and precipitation derived from WorldClim 2 (Fick & Hijmans, 2017)), but daily temperatures can vary more than 30°C in the dry season, depending on the topography (Finckh *et al.*, 2016). In the dry season, open areas, i.e., geoxyle grasslands and woodland ecotones, are particularly prone to frequent nocturnal frosts (up to 40 events per year with down to -7.5°C and an occurrence peak in July (Finckh *et al.*, 2016, 2021)) and to anthropogenic fires, which are ignited annually. Time of fire depends on its purpose: early dry-season fires (June-July) are set to clear the area around settlements and to facilitate hunting, and late dry-season fires (August-September) often escape from slash-and-burn agricultural and charcoal-producing practises in the woodlands (Schneibel *et al.*, 2013; Catarino *et al.*, 2020). Because hunting pressure is high, there are no large native herbivores in the area (Huntley *et al.*, 2019), and cattle is mostly absent in the Leguminosae-dominated geoxyle grasslands (personal observation).

Experimental design

The experimental site is located on a slope at -13.705° N, 17.053° E at 1550 m a.s.l. and encompasses a square of 100 m by 100 m, containing 36 plots (15 m by 15 m) with a 5-m-wide firebreak all around (**Fig. 6.1a, b, c**). Of these 36 plots, one third were randomly assigned an early dry-season fire treatment, another third a late dry-season fire treatment, and in the remaining 12 plots, fire was excluded (**Fig. 6.1c, d**). To minimize edge effects, a central 5 m by 5 m subplot was nested in each plot for vegetation assessments. Early burning always took place in June, whereas late burning was usually done in September, except in the first year when it had to be done in July
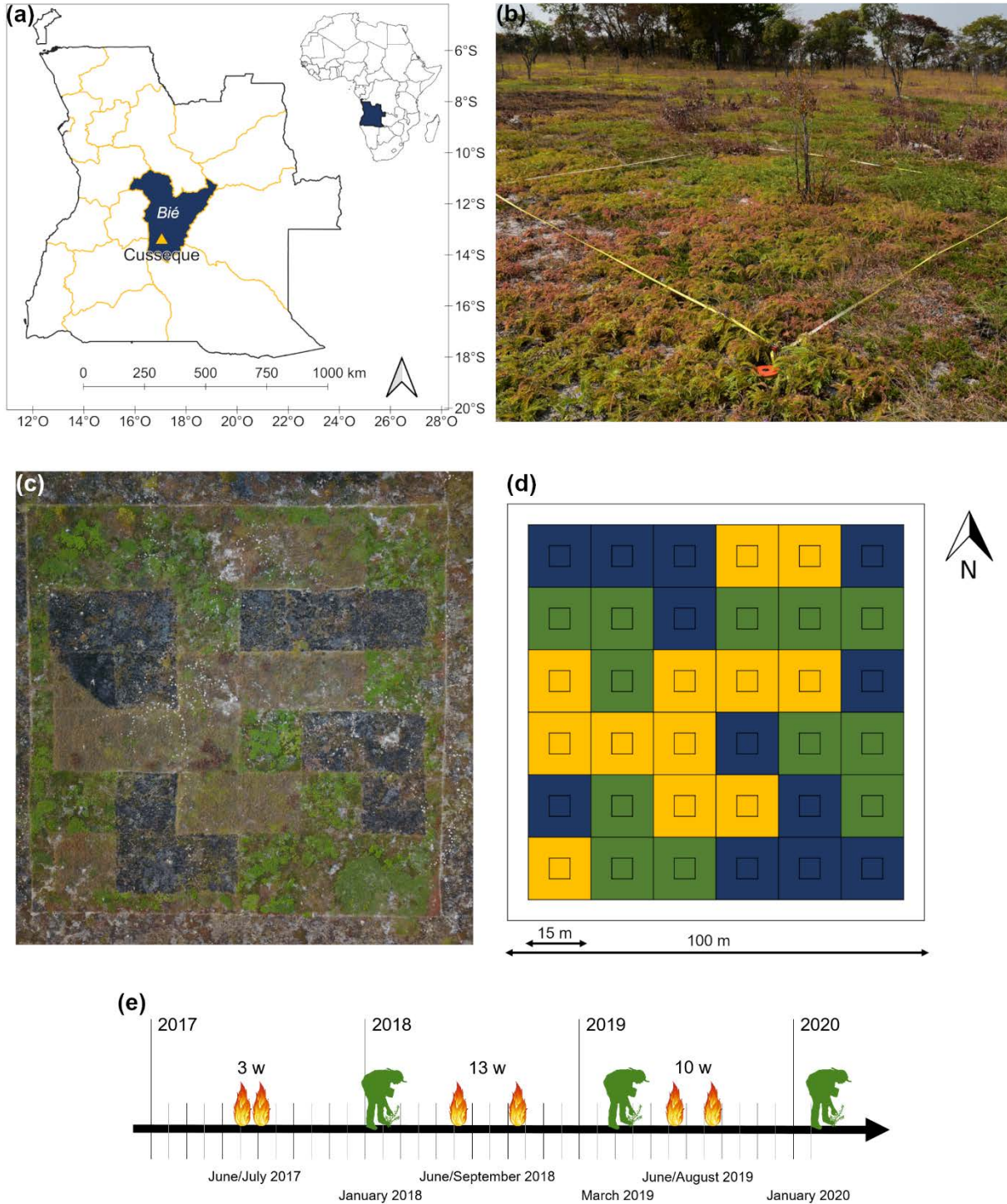
Figure 6.1: (a) Location of Cusseque in Angola. (b) Photo of an early burning 25 m² plot, showing the dominance of *Brachystegia russelliae* (reddish-green patches) and *Cryptosepalum* aff. *maraviense* (low patches, dark green) and a protruding stem of *Monotes africanus*. (c) Aerial image of the experimental area in September 2018, after late burning. One fire exclusion plot (third row left) was partly burnt by accident. (d) Spatial layout of the experiment. The whole square measures 1 ha, the northward side faces the upper slope, the southward side points to the valley bottom. Yellow denotes fire exclusion plots, blue defines early burnt plots, and green reflects late burnt plots. (e) Timeline of the experiment, indicating when burning and vegetation assessments took place (w = weeks between early/late burning). Exact dates for burning are provided in **Tab. S6.1**.

due to logistical constraints (**Fig. 6.1e**). Early burning of plots happened during the main and most severe occurrences of frost (June and July), and late burning afterwards, when geoxyles started to resprout. Usually, plots were burnt in a controlled way by burning only in the cooler mornings and evenings and creating first a 1 m firebreak against the wind, protecting adjacent plots of different treatment. Afterwards, the isolated interior was burnt in one rush. Several people always stood ready with fire beaters to keep the fire front in line. We could not avoid minor burning errors, but these affected the central subplots only in one incident, after which the respective subplot was removed from analysis (**Fig. 6.1c**).

We assessed the effects of the fire treatments by using recurrent standardized vegetation surveys in the following rainy seasons. Due to logistic constraints, rainy-season assessment times differed over the years: In 2018 and 2020, assessments were done in January, whereas in 2019 it was done in March, which affects interannual comparability of grass-cover values. We visually estimated total vegetation cover and species-specific cover percentage for each 5 m by 5 m subplot. We identified plant species as far as possible in the field and assigned them to a functional group (grass, geoxyle, herb and tree). We did not use the term "forb" because both herbs and geoxyles had been named as such in previous studies. Instead, we defined resprouting species with woody underground structures as geoxyles, and non-woody, non-graminoid perennial and annual species as herbs.

When *in-situ* identification was not possible, we took photos and collected specimens that we deposited in the herbaria Lubango (LUBA) and Hamburg (HBG). We identified species by comparing them with specimens from our own and other collections (accessed via Global Plants JSTOR https://plants.jstor.org) and by using online references (Kew Flora Zambesiaca http://apps.kew.org/efloras/search.do) and guides (Senckenberg African Plants http://www.africanplants.senckenberg.de; Field Guide to the (Wetter) Zambian Miombo Woodlands) (Vollesen & Merrett, 2020).

We collected additional data on (a) stem heights of two common taxa, *Monotes africanus* and *Syzygium guineense* subsp. *macrocarpum*, which are able to outgrow the shrub state to become trees under favourable conditions, and we counted and measured all living stems of at least 50 cm in height within the 5 m by 5 m subplot. In 2019, we additionally counted the ratio of vital to dead stems; (b) number of flowering culms per grass species that grow in the square meter of the northwest corner of each subplot; and (c) shoot length, leaf length and leaf number of the two dominant geoxyle species, *Brachystegia russelliae* and *Cryptosepalum* aff. *maraviense,* and we measured 4 shoots per species per plot, measuring always the shoot closest to the corner within 1 m distance outside of the subplot (**Fig. 6.2**).
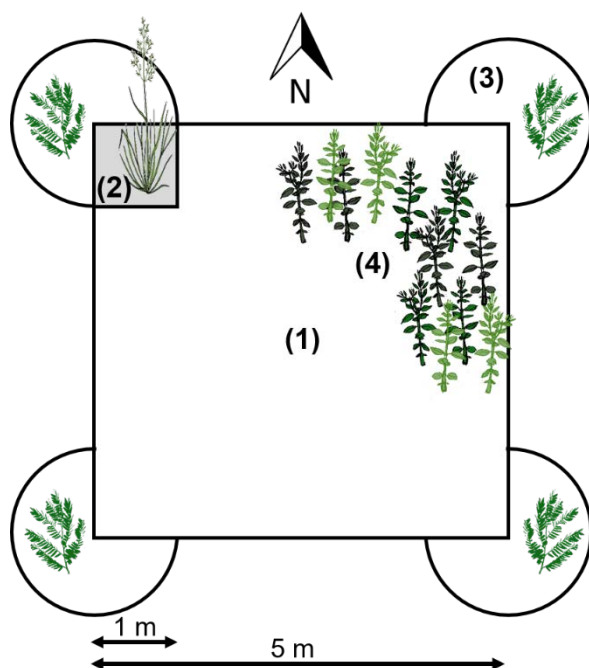
Figure 6.2: Scheme of a 5 m by 5 m subplot, showing the sampling design. We compiled a species list including visual estimation of cover per species of the whole subplot (1). In the NW corner of the subplot, flowering grass culms were counted on 1 m² (2). Outside every corner within 1 m distance, shoot and leaf length, and leaf number, were measured from the closest shoot of *Brachystegia russelliae* and of *Cryptosepalum* aff. *maraviense* (3). Every living stem of at least 50 cm height of *Monotes africanus* and *Syzygium guineense* subsp. *macrocarpum* within the subplot was counted and its height measured (4).

Data analysis

If not specified otherwise, we conducted all analyses in R v4.0.3 (R Core Team, 2020). We tested for differences in plot cover among and within functional groups (geoxyle, grass, herb) and treatment (early, late, no burning), and for significant developments over time for each group. The group-specific cover values were created by summing up individual species covers grouped by functional group for each plot. As a result, cover values may exceed 100% due to overlapping vegetation strata.

Beforehand, we tested for a normal distribution of the data using QQ-Plots, for homogeneity of variances using Levene's test (Brown & Forsythe, 1974), and for extreme outliers that could have a strong influence on the outcome. This was done with ggqqplot() from package ggpubr (Kassambara 2018), and levene_test() and identify_outliers() from rstatix (Kassambara 2021). We $\log_{10}$-transformed the data to meet the assumptions. Subsequently, we used a two-way mixed ANOVA as implemented in anova_test() from rstatix with "treatment" as between-subjects variable, "year" as within-subjects variable, and "plot" as subject identifier. The ANOVA outcomes were further investigated by running a one-way model on the significant variable for each level of the second variable, and by pairwise comparisons using t-tests. Both posthoc tests used Benjamini-Hochberg correction (Benjamini & Hochberg, 1995) with α = 0.05 as threshold to significance.

To analyse the species diversity in our experiment, we calculated and compared three commonly used metrics: species richness (number of species per plot), diversity (Shannon index) and evenness (equitability of individual covers). We created a species-by-plot matrix including all species for a general analysis, and specific matrices only for grass, geoxyle and herb species, respectively. In the matrices, zeros indicated the absence of a species in a given plot; otherwise

cover values (in %) indicated the presence and dominance of a species. Using the package vegan (Oksanen *et al.*, 2007), we calculated species richness, diversity and evenness upon these matrices. We then tested for differences among and within treatments over time with the same ANOVA and posthoc test approach as described above, after making sure that requirements for these tests were met.

Analogously, the number of all grass culms per m² among and within treatments over time was tested with two-way mixed ANOVA and posthoc t-tests, after the values had been $\log_{10}$-transformed to conform to the test requirements. In a second step, we repeated this analysis for the eight grass species with enough culm counts to allow for testing.

We assessed the response of geoxyles to the treatments by comparing selected performance metrics (shoot and leaf length, and leaf number) of the two dominant taxa among and within treatments over time. For each taxon, we made sure that the metrics met the test requirements, by applying $\log_{10}$-transformation and removal of extreme outliers, before proceeding with the same two-way mixed ANOVA and posthoc test approach as described above. Additionally, we tested the plot cover of *B. russelliae* and *C.* aff. *maraviense* in the same way.

Performance of herbs was investigated by examining cover development of the most abundant species among and within treatments over time. Additionally, development of herb species richness, particularly with regard to annual species, was assessed. We used the same two-way mixed ANOVA and posthoc test approach for the assessment as described above. Lastly, we evaluated the shrub and tree development in our experiment. Differences in stem heights among and within treatments over time were tested with non-parametric Kruskal–Wallis and subsequent pairwise Dunn tests (Dinno, 2015) because no transformation could conform to a normal data distribution.

Results

Cover balance

In most plots, the vegetation cover was dominated by geoxyles, ranging from 36.5% to over 100% (multilayered, cumulative cover). Grasses covered less on average, with 12.8% to 72.4%, and herbs had the lowest shares with 1.6% to 7.7%. Both the burning treatments (ANOVA $F_{(2,32)} = 4.670$, $p = 0.017$, $\eta^2_g = 0.156$) and the time passed (ANOVA $F_{(1.6,51.14)} = 3.647$, $p = 0.042$, $\eta^2_g = 0.040$) had strong specific effects on the vegetation cover. In general, unburnt plots showed denser total cover than early-burnt (on average 7.4% lower, t-test $p_{adj} = 0.061$), and late-burnt plots (on average 15.5% lower, t-test $p_{adj} \ll 0.001$), which had the overall lowest covers.

Functional groups responded differently to the treatments (**Fig. 6.3**). With early burning, grasses showed the lowest cover values compared to other treatments, and even decreased over time, whereas herbs showed intermediate but increasing cover levels. There was a non-significant increasing trend for geoxyles. Late burning had little effect on grasses; their cover remained stable over time, whereas geoxyle cover dropped sharply over time and stayed comparably low. Overall,

herb cover increased slightly over time and was highest for the late fire treatment. Fire exclusion had a strong promoting effect on grass cover, increasing it over time, and a negative effect on geoxyle cover, comparable to that of late burning. Herb cover varied over time with no discernible trend, but remained lower than with burning. Generally speaking, geoxyle cover thrived under early burning, herb cover thrived under late burning and grass cover thrived under fire exclusion.
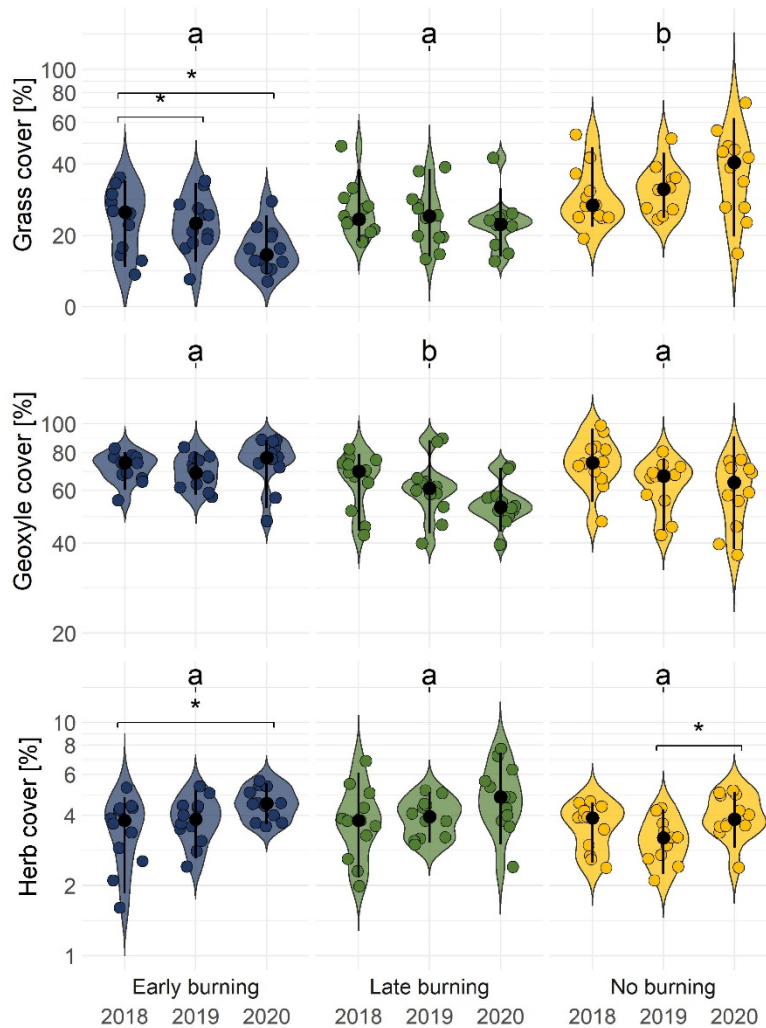
Figure 6.3: Cover balance between grasses, geoxyles and herbs throughout the experiment. The violins show differences between treatments and development over time for each functional group separately (top: grasses, centre: geoxyles, bottom: herbs), plus statistical evaluation. The black ranges represent 95% confidence intervals, with the dot being the median. All cover values have been log_{10}-transformed to meet test requirements. Testing for significant dif-ferences among treatments and among years within a treatment was done with a mixed ANOVA (significant differences between treat-ments indicated by different letters, threshold $\alpha = 0.05$) and posthoc pairwise t-tests with Benjamini-Hochberg cor-rection (significance level as follows: $p < 0.0001$ ***; $p < 0.001$ **, $p < 0.05$ *, $p \leq 0.1$ °, $p > 0.1$ ns).

Plant performance metrics
Grasses:

The number of flowering grass culms differed among treatments (ANOVA $F_{(2,29)} = 4.545$, $p = 0.019$, $\eta^2_g = 0.141$), with the highest numbers in late and unburnt plots (**Fig. 6.4**). Differences between years were negligible and nonsignificant (ANOVA $F_{(2,58)} = 1.535$, $p = 0.224$, $\eta^2_g = 0.025$). With a more thorough look at single species, it is apparent that grass species responded differently to the treatments. All species developed only few culms under early burning treatment, and some species, e.g., *Loudetia simplex* or the annual *Microchloa kunthii*, performed much better with late burning than with no burning (on average 4.7 culms more, t-test $p_{adj} = 0.009$). However, we also found examples for the opposite, in that *Trachypogon spicatus* clearly produced more culms under fire exclusion (on average 3.4 culms more, t-test $p_{adj} = 0.006$). The same trends

that we observed for culm numbers were also reflected in the respective cover values of grasses, also for individual species (i.e., increasing culm numbers went along with increasing cover).
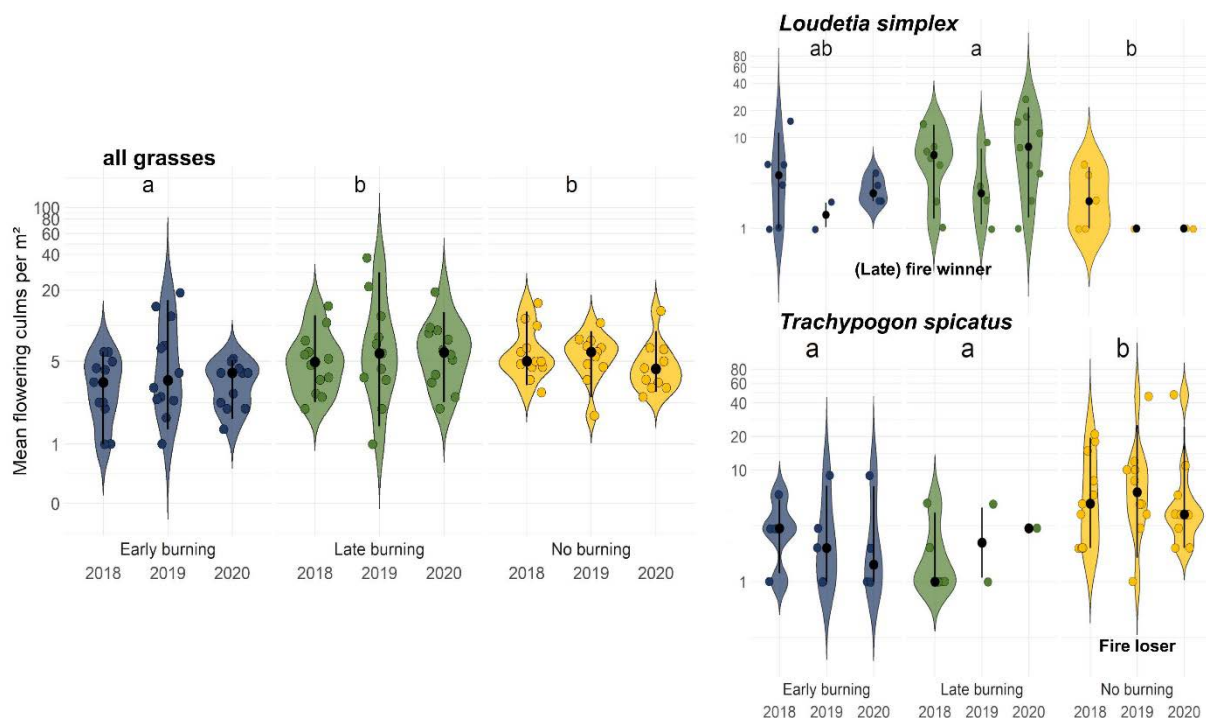
Figure 6.4: Comparison of average grass culm numbers among treatments and years. Values have been log$_{10}$-transformed to meet test requirements. Significance of differences was assessed with a mixed ANOVA (significant differences indicated by different letters, threshold α = 0.05) and with posthoc pairwise t-tests with Benjamini-Hochberg correction for within treatment developments over time. The latter showed no significant changes over time. As grass species reacted differently to the treatments, we give examples of fire winners (*Loudetia simplex,* top right) and fire losers (*Trachypogon spicatus,* bottom right).

Geoxyles:

Brachystegia russelliae had slightly higher cover than *Cryptosepalum* aff. *maraviense* in the experimental area. The first covered up to 85% per plot (on average: 26.6%), the second followed with up to 70% per plot (on average: 25.9%). The two taxa responded quite differently to the treatments (**Tab. 6.1, S6.2**): *B. russelliae* profited from early burning in that shoot length, leaf length and leaf number were greater under this treatment and increased over time (on average by 3.2 cm shoot length, 1.8 cm leaf length and 0.8 leaves in 3 years, t-test p$_{adj}$ = 0.033). Under fire exclusion, similar, but not increasing, values were reached, whereas under late burning, performance metrics were lower in comparison (ANOVA, shoot length: $F_{(2,91)}$ = 7.303, p =0.001, η²$_g$ = 0.138; leaf length: $F_{(2,91)}$ = 11.013, p << 0.001, η²$_g$ = 0.195; leaf number: $F_{(2,91)}$ = 4.316, p = 0.016, η²$_g$ = 0.087). Cover did not differ among treatments (ANOVA $F_{(2,32)}$ = 1.985, p = 0.154, η²$_g$ = 0.093) and did not change over time ($F_{(2,64)}$ = 1.353, p = 0.266, η²$_g$ = 0.007).

For *C.* aff. *maraviense*, the picture is less apparent in that cover and performance metrics responded less clearly. Most conspicuously, shoot and leaf length were greatest under fire exclusion and lowest with late burning (ANOVA, shoot length: $F_{(2,96)}$ = 17.311, p << 0.001, η²$_g$ = 0.265; leaf length: $F_{(2,96)}$ = 15.578, p << 0.001, η²$_g$ = 0.348). Leaf number did not differ

among treatments (ANOVA leaf number: $F_{(2,96)} = 0.910$, $p = 0.406$, $\eta^2_g = 0.019$), and barely among years ($F_{(2,96)} = 2.469$, $p = 0.095$, $\eta^2_g = 0.019$) (**Tab. 6.1, S6.2**). The cover of this taxon remained stable and unchanged among treatments (ANOVA $F_{(2,66)} = 1.421$, $p = 0.248$, $\eta^2_g = 0.007$) and over time (ANOVA $F_{(2,103)} = 2.322$, $p = 0.103$, $\eta^2_g = 0.043$). Collectively, both geoxyle species showed poorer performance metrics under late burning, and the best metrics under early burning (*B. russelliae*) and fire exclusion (*C.* aff. *maraviense*), respectively.

Table 6.1: Development of three selected performance metrics from the two dominant geoxyle taxa in Cusseque according to time and treatment. Please see **Tab. S6.2** for the actual numbers behind the trends shown here. The metrics are shoot length (SL), leaf length (LF) and leaf number (LN). The arrows give information about how the metrics relate between different treatments, e.g., "Early vs. Late – SL: ↑**" refers to higher shoot lengths in early compared to late burning treatment. Testing for significant differences among treatments and among years within a treatment was done with a mixed ANOVA and posthoc pairwise t-tests with Benjamini-Hochberg correction. Levels of significance are as follows: $p < 0.0001$ ***; $p < 0.001$ **, $p < 0.05$ *, $p \leq 0.1$ °, $p > 0.1$ ns.

	Treatment/over time	Early	Late	No
Brachystegia russelliae	**Early vs.**	SL over time: ↑*	SL: ↑*	SL: ns
		LL over time: ↑*	LL: ↑**	LL: ↑**
		LN over time: ns	LN: ns	LN: ↓ *
	Late vs.		SL over time: → ns	SL: ↓ *
			LL over time: → ns	LL: ns
			LN over time: → ns	LN: ↓ *
	No vs.			SL over time: ↑*
				LL over time: → ns
				LN over time: → ns
Cryptosepalum aff. maraviense	**Early vs.**	SL over time: → ns	SL: ↑ *	SL: ↓ *
		LL over time: → ns	LL: ↓ *	LL: ↓ ***
		LN over time: → ns	LN: ns	LN: ns
	Late vs.		SL over time: ↓ °	SL: ↓ ***
			LL over time: ↓ ns	LL: ↓ ***
			LN over time: ↓ ns	LN: ns
	No vs.			SL over time: ns
				LL over time: ns
				LN over time: ns

Herbs:

Herb species varied in their reactions to the fire treatments. Some showed stronger increasing covers over time after being burned than not being burned, e.g. the annual *Emilia baumii* (Asteraceae) (**Fig. S6.1a**). Others like the perennial *Spermacoce dibrachiata* (Rubiaceae) showed strongly increasing cover under fire exclusion (**Fig. S6.1b**). Both herb cover and herb richness differed more strongly among years (ANOVA herb richness over time: $F_{(2,64)} = 8.780$, $p < 0.001$, $\eta^2_g = 0.074$) than among treatments (ANOVA herb richness among treatments $F_{(2,32)} = 0.748$, $p = 0.481$, $\eta^2_g = 0.032$). Furthermore, numbers of annual herb species increased over time (ANOVA $F_{(2,64)} = 27.425$, $p << 0.001$, $\eta^2_g = 0.283$) in burned plots (pairwise t-test $p_{adj.} = 0.001$), but not

in fire protected plots (pairwise t-test $p_{adj.}$ = 0.489) (**Fig. S6.2**). Generally, we observe a better performance and higher richness of (annual) herbs in burned plots, but with a high variance over time due to species-specific responses.

Stem heights:

The median stem heights of *Syzygium guineense* subsp. *macrocarpum* and *Monotes africanus* did not differ between treatments (Kruskal–Wallis: X^2 = 2.650, df = 2, p = 0.270). However, marked patterns emerged regarding the height distribution over time (**Figure 6.5**). Under early-burning treatment, upper bound of the variance increased and a greater proportion of taller stems occurred over time, although the majority of stem heights remained between 50 cm and 100 cm (Kruskal–Wallis: X^2 = 17.212, df = 2, p = 0.019). The opposite was observed under late burning, where variance decreased over time so that the majority of stems ranged between 50 cm and 80 cm (Kruskal-Wallis: X^2 = 24.232, df = 2, p < 0.001). Under fire exclusion, main stem heights decreased over time, ranging between 50 cm and 80 cm at the end, but a single stem escaped this pattern and continues to grow (Kruskal-Wallis: X^2 = 5.704, df = 2, p = 0.012). All stems that protrude so strongly from the main height range under early burning and fire exclusion belong to *Monotes africanus*. Furthermore, a one-time assessment of stem mortality for *S.g.* subsp. *macrocarpum* in 2019 revealed 59.8% and 65.9% of stems dead under early and late burning treatment, respectively, and 72.9% of stems dead under fire exclusion.
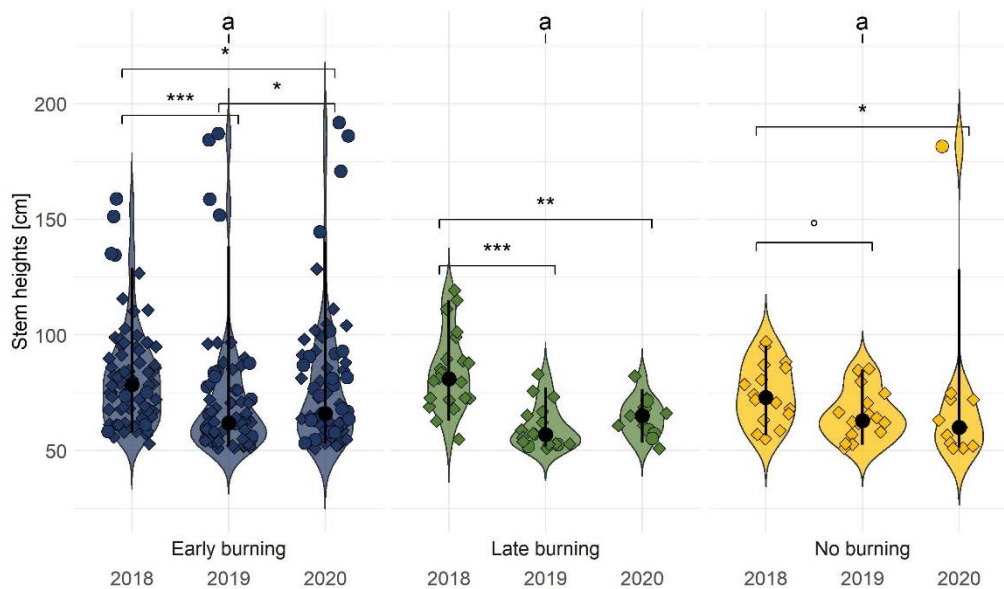
Figure 6.5: Comparison of the distribution of stem heights among treatments and years. Stems of at least 50 cm height from two taxa were measured: *Syzygium guineense* subsp. *macrocarpum* (diamonds) and *Monotes africanus* (circles), which are able to outgrow the dwarf shrub form to become trees, if disturbances cease long enough. The black ranges represent 95% confidence intervals, with the dot being the median. Testing for significant differences was done with non-parametric Kruskal–Wallis tests (significant differences indicated by different letters, threshold α = 0.05) and posthoc pairwise Dunn tests (significance level as follows: p < 0.0001 ***; p < 0.001 **, p < 0.05 *, p ≤ 0.1 °, p > 0.1 ns).

Species diversity

Over time, we recorded 187 different plant taxa within the experimental area (45 grasses, 50 geoxyles, 72 herbs, 11 trees, 9 others). Species numbers (S) ranged from 35 to 72, with on average 49.5 different species per 25 m² plot. However, S differed significantly among treatments over time (ANOVA $F_{(4,64)} = 2.594$, $p = 0.045$, $\eta^2_g = 0.039$) (**Tab. 6.2, S6.3**). The lowest numbers were recorded in unburnt plots (ranging from 36 to 59), the highest numbers in late-burnt plots (on average 5 species more than in unburnt plots, t-test $p_{adj.} = 0.012$) and early-burnt plots were intermediate (on average 3.3 species more than in unburnt plots, t-test $p_{adj.} = 0.076$). S increased over time under early burning (on average 5.5 species more in 2020 than in 2018, t-test $p_{adj.} = 0.061$) but not in late burning (t-test $p_{adj.} = 0.197$), and remained stable in unburnt plots. This observation is particularly driven by herb species, whereas grasses showed rather uniform species numbers among treatments and over time. All functional groups had their lowest S in unburnt plots, but this was significantly so only for geoxyles (ANOVA $F_{(2,104)} = 4.268$, $p = 0.017$, $\eta^2_g = 0.076$; grasses: $F_{(2,104)} = 1.965$, $p = 0.145$, $\eta^2_g = 0.036$; herbs: $F_{(2,104)} = 2.399$, $p = 0.096$, $\eta^2_g = 0.044$). Across all treatments, geoxyles and grasses had similar means of 14.9 ± 3.2 and 15.3 ± 3.0 species per plot, respectively, while herbs had 17.5 ± 3.4 species.

Species diversity, measured by the Shannon index (H'), differed among treatments (ANOVA $F_{(2,32)} = 4.087$, $p = 0.026$, $\eta^2_g = 0.145$) and among years (ANOVA $F_{(2,64)} = 5.142$, $p = 0.008$, $\eta^2_g = 0.051$) (**Tab. 6.1, S6.2**). On average, H' was lower by 0.200 in early burnt (t-test, $p_{adj.} = 0.002$) and by 0.218 lower in unburnt (t-test, $p_{adj.} = 0.001$) than in late-burnt plots, making this treatment the one with highest, and over time increasing, species diversity (by 0.228 from 2019 to 2020, t-test, $p_{adj.} = 0.049$). Unburnt plots showed lowest H', particularly with regard to grasses, whereas both fire treatments had a strongly promoting effect on herb diversity. Herbs showed the overall highest H' (ranging between 1.8 and 3.1), followed by grasses (between 1.1 and 2.8) and geoxyles (between 0.5 and 1.9).

Similarly, species evenness (J') differed among treatments (ANOVA $F_{(2,32)} = 3.332$, $p = 0.048$, $\eta^2_g = 0.119$) and years (ANOVA $F_{(2,64)} = 2.913$, $p = 0.062$, $\eta^2_g = 0.031$) (**Tab. 6.2, S6.3**). Late-burnt plots showed higher J' than early burnt (by 0.048, $p = 0.004$) or unburnt plots (by 0.041, $p = 0.009$). There was little change over time, only J' in early-burnt plots declined slightly (by 0.04 from 2018 to 2020, $p = 0.059$). Stronger effects become apparent with regard to the functional groups. Geoxyle J' declined slightly over time in early-burnt plots, and grass J' drops strongly (but insignificantly) in unburnt plots. Increasing J' can be observed for grasses in early burnt plots and in general for herbs, which show strong gains in all treatments, especially from 2018 to 2019.

Table 6.2: Species richness (S), diversity (Shannon index, H') and evenness (J') according to functional group, time and treatment. Please see **Tab. S6.3** for the actual numbers behind the trends shown here. The calculations are done separately for grass (top), geoxyle (middle) and herb species (bottom). The arrows give information about how the values relate between different treatments, e.g., "Early vs. No – H': ↑***" refers to higher species diversity (Shannon index) values in early compared to no burning treatment. Testing for significant differences among treatments and among years within a treatment was done with a mixed ANOVA and posthoc pairwise t-tests with Benjamini-Hochberg correction. Where necessary because parametric requirements were not met, results were confirmed with non-parametric Kruskal–Wallis and posthoc Dunn tests. Levels of significance are as follows: $p < 0.0001$ ***; $p < 0.001$ **, $p < 0.05$ *, $p \leq 0.1$ °, $p > 0.1$ ns.

Treatment/ over time		Early	Late	No
Grasses	**Early vs**	S over time: → ns	S: ns	S: ns
		H' over time: ↑ **	H': ns	H': ↑ ***
		J' over time: ↑ *	J': ns	J': ↑ ***
	Late vs.		S over time: ↑ *	S: ns
			H' over time: ↓ns	H': ↑ ***
			J' over time: → ns	J': ↑ ***
	No vs.			S over time: → ns
				H' over time: → ns
				J' over time: → ns
Geoxyles	**Early vs.**	S over time: → ns	S: ns	S: ns
		H' over time: ↓ *	H': ↓ °	H': ns
		J' over time: ↓ *	J': ns	J': ns
	Late vs.		S over time: → ns	S: ↑ *
			H' over time: → ns	H': ↑ *
			J' over time: → ns	J': ↑ *
	No vs.			S over time: → ns
				H' over time: → ns
				J' over time: → ns
Herbs	**Early vs.**	S over time: ↑*	S: ns	S: ns
		H' over time: ↑ ***	H': ns	H': ns
		J' over time: ↑ ***	J': ns	J': ns
	Late vs.		S over time: ↑ ns	S: ns
			H' over time: ↑ ***	H': ns
			J' over time: ↑ ***	J': ns
	No vs.			S over time: → ns
				H' over time: ↑ °
				J' over time: ↑ ***

Discussion

Different fire treatments have specific effects on the functional groups within the ground layer

Fire experiments have been running for decades in various savanna and woodland systems in Africa. However, few studies have addressed the components of the ground layer, and those were conducted in South Africa (Uys *et al.*, 2004), Zimbabwe (Matayaya *et al.*, 2017) or comparable ecosystems in the Cerrado in Brazil (Pilon *et al.*, 2021). No ground-layer studies are published so far from the wetter Miombo region. Thus, we here present the first experimental study on the effects of fire seasonality in a miombo geoxyle grassland, though the short running time of the experiment has to be kept in mind.

Each of the applied fire treatments seemed to promote a different functional group, in that it performed better (**Figs. 6.4** and **6.5**; **Tab. 6.1**) and increased cover (**Fig. 6.3**). Over three years, grasses benefitted from fire exclusion, geoxyles from early burning, and herbs from late burning. For geoxyles, our results are hard to compare with those of other studies because this functional group tends to be treated either as (sub)shrubs (Ratter *et al.*, 1997; Durigan *et al.*, 2020), as forbs (Uys *et al.*, 2004; Smith *et al.*, 2013; Trollope *et al.*, 2014), or as non-existent. We chose to look at geoxyles separately because (a) they constitute an important part of tropical grasslands in Angola (Zigelski *et al.*, 2019), and (b) they behave ecologically differently from shrubs, non-woody herbs or forbs, and grasses, as shown in this study.

Geoxyles resprout quickly after the end of the main frost season (August onwards) and start to bloom and fruit before the grasses do so in the peak rainy season (January onwards), which gives them the advantage of mostly concluding their annual cycle before the grasses overshadow them (Trapnell, 1959; Fidelis & Blanco, 2014; Zigelski *et al.*, 2019). This head start is particularly advantageous if it follows the burning of the grassland. Reduced competition for light and nutrients, brimming underground storage organs and bud banks, plus a nutrient boost from the ashes, promote rapid resprouting (Pausas *et al.*, 2018; Buisson *et al.*, 2019). Thus, geoxyle cover thrived under an early burning regime, which was mostly attributed to the particularly well-performing *Brachystegia russelliae*, the dominant geoxyle species in this ecosystem.

However, if no burning takes place, the head start advantage dissipates in the dense grass layer. Likewise, when burning occurs too late in the dry season, the geoxyles have already resprouted and partially depleted their underground reserves (West, 1965; Miyanishi & Kellman, 1986; Schutz *et al.*, 2011). The second resprouting after late burning was therefore poorer (**Tab. 6.1**), further depleting the reserves, and the seasonal head start was nullified. In addition, late burning shortened the period of lower competition by 4 to 6 weeks and affected the annual assimilation balance correspondingly. This effect was strong: after the short time of 3 years, the geoxyles' aboveground cover decreased by about 20% (**Fig. 6.3**).

The reduction of geoxyle cover was consistent with the increased cover of grasses and herbs. As occurred in other studies, we observed that fire exclusion did not benefit herbs whereas burning

did, regardless of the timing (Uys *et al.*, 2004; Sawadogo *et al.*, 2005). The reduced competition by either grasses or geoxyles were likely reasons for this observation (Overbeck *et al.*, 2005), even allowing for annual species to germinate on burned, ash-fertilized patches. The observed decline of (perennial) grasses under early burning treatment has also been reported from wet savannas in West Africa (Sawadogo *et al.*, 2005; Laris & Wardell, 2006), in response to increased tree cover. Analogously, the increased "underground tree" cover in our experiment might result from a tipped balance between geoxyles and grasses due to poorer performance from the latter. The dominance of grasses in the unburned plots was probably just the effect of accumulated grass biomass over the 3 years. Most studies of tropical grasslands report a decline of grasses if not burned over a longer time (Fynn *et al.*, 2004; Smith *et al.*, 2013; Durigan *et al.*, 2020), and 3 years is a too-short time span for robust inferences in this regard.

   All other publications on fire experiments from savannas report that trees and shrubs profit from fire exclusion, if no other disturbances like herbivory are in place (Bond & Keeley, 2005; Mills & Fey, 2005; Archibald & Hempson, 2016). Strikingly, we did not observe this. Tree cover and species number did not change significantly over time for all treatments (not shown), and stem heights declined on average under fire protection (**Fig. 6.5**). Only the negative effect of a late fire treatment on trees was in line with previously reported findings (Aubréville, 1953; West, 1965; Brookman-Amissah *et al.*, 1980; Laris & Wardell, 2006; Laris *et al.*, 2017). However, tree growth being stimulated more by early burning than by fire exclusion stood out because in the studies cited here it has always been reported the other way around. We interpret this as an effect of ash fertilization for the trees after burning (Jensen *et al.*, 2001; Pivello *et al.*, 2010; Oyedeji *et al.*, 2016), in combination with another disturbance acting on all plants: nocturnal frosts (Finckh *et al.*, 2016). Because the study area is not home to big domestic or native herbivores (Huntley *et al.*, 2019), frost is very likely the key factor in keeping the majority of the stems so low. Moreover, frost affects densely grass-covered sites more severely than bare (burnt) patches, because at night, the air-filled grass layer reduces thermal radiation from the ground, while radiation from the grass layer to the open sky continues (Leuning, 1988). This causes lower minimum temperatures above the grass layer, with more frost damage and photoinhibition impairing tree growth (Ball *et al.*, 1997). This is in line with our finding that, although most stems of *Syzygium guineense* die back during the frost season (personal observation), the highest proportions of dead stems occurred in unburnt plots. Frost occurs reliably and often from end of May to beginning of September at the study site, with up to 40 events per dry season and an occurrence peak in July (Finckh *et al.*, 2021). Fires in contrast are set only after the first frosts, when more frost-killed, combustible biomass is available. For trees, particularly those with a tropical background and little frost resistance like *Syzygium guineense* or *Monotes africanus*, early fires are beneficial because they offset the effect of frost. Increased nutrient availability on burnt plots might also allow more stems to escape the fire and frost trap due to faster growth (Wakeling *et al.*, 2011).

Specific effects of the fire treatments on the functional groups are reflected in their performance metrics

Looking at the species and their performance level, we observed marked differences, for example regarding increased flowering of some grass species. Fire-stimulated flowering in grasses has been reported before (Lamont & Downes, 2011), and Fidelis and Blanco (2014) reported increased flowering vigour of burnt compared to unburnt grasses. However, we also observed stronger flowering for some grass species under fire protection, which contradicts previous long-term observations of increased fire-stimulated flowering (Zirondi *et al.*, 2021). *Trachypogon spicatus* has been reported as a fire winner (Furley *et al.*, 2008), but appeared in our study as a fire loser (**Fig. 6.4**), which points either to a site specific or short-term effect. The majority of the grass species, however, increased the number of flowering culms under the late-fire regime, which was in line with previous studies (Zirondi *et al.*, 2021).

As shown and discussed above, geoxyle species also responded differently to fire treatments. In contrast to *B. russelliae*, the second dominant species, *Cryptosepalum* aff. *maraviense*, remained quite unchanged and showed increased growth only under fire exclusion (**Tab. 6.1**), but with unchanged cover (not shown). We interpret this as increased versatility compared to *B. russelliae*, in that this very low and dense growing species (max 10 cm height) is adapted to light conditions in the understorey of grasses and does not need special fire treatments, at least not at the time scales studied so far. *Cryptosepalum* and *Brachystegia* both form a massive network of underground woody rhizomes in the study area (Revermann *et al.*, 2017, Meller *et al.*, 2021b), implying that the poorer aboveground performance under late burning treatment (**Tab. 6.1**) might in the long run also go along with a decline on woody belowground biomass.

Burning enhances species richness and diversity

There is ample evidence in the literature that in fire-adapted ecosystems, burning has a positive effect on richness and diversity of flora and fauna (He *et al.*, 2019), at least under the condition that the fire regime represents an intermediate disturbance regime (Connell, 1978; Huston, 1979). Fire suppression on the other hand leads to diminished diversity (Smith *et al.*, 2013), structural change (Higgins *et al.*, 2007) and changed species compositions (Brookman-Amissah *et al.*, 1980; Uys *et al.*, 2004; Van Wilgen *et al.*, 2007), all of which we also observed in our experiment (changes in species composition will be published separately).

It is important to take the seasonal timing of burning into account. Early dry-season fires promote native plant diversity against invasive species (Kral *et al.*, 2018) and allow for enhanced tree and shrub growth (Laris & Wardell, 2006; Furley *et al.*, 2008), as they are not as severe as late dry-season fires due to lower and wetter fuel loads (Govender *et al.*, 2006; Rissi *et al.*, 2017). Other studies reported highest diversity at fire-protected sites due to recruitment of shade-tolerant species (Brookman-Amissah *et al.*, 1980). These studies were conducted in woodland or savanna contexts, however, where larger shrubs and trees come into play. In the geoxyle grassland of our study, we observed highest plant diversity at late-burned sites, which can easily be explained by

reduced competition from perennial grasses and geoxyles, which allowed annual and herb species to step up (Savadogo *et al*., 2008; Fidelis & Blanco, 2014).

Although grasses dominated the unburnt plots cover-wise, their richness and diversity were lower than in the burnt plots (**Tab. 6.2**). In contrast, herb cover, richness, diversity and evenness increased in all three treatments over time. Similar findings have been reported from long-term experiments in South African grasslands (Fynn *et al.*, 2004), and these too were due to changed species compositions between burnt and unburnt plots (not shown). Either recruitment of more shade-tolerant herb species might have happened here, or we measured an artefact caused by surveys taking place some weeks later in the year in 2019 and 2020. The pattern for geoxyles was controlled by the response of the dominant geoxyle *B. russelliae*. Because it thrived under early burning, the evenness for all geoxyle species was reduced in such plots. Contrariwise, geoxyle richness, diversity and evenness were increased under late burning, because *B. russelliae* was disadvantaged and offered space to other geoxyle species. Likely, the overall plant diversity was high in our study area because at landscape level, different fire regimes occur over space and time that offer a suitable level of pyrodiversity (Parr & Brockett, 1999; Parr & Andersen, 2006).

Conclusion

We show the effects of early and late dry-season fires and fire exclusion on the vegetation structure of a geoxyle grassland in Angola. Although we can only infer short-term effects from our findings, as much longer observation times are needed for more robust, long-term conclusions, we nevertheless reveal grassland dynamics that were not reported before. The high beta diversity of the study site is likely a product of the variable use of fire by the locals, leading to a patchy and pyrodiverse landscape (Trauernicht *et al.*, 2015). The timing of fire balances the structure and composition of the ground layer, and tips the scales towards different functional groups. Strikingly, tree and shrub growth did not improve in fire protected plots, like reported from numerous other fire experiments. Rather, tree growth is impaired even in the absence of fire, which implies that a different disturbance type, most likely frost, is keeping the grasslands open.

-VII-

Basananthe baumii
var. caerulescens
(Passifloraceae)

Frost-driven lower treelines in Angola and their implications for tropical forest-grassland mosaics

Manfred Finckh, Janika Wendefeuer, **Paulina Meller**

Abstract

Questions: Forest-grassland boundaries in the tropics are primarily interpreted as driven by fire and herbivory. So far, frost has received little attention as driver of tropical vegetation boundaries. Here, we study mid-altitudes in south-central Africa and ask the following questions: a) Is there a lower treeline between grasslands and forests on the Angolan Plateau? b) If so, do topoclimatic differences play a role in it? c) What do our results imply for tropical highlands globally?

Location: The Angolan Plateau (10°-16°S and 13°-21°E).

Methods: We mapped vegetation by applying a supervised support vector machine based classification on a Landsat satellite image. We used a 1000 m spaced point grid to extract the mean vertical distribution of the vegetation units from a digital elevation model. The topographic position of each point was calculated using a channel network approach. Microclimatic data were collected across topographic gradients at two sites along the Plateau. Analyses focused on the number of nights where temperature dropped below 0°C, median and minimum temperatures, and diurnal temperature ranges.

Results: Lower treelines separate miombo forests from geoxyle grasslands in all major valley systems. Treelines are located 150–200 m below the headwater divides. Nocturnal outgoing net longwave radiation and resulting cold-air pooling cause frequent frosts in the valleys during the dry season. Topography controls frost patterns, with minima of down to -7.5°C and diurnal temperature amplitudes up to 40°C.

Conclusions: The results show that vegetation patterns in central Angola are shaped by frost. The processes causing frost depend on air humidity. Drier atmosphere and lower global temperatures indicate a longer frost season, lower minima and frost extending to lower elevations and latitudes for the Pleistocene. Pleistocene forest fragmentations and the rise of endemism-rich grasslands in comparable tropical highlands worldwide may be explained by crossing thermic thresholds via increasing seasonal aridity.

Keywords: Climate seasonality, cold-air pooling, forest–grassland mosaics, geoxyle grasslands, lower treelines, miombo ecosystems, Pleistocene forest fragmentation, radiation frost, south-central Africa, topography, tropical highlands, vegetation patterns.

Introduction

The altitudinal position of climate-driven treelines and their ecological explanation has fascinated researchers since Alexander von Humboldt. The essence of a treeline is hereby a boundary along an elevation gradient between tree-favourable (forests) and tree-adverse habitats (e.g. alpine grasslands). Despite sound global syntheses of upper treeline positions (e.g., Körner, 1998; Troll, 1973), new aspects are still appearing (e.g., the study by Irl *et al.* (2016) on upper treelines of oceanic islands).

Lower treelines, where forests occur at higher elevations than treeless habitats, have been less studied. This is due to the fact that lower treelines have, in most cases, been modified by pastoral land uses and anthropogenic fires, as they are normally drought and not temperature driven (e.g., Means, 2011). However, especially in boreal and temperate continental areas, temperature-driven inversions of vegetation zones occur in high-lying closed valleys, dolines or poljes. Such depressions, where cold air accumulates during clear, winter nights, can be among the coldest places in mountain ranges (e.g., Ogrin (2007) for Slovakia; Lehner *et al.* (2017) for Austria) and frequently show vegetation inversion (Clements *et al.* (2003) for Utah and Finckh (1993) for Chile) or lower treelines (Coop and Givnish (2007) for New Mexico).

Forest–grassland boundaries also occur in other contexts, where they are not addressed as treelines. In tropical regions throughout the world forest–grassland mosaics cover a substantial part of the land surface. In general, such landscapes are considered "savannas" and interpreted as results of a fine balance of fire, waterlogging and/or megaherbivory (Oliveras & Malhi, 2016). This dominant narrative obscures the discussion on other drivers of forest–grassland boundaries, particularly in tropical highlands.

Joint features of forest–grassland mosaics in tropical mid-altitudes are their high diversity and high share of endemic taxa, such as in the biodiversity hotspots of the Brazilian Cerrado (Myers *et al.*, 2000), the Indian Western Ghats (Sankaran, 2009), the Patana highlands of Sri Lanka (Mueller-Dombois & Perera, 1971) and the Ethiopian highlands (Wang *et al.*, 2020). The Angolan Plateau is such a biodiverse tropical forest–grassland mosaic and, like the Brazilian Cerrado, contains a striking diversity of geoxylic suffrutices (i.e., dwarf shrubs with belowground bud banks and extensive woody storage organs in the form of roots, rhizomes or tubers — referred to as geoxyles) which evolved in both regions convergently from many different lineages (Simon & Pennington, 2012; Maurin *et al.*, 2014). These features indicate that the above-listed grassland ecosystems have a long evolutionary history (Veldman *et al.*, 2015; Nerlekar & Veldman, 2020).

The forest–grassland mosaic on the Angolan Plateau occurs in a rolling landscape with wooded hills and open valleys. Although grassland fires in the dry season are a common aspect of these landscapes, they are unlikely to be responsible for the forest–grassland layout (Finckh *et al.,* 2016), because their spatial patterns do not respond to the physical logics of wildfires. The stunning diversity of geoxyles on the Angolan Plateau (Zigelski *et al.*, 2019a), which Maurin *et al.* (2014) interpreted as the result of an evolutionary adaptation to fire, can just as well constitute an

avoidance strategy against frost (Gomes *et al.*, 2019; Hoffmann *et al.*, 2019). The forest–grassland boundaries look strikingly like the lower treelines in the temperate regions described above. Yet, temperature–controlled lower treelines from tropical regions are not well studied, with the exceptions of Young (1993) who reported on lower treelines in the Peruvian Andes and Duker *et al.* (2015, 2020) who pointed at frost as a principal driver for the (lower) vegetation boundary between the Albany subtropical thicket and Nama-Karoo semi-desert shrubland. Such treelines, however, are likely to be more common, because tropical taxa are very sensitive to low and strongly varying temperatures (Sakai & Larcher, 1987).

We therefore aim to broaden the discussion about tropical forest–grassland mosaics by analysing a stunning and thus far ignored example of lower treelines in tropical highlands. We combined a remote sensing approach to classify vegetation units and infer their altitudinal preferences with in-situ microclimatic measurements at different scales across the Angolan Plateau. By quantifying the extent of forest–grassland boundaries and the occurrence of frost across these boundaries, we aim to provide answers to the following questions: is there a) a frost-driven boundary (i.e., treeline) between grasslands and forests on the Angolan Plateau, and if so b) do topoclimatic differences play a role in it? c) What do our results imply for similar tropical highlands around the world?

Materials and Methods

Study area

The Angolan Plateau extends from Huíla Province in western Angola to Moxico Province in eastern Angola, from approximately 10°–16°S and 13°–21°E. We selected an area from 12°–14°S and 18°–20°E for a treeline analysis (**Fig. 7.1**). We chose this area because it is one of Angola's most remote and least populated regions with forest–grassland patterns that are widely undisturbed by agriculture or settlements.

The vegetation of the study area is dominated by wet miombo forests, intersected by geoxyle grasslands in the valleys and narrow bands of peaty wetlands along the small streams (Stellmes *et al.*, 2013b). Miombo forests are mostly dense stands dominated by *Brachystegia spiciformis*, *Cryptosepalum exfoliatum* subsp. *pseudotaxus* and *Julbernardia paniculata* (Revermann *et al.*, 2018) whereas geoxyle grasslands are dominated by species like *Brachystegia russelliae* on Plinthosols and *Parinari capensis* on Arenosols (Gomes *et al.*, 2019).

Climate measurements were conducted in two different sectors of the Angolan Plateau, namely at Bicuar National Park (15.1°S 14.8°E, 1235 m asl) and Cusseque (13.7°S 17.1°E, approximately 1530 m asl), covering a broad west–east extension and an altitudinal span of approximately 300 m (see **Fig. 7.1**).

There are two reasons for the spatial mismatch between the area used for our remote sensing analysis and the main logger transect in the neighbouring upper Cusseque valley. First, the disparity is caused by the inaccessibility of the former, which is also the main reason for its intactness. When we started the logger transect in 2011, the area was still littered with minefields, leftovers of the

decades-long civil war. The interprovincial road EN140, which cuts across the Cusseque valley, allowed for safe and easy access for logger maintenance but had already started to cause degradation of the forest landscape (see **Fig. 7.2**, wherein the patches indicate fallows and cut-down forest). The second reason for the spatial mismatch between the two areas is that we looked for a mostly intact and little disturbed Landsat image for the remote sensing analysis. The next Landsat path to the west, which would have included the Cusseque area, was largely transformed by agricultural land use and has lost its natural vegetation patterns. However, the spatial configuration of forests and grasslands in the Cusseque area is comparable to the still-intact landscapes further east (see **Fig. S7.1**). For the sake of comparison, we included microclimatic measurements from Bicuar National Park which is approximately 295 km south-west of the Cusseque area but corresponds in elevation to the lower parts of the remote sensing study area. We are not aware of any other microclimatic measurements from valleys on the Angolan Plateau at this elevation.

All taxon names follow The Plant List (http://www.theplantlist.org).
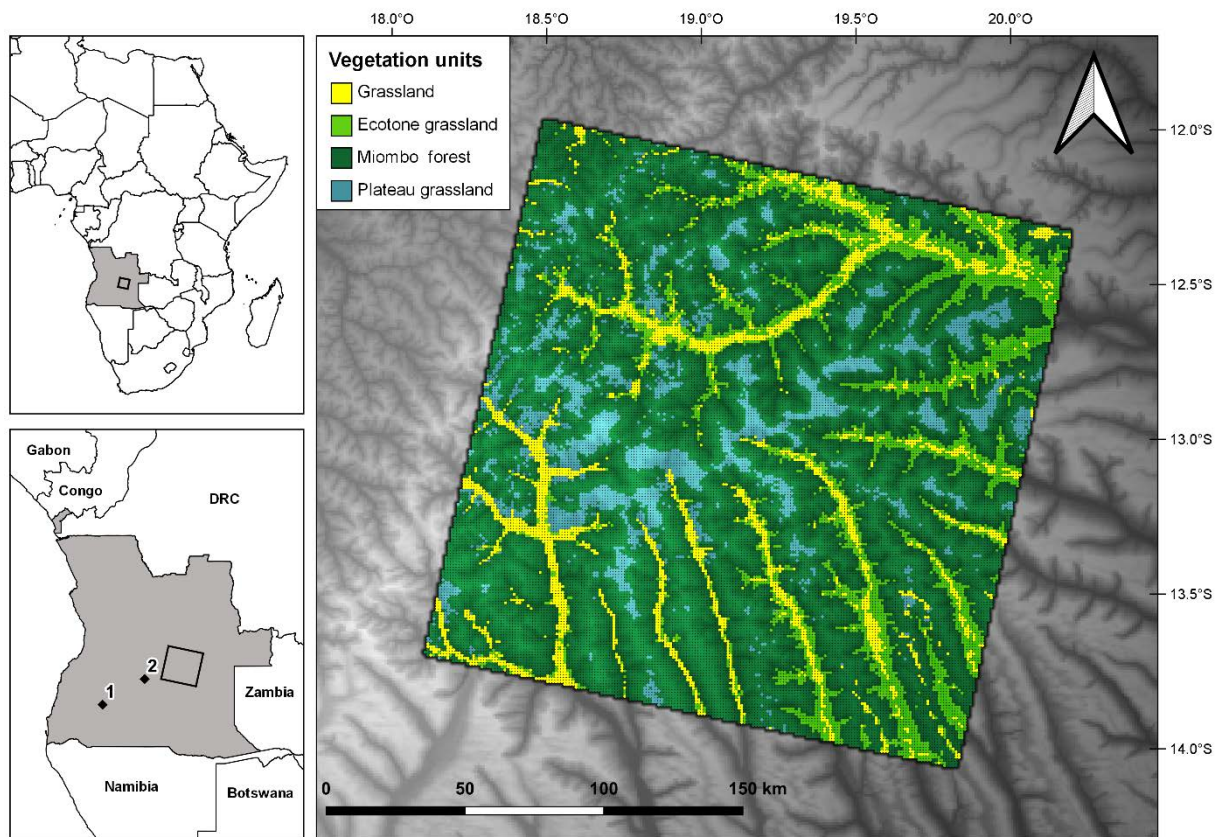
Figure 7.1. Upper and lower left: location of the study sites on the Angolan Plateau: square) study site for the spatial treeline analysis; numbers) sites of microclimatic measurements on the Angolan Plateau: 1 - Bicuar National Park, 2 - Cusseque. Right: vegetation units of the study site on the Bié Plateau following a support vector machine based classification (SVM) (Kappa-value of 0.79 and an overall-accuracy of 0.86) (Landsat 8 Level-1C, path/row 178/70).

Satellite data acquisition and analysis

We used a recent Landsat 8 Level-1C tile (path/row: 178/70; 2017-08-10T14:49:22z) covering an area from approximately 12°–14°S and 18°–20°E from the USGS Earth Resources Observation and Science Center archive (https://earthexplorer.usgs.gov/). We chose a dry season scene with the lowest cloud cover (<10%) and used only Operational Land Imager bands 2, 4 and 5. The phenological state of the vegetation in the advanced dry season (10 August) allowed for clear differentiation between forest and grassland vegetation. Additionally, we used the digital elevation model (DEM) from the Shuttle Radar Topography Mission (SRTM) (https://www2.jpl.nasa.gov/srtm/) with a 90 m resolution. The Landsat 8 images were resampled into a 90 m resolution using the nearest neighbour algorithm (Cover & Hart, 1967).

We calculated the normalized difference vegetation index (NDVI) (Tucker, 1979; Silleos *et al.*, 2006) for the scene and conducted a supervised support vector machine (Muñoz-Marí *et al.*, 2010) based classification, including the DEM and training and test polygons. Based on existing information from the upper Cubango basin (vegetation map by Stellmes *et al.* (2013b), and vegetation classification by Revermann *et al.* (2018)), we identified the four structurally defined dominant vegetation types (i.e., Miombo forests, Ecotone grasslands, Grasslands and Plateau grassland) in the area and selected corresponding training polygons. *Miombo forest* includes all close-canopy stands, *Ecotone grassland* refers to sparse open-canopy woodlands, *Grassland* refers to open geoxyle-grasslands with a high cover of broad-leaved geoxyle species, and *Plateau grassland* refers to more densely covered open lands, dominated by graminoids, with higher standing biomass. We calculated the overall accuracy and Kappa-value of the classification (Congalton, 1991).

We placed a point layer grid with a rectangular distance pattern of 1000 m x 1000 m over the classification and the DEM. Due to the spatial resolution of the SRTM data and the corresponding resampling of the Landsat data, we classified the vegetation according to broad structural types. We extracted the vegetation unit, elevation and geographical coordinate for each point and calculated mean vertical distribution and vertical distribution along a west–east gradient for the vegetation units. We conducted a one-way analysis of variance with Tukey's method for multiple comparisons to test for differences in mean altitude between vegetation units.

Furthermore, we sampled the gradient along valley slopes by creating a valley depth grid. Therefore, the altitudinal distance to the next (interpolated) ridgeline was calculated for each grid cell using the DEM. Results gave a measure of how deep each grid cell was inserted in a valley, with the drainage lines always having the lowest depths. This valley depth grid was then transferred into polygons with an altitudinal equidistance of 50 m ranging from 0 m at the headwater divides, which constitute the highest ridges between hydrographic basins, to less than -250 m for the lowest valley bottoms. Finally, we calculated the proportion of each vegetation unit according to its altitudinal position.

Calculation were conducted with SAGA 2.1.4 (Conrad, 2012; Conrad *et al.*, 2015) (see **Fig. S7.2**

for settings used) and R version 3.6.0 (R Core Team, 2019). Maps were drawn with the geographic information system (GIS) QGIS 3.2.0 (QGIS Development Team, 2019).

Microclimatic measurements

In November 2011, we established a network of Gemini Tinytag® PLUS 2 temperature data loggers (TT) in the Cusseque and Sovi valleys in Bíe province forming three valley cross sections (transects) (**Fig. 7.2**). The probes were mounted below wooden boards 0.3 m above ground and recorded the mean temperature per 15 min interval. The height above ground corresponded to the upper grass layer, where we expected the lowest temperatures during night frosts in the dry season (Ball *et al.*, 1997). In addition, the low height reduced the visibility of the logger stations and thus also vandalism by curious youths. For this study, we used the data from 12 selected loggers with a complete seasonal time series between 2012 and 2016. Four loggers were located in the closed canopy Miombo forest, three in the Ecotone grassland and five in the Grassland (**Fig. 7.2, Tab. S7.1**). Plateau grasslands were not found in the Cusseque area, which is why we did not provide microclimatic measurements for this vegetation unit. Additionally, from 2015 onwards, ambient temperatures were measured with an automated weather station (AWS) from the SASSCAL WeatherNet network (Muche *et al.*, 2018). An Adcon TR1 Temp/Rh Sensor at a height of 2 m recorded temperatures from March 2015 to June 2017.
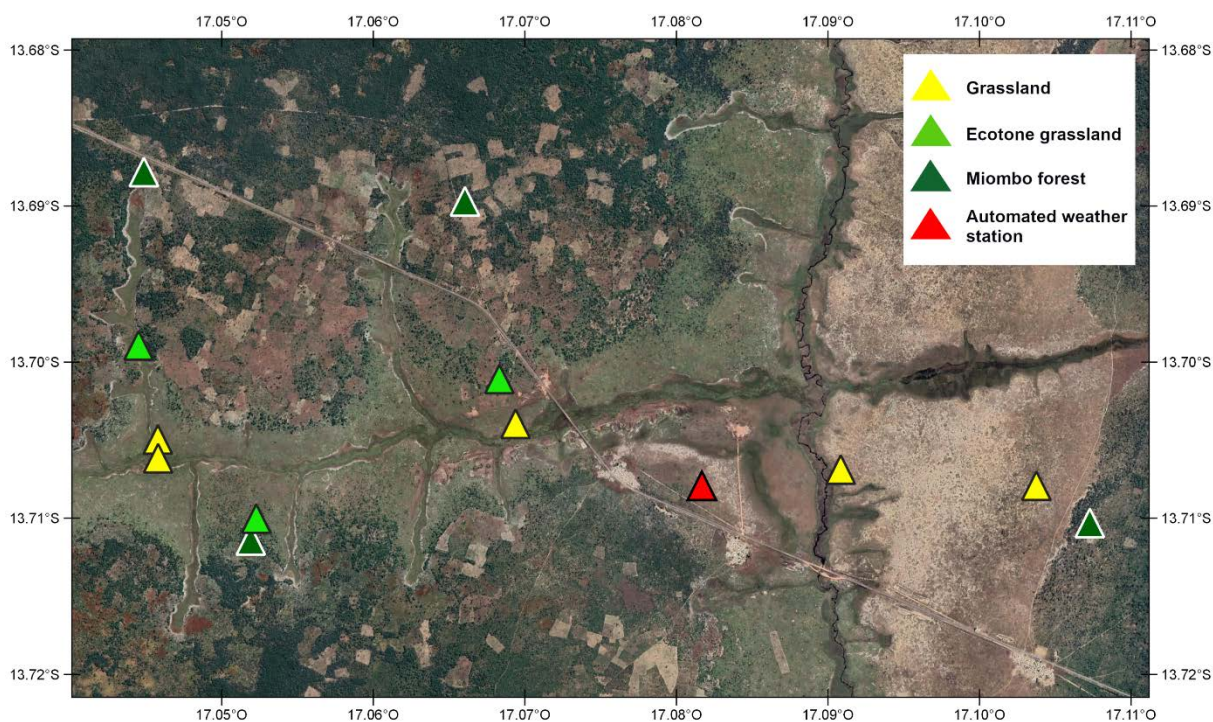
Figure 7.2. Detailed positions of the temperature data loggers in the Sovi (east-west) and Cusseque (north-south) valleys, Bié Province, Angola, coloured according to habitat. The red triangle marks the position of the AWS in Ecotone grasslands. The wider surroundings and landscape configuration of the study area are shown in **Fig. S7.1**. Image © Maxar (Vivid) imagery captured on 28 Mai 2019.

We cleaned the data by removing time periods with missing or erroneous data, caused by vandalised or defective probes or temperature peaks due to fires. Afterwards, we calculated the number of nights where temperature dropped below 0°C (hereafter referred to as frost nights), annual minimum temperature, daily mean temperature and the highest diurnal temperature range during frost season (1 May–1 October) for each logger. We tested these parameters for differences between habitats at a significance level of $\alpha \leq 0.05$, using Kruskal-Wallis and post-hoc Dunn tests with Bonferroni correction (Dunn, 1961). Analysis was done using the R package dunn.test (Dinno, 2015). Furthermore, for illustration purposes, we plotted the temperature profiles for the frost night on 10–11 August 2015.

For all logger locations at the Cusseque site, including the AWS, we established the fire history based on data from the Moderate Resolution Imaging Spectroradiometer. We used the Google Earth Engine to retrieve the MCD64A1 Version 6 Burned Area data product. We used the middle date of the 8-day window given by the burned area data product to simultaneously plot the seasonal occurrence of all fire and frost events. The recording periods for frost and fire events are given in **Tab. S7.1**, data of fire events in **Tab. S7.2**.

In contrast to the logger network at Cusseque, which included forest, ecotone grassland and grassland, only grassland sites were measured in Bicuar National Park. The compiled climate parameters were the same as listed above for Cusseque. Temperature data was again acquired with an AWS from the SASSCAL WeatherNet network with the same sensors and sensor height, installed on the mid-slopes of the geoxyle grassland, and with a single Gemini Tinytag® PLUS 2 Logger at ground level. The AWS has provided continuous climate data since March 2015. The Tinytag® Logger was installed in June 2017 at a distance of 400 m from the AWS in a similar topographic position and recorded the mean temperature at 15 min interval. Because the temperature sensors for AWS and TT were placed at different heights, they recorded slightly divergent temperatures, particularly for high temperatures. For precise positions and available data per logger, please see the list of loggers and AWS in the supporting information given in **Tab. S7.1**.

Results
Vegetation patterns

Four vegetation types were identified in the GIS study area (**Fig. 7.1**): a) grasslands on the high-lying inter-watershed plains of the Bié Plateau (Plateau grassland) dominated by C4-grasses, sedges and geoxyles like *Protea spp.* and *Pygmaeothamnus zeyheri*; b) closed-canopy Miombo forest, dominated by *Cryptosepalum exfoliatum ssp. pseudotaxus* and *Brachystegia spp.*; c) geoxylic Ecotone grassland sparsely interspersed with trees, dominated by savanna tree taxa like *Monotes spp.* and *Combretum spp.*, geoxyles like *Brachystegia russelliae*, and tall C4-grasses (here, trees tend to be located at elevated positions such as large termite hills); d) dry geoxyle Grasslands, dominated by *Brachystegia russelliae* or by *Parinari capensis* together with many other geoxyle species and C4-grasses (for detailed vegetation descriptions, see Revermann *et al.* (2018)).

Settlements, agricultural and silvicultural land uses were virtually absent in the area. The supervised support vector machine based classification showed an overall accuracy of 0.86 and a Kappa-value of 0.79. This satisfactory classification accuracy is due to the marked differences in vegetation structure on which the classification scheme is based. Visual interpretation of the results indicated that most errors were related to misclassifications between Grassland and Plateau grassland.

The four vegetation types differ significantly in altitudinal distributions (**Tab. 7.1**). Plateau grassland is dominant above 1600 m. Miombo forest and Plateau grassland coexist between 1450 m and 1600 m. Grassland does not occur above 1350 m and Miombo forest is absent below 1250 m. The limit between Miombo forests and Grasslands at the slopes is sharp. The first quartile of the former is more than 30 m above the third quartile of the latter. The altitudinal distance towards the Ecotone grassland is still larger, with their third quartile at 1304 m. The sharp lower treeline is also discernible on the vegetation map (**Fig. 7.1**), where the open habitats (in light green and yellow) delineate the valley network of the Angolan Plateau.

Table 7.1: Distribution of vegetation units along the altitudinal gradient on the Angolan Plateau, with minimum, first quartile, mean, third quartile and maximum altitude of each vegetation unit. The number of points used for unit classification and analysis is also provided. A one-way ANOVA, followed by Tukey HSD post hoc test with 95% family-wise confidence level, was used to test for significant differences between the mean altitudes of vegetation units. All vegetation units had significantly different altitudinal occurrences ($F_{3,37345}$ = 13347, p < 0.001).

Vegetation unit	n of points	minimum altitude [m]	1st quartile [m]	mean altitude [m]	3rd quartile [m]	maximum altitude [m]
Grassland	3377	1175	1244	1289 [a]	1336	1398
Ecotone grassland	4945	1172	1247	1277 [b]	1304	1387
Miombo forest	25455	1271	1369	1416 [c]	1461	1650
Plateau grassland	3572	1372	1429	1478 [d]	1522	1673

The Ecotone grasslands are primarily found in the mid to lower elevation range of the Grasslands, and the second and third quartiles of the Ecotone grasslands have a much narrower elevation spread (57 m) than is the case for the Grasslands (92 m) (**Tab. 7.1**). Thus, Grassland and Ecotone grassland co-occur in the broader valleys at mid to low elevation ranges but less so in the narrow upstream valleys. The upper altitudinal limit between Miombo forest and Plateau grassland is not so well-defined. The third quartile of the former (1461 m), lying 32 m above the first quartile of the latter (1429 m), indicates a notable overlap in altitudinal extension.

All vegetation classes' mean elevation decreases from west to east, while their relative position to each other is maintained (**Fig. 7.3**). Plateau grasslands show a parabolic longitudinal distribution, with the highest sites between 18.5°–19.0°E. Their upper limit is defined by the crest of the Angolan Plateau, whereas the lower limit of their distribution lies consistently at about 1380 m. As

the crest line of the plateau is descending towards the east, its altitudinal amplitude is declining in this direction. Grasslands showed the strongest altitudinal decline along the longitudinal gradient with 71 m, followed by Ecotone grasslands with 68 m and Miombo forests with 60 m. Accordingly, the lower treeline between Miombo forests and the open habitats is descending downstream within valley systems (**Figs. 7.3, 7.4**).
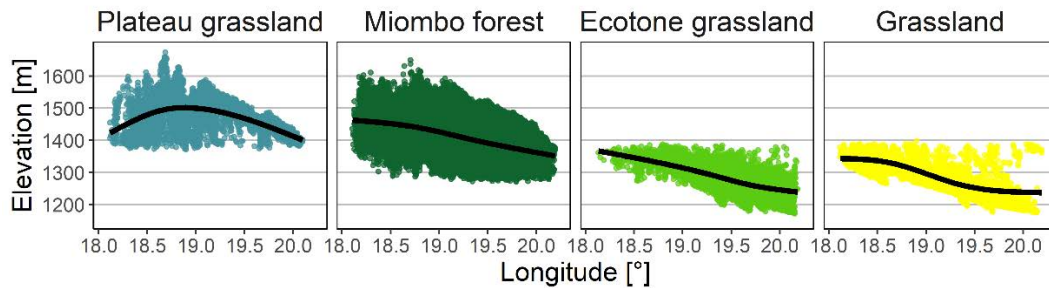
Figure 7.3. Distribution of vegetation units along the west-east gradient of the Bié Plateau, Angola. All classified points are shown in the plot. Additionally, each units' mean distribution is indicated with cubic GAM smoothing lines (k = 3) and 95 % confidence intervals (very narrow due to the high number of points per unit: $n_{Grassland}$ = 3377, $n_{Ecotone\ grassland}$ = 4945, $n_{Miombo\ forest}$ = 25455, $n_{Plateau\ grassland}$ = 3572).
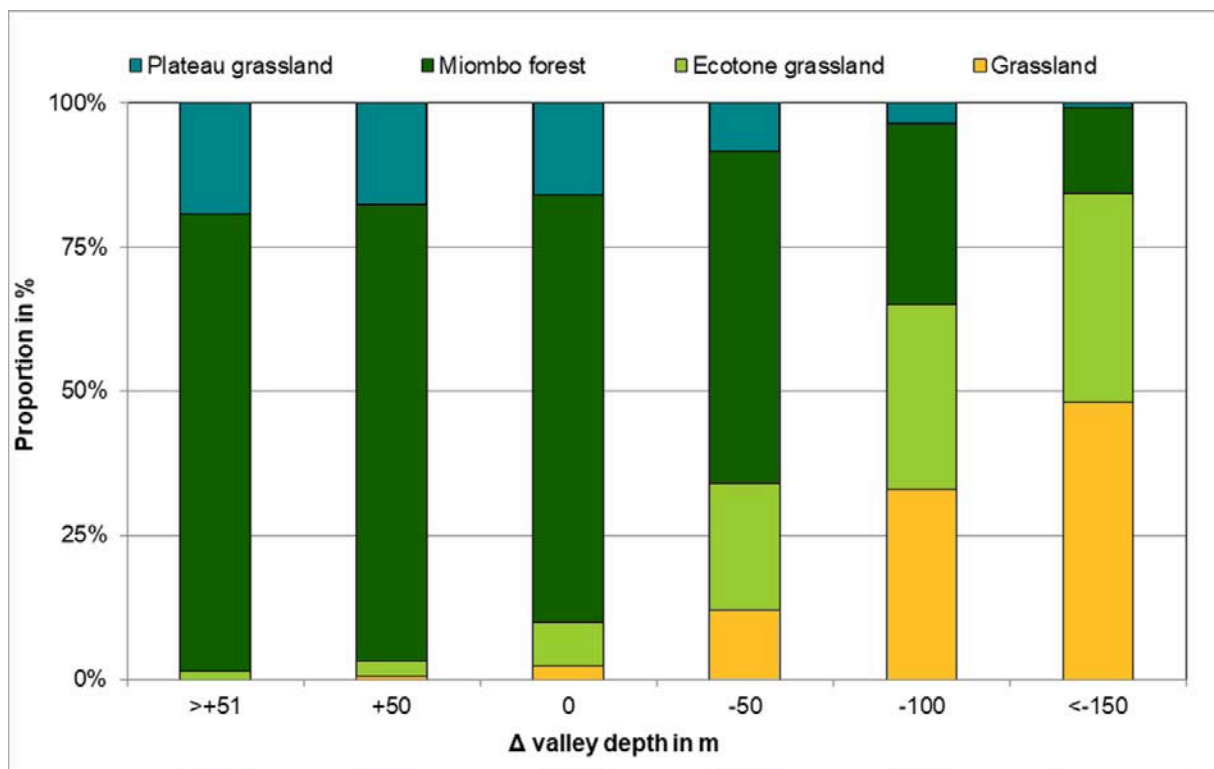
Figure 7.4. Distribution of the vegetation units along the valley systems on the Bié Plateau, Angola (proportional cover per valley depth class).

We also found upper treelines on the high plateaus of our study area. The altitudinal range of the Plateau grasslands on the high-lying plains between the valley systems overlaps strongly with the upper range of the Miombo forests that occupy the fringes of these plains and the top slopes. The analysis of vegetation units according to their topographic position in valley systems (**Fig. 7.4**)

reflects this observation. Plateau grasslands are the highest-lying vegetation unit and do not follow the west–east pattern of the other units. They seem to be restricted to ranges above 1400 m, which are limited to the western parts of the Angolan Plateau.

Microclimate

Frost occurs on the Angolan Plateau during the dry season from May to September (**Fig. 7.5**), with the highest frequency in June and July. The diurnal temperature profiles at all sites and for both TT and AWS measurements follow a general pattern (**Fig. 7.6**): air temperature starts to drop rapidly at about 4 p.m. and then continues to decrease throughout the night, reaching absolute minima down to below 0°C directly before sunrise. A temperature inversion begins to form at the lower slopes and in the valleys around sunset and is rapidly broken up between 7 a.m. and 9 a.m. Temperatures continue to rise rapidly and peak between 12 a.m. and 2 p.m. with temperatures above 30°C.
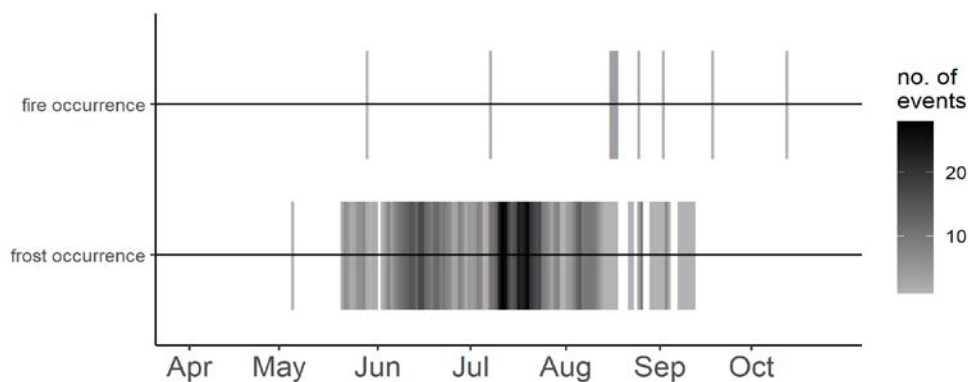
Figure 7.5. Seasonal occurrence of frost and fire at the logger locations of the study site Cusseque, based on the recording periods detailed in Appendix S1. Fire events are indicated as mid date of the 8-day window given by the burned area data product. Frost events are defined as days with temperature below 0°C.
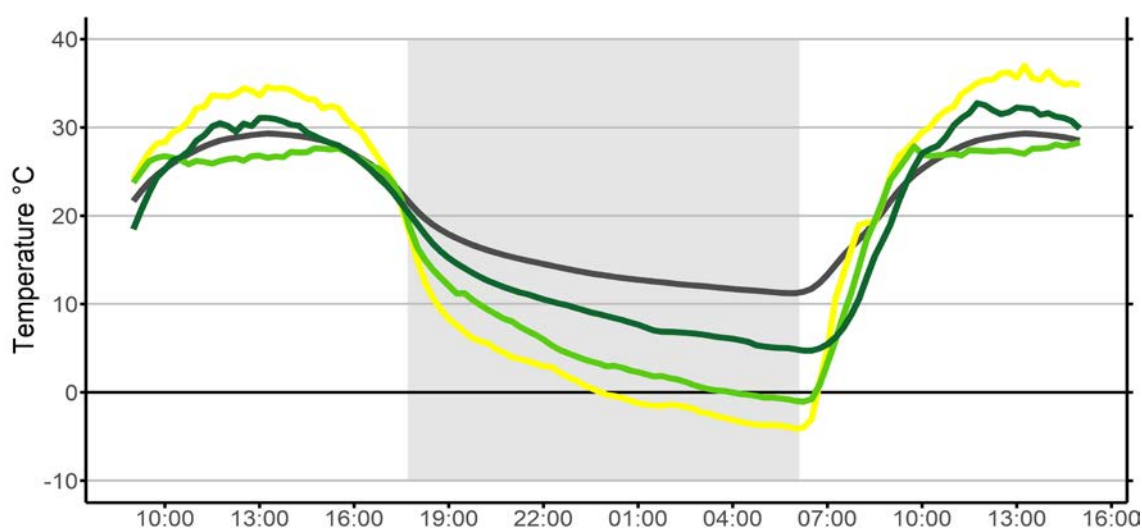
Figure 7.6. Daily temperature profiles along a transect from closed-canopy Miombo forest to open grasslands in the Sovi Valley (Bié Plateau, Angola) from 10–11 August 2015. Temperature profiles are given for a forest site (1601 m a.s.l.), a forest-grassland ecotone site (1555 m a.s.l.), a grassland site (1526 m a.s.l.) and the annual mean across all three habitats. Time between sunset (17:42) and sunrise (06:07) is shaded.

A good example of a frost night with the corresponding temperature profiles for the different vegetation units was recorded in the Sovi Valley from 10–11 August 2015 (**Fig. 7.6**). The profiles show the nocturnal build-up of the temperature inversion with minimum temperatures of 4.7°C in the forests on the hills, temperatures of -1.1°C at the ecotones upslope and temperatures down to -4.1°C in the grasslands at the valley bottom. Likewise, the daily temperature range is highest in the grassland at -4°C–36°C and lowest in the forest at 5°C–31°C. Concomitantly, the temperature drop in the evening and the increase after sunrise are steepest in the open grasslands. Disregarding the seasonally different and habitat-specific temperature profiles along the transect, the annual means of daily minimum and daily maximum temperature only range between 11°C and 29°C (**Fig. 7.6**, solid line).

Frost nights occurred reliably in every dry season. For the valley confluence of Cusseque and Sovi rivers in Bié, where detailed habitat-related records were available from 2012–2016, we recorded an increasing number of frost nights towards the valley bottom (**Tab. 7.2**), with up to 49 events per season. Extreme temperatures reached -7.5°C and diurnal temperature ranges exceeded 40°C at ground level. Overall, we observed a significant temperature difference between closed and open vegetation units. All analysed frost-related variables implied that Grasslands, and to a lesser extent Ecotone grasslands, experienced more frost nights and harsher temperatures regimes than Miombo forests, in particular lower minimum temperatures and higher diurnal temperature ranges (**Fig. S7.3**).

We measured similar numbers of frost events at the other site on the Angolan Plateau: in Bicuar National Park, 36–43 frost nights per year were recorded 2015–2018, with values comparable to those found in Cusseque.

Table 7.2. Frost events in the Sovi and Cusseque area from 2012 to 2016, differentiated by habitats, and frost events in Bicuar NP from 2015 to 2018. For Tinytag loggers (TT) and automated weather stations (AWS), we provide the median and maximum number of frost nights per year, the median and minimum daily minimum temperatures in the frost season (1 May to 1 October), the median and maximum daily temperature range in the frost season, plus minus standard error. We tested for significant differences in the variables' medians between vegetation units in Cusseque. For this, we used Kruskal-Wallis tests and superscript letters indicate outcomes of the pairwise post-hoc Dunn tests. In Cusseque, a single logger (most right in Fig. 7.2) recorded all frost events in Miombo forest, while no other forest loggers recorded any frost. The AWS in Cusseque is situated in an Ecotone grassland environment.

Site / system	Altitude [m]	n_{median}	n_{max}	Median T_{min} [°C]	Minimum T_{min} [°C]	Median ΔT [°C]	Maximum ΔT [°C]
Cusseque AWS	1529	9.0 ± 0.0 (2015-16)	9	5 ± 0.2	-1 (11.08.2015)	23.5 ± 0.2	29.9 (13.08.2015)
Miombo forest (TT)	1575.2 (mean)	0.0 ± 1.0 [a] (2012-13, 2015)	13 (2012)	7.4 ± 0.1 [a]	-4.4 (18.07.2012)	24.5 ± 0.1 [a]	40.9 (11.08.2015)
Ecotone-grassland (TT)	1549.8 (mean)	10.0. ± 4.5 [b] (2012-16)	43 (2012)	4.0 ± 0.1 [b]	-6.5 (12.06.2012)	28.6 ± 0.1 [b]	41.5 (28.08.2013)
Grassland (TT)	1542.9 (mean)	25.0 ± 4.5 [b] (2012-16)	49 (2016)	2.8 ± 0.1 [c]	-7.5 (12.06.2012)	31.1 ± 0.1 [c]	44.9 (12.07.2014)
Kruskal-Wallis test		X^2 = 21.449, p << 0.001		X^2 = 1025.497, p << 0.001		X^2 = 915.065, p << 0.001	
Bicuar AWS	1235	40 (2015-18)	43 (2015/16)	2.20	-4.1 (21.07.2016)	21.85	31.2 (21.07.2016)
Bicuar TT	1238	39 (2018)	39 (2018)	2.60	-3.3 (08.06.2018)	33.0	40.3 (08.06.2018)

Discussion

Drivers of the lower treeline on the Angolan Plateau

We have shown that the forest–grassland distribution along the valleys of the Angolan Plateau is not a random mosaic but is instead controlled by topography. Treelines divide open vegetation units on lower slopes and valley bottoms as well as on high-lying inter-catchment plateaus from dense Miombo forests on top slopes and mountain ridges.

Water-logged sites can prevent tree growth. Revermann *et al.* (2018) briefly describe the high-lying inter-catchment Plateau grasslands and mention that underlying hardpans can lead to seasonal waterlogging and peaty mineral topsoil. Lack of climate data and comparable studies makes it difficult to determine if nocturnal radiation frost and/or deficient drainage prevent forest growth on these plateaus, and we will not discuss the Plateau grasslands further. However, water-logged soils at the slopes of the Angolan Plateau are restricted to peatlands along the drainage lines (Gröngröft *et al.*, 2013). As neither the typical miombo trees nor the dominant geoxyle species tolerate water logging (Zigelski *et al.*, 2018, 2019a), water-logging does not explain the lower treeline on the Angolan Plateau.

The prevailing explanation for forest–grassland mosaics in the sub-humid tropics is disturbance by fire and megafauna (Oliveras & Malhi, 2016). These factors are also regarded as key drivers for the evolution of tropical old growth grasslands (Veldman *et al.*, 2015). The Angolan highlands, however, have historically been described as being mostly free of megaherbivores larger than antelopes (Huntley *et al.*, 2019). Fire would also not sufficiently explain the forest–grassland distribution on the Angolan plateau. The spatial layout of forest–grassland distribution in the study area with open habitats below forested slopes is inconsistent with the physical dynamics of fire. Lightning would not preferentially strike low-lying valleys, nor would hot forest fires remain on the valley floors but rather run uphill with thermic winds (Linn *et al.*, 2007). The chronosequence of frost and fire at Cusseque supports this reasoning. Data show that fires start slowly after the onset of the frost season and peak at its very end (**Fig. 7.5**). These dry-season fires, though, preferably run through the dry fuel bed of frost-damaged grasses and leaves of open vegetation types (Joshi *et al.,* 2020) instead of intruding in the still humid denser forest (Stellmes *et al.*, 2013a). Under natural conditions, fires may not cause forest-grassland transitions but rather follow and accentuate the treelines already drawn by frost, according to the topographic layout of the landscapes.

Frost, however, easily explains the forest-grassland distribution in the study area. It typically occurs in the dry season, when the inflow of cold, dry air from the south-east allows for clear nocturnal skies, facilitating outgoing thermal radiation (**Fig. S7.4**). Comparable mechanisms of dry-season frost generation with inflow of dry air and resulting temperature minima at dawn have been described for the Brazilian Cerrado (Hamilton & Tarifa, 1978). The measured topographic gradients in temperature correspond with the mechanisms of nocturnal build-up of cold-air pools in basins and closed valleys through outgoing net longwave radiation as described and analysed in detail

from temperate mountain ranges (Clements *et al.*, 2003; Steinacker *et al.*, 2007; Lehner *et al.*, 2017) and South African highlands (Duker *et al.*, 2015). Microtopography channels the flow of cold air down the slopes and thus controls the spatial pattern of frost occurrence and severity. The descending treeline indicates that its exact position is not determined by a macroclimatic threshold but follows the topographic outline of the Angolan Plateau and its local topoclimatic conditions.

We measured particularly frequent and strong frost events in the deepest valleys and valley confluences. It is probable that the small peat bogs in the headwater sections and along the many small streams, which are treeless because of waterlogging, play a role in strengthening the generation of cold air. The more cold-air-generating area there is above a given point in a valley, and the more that cold air accumulates, the more it suppresses the tree growth and thus directly influences the extension of the open habitat types (Ecotone grassland and Grassland) (see **Figs. 7.1, 7.4**). Regarding our findings and those of Clements *et al.* (2003), Steinacker *et al.* (2007) or Lehner *et al.* (2017), it is reasonable to argue that the deeper and more treeless a valley is, the more is it prone to frost. The shallower valleys at the south-eastern fringes of the Angolan Plateau seem to facilitate rather patchy frost pockets, as shown by the coexistence of Ecotone grasslands and Grasslands.

Frost prevents forest growth on the Angolan Plateau because in contrast to tree taxa from temperate and boreal zones, most woody wet-tropical forest taxa never developed physiological adaptations to frost (Sakai and Larcher, 1987), and many tropical trees are sensitive to chilling at low temperatures even above 0°C (Allen & Ort, 2001; Larcher, 2005). The dominant miombo taxa like *Isoberlinia*, *Julbernardia*, *Brachystegia* and *Cryptosepalum* all belong to the group of the Afrotropical legume subfamily Detarioideae (Azani *et al.*, 2017). Frost damage to woody species from an Afrotropical background may be amplified by the sequences of extreme diurnal temperature changes of more than 30°C, thereby overstressing the repair mechanisms for damaged bio-membranes and enzymatic systems (Sakai and Larcher, 1987). Furthermore, the difference in daily temperature ranges between AWS (2 m height) and TT (0.1–0.3 m height) in Bicuar National Park and Cusseque (**Tab. 7.2**) highlights the more extreme temperatures and more stressful conditions at ground level, which, additionally, hamper seedling establishment and sapling development (Körner, 1998; Rehm & Feeley, 2015; Joshi *et al.*, 2020).

Frost events are a frequent cause of topkill for woody taxa of tropical origin in south-central Africa (e.g., Whitecross *et al.* (2012) for Mopane forests; Muller *et al.* (2016) and Duker *et al.* (2015) for the Nama Karoo; Wakeling *et al.* (2012) for the Albany thicket), the climatically comparable Brazilian Cerrado (Brando & Durigan, 2005; Rorato *et al.*, 2018; Hoffmann *et al.*, 2019) and other tropical regions (e.g., Bojórquez *et al.,* (2019) for north-western Mexico). Hoffmann *et al.* (2019) concluded that the damaging effects of frost to trees, though irregular at the authors' study site, contribute to the maintenance and formation of savanna–forest boundaries. Because frost occurs at much higher frequencies at our study site, we considered frost as the main environmental constraint shaping the lower treeline on the Angolan Plateau. Though the Ecotone grasslands at

the slopes allowed for occasional survival of tree seedlings and saplings due to their less extreme temperature conditions, the harsher conditions at the foot slopes and valley bottoms of the Angolan Plateau excluded tree growth to a large extent and thus constituted topoclimatic microrefugia (Dobrowski, 2011) for frost-adapted biota of open habitats.

Biogeographic implications for tropical highlands worldwide

Studies on tropical lower treelines are scarce but widely distributed (e.g., Young, 1993 for Peruvian Andes; Mueller-Dombois & Perera, 1971 for Patana grassland valleys of Sri Lanka; Caner *et al.,* (2007) for the Western Ghats; and Brando and Durigan (2005) for the Brazilian Cerrado) (**Fig. 7.7**). Most of these studies concerned grassland biodiversity hotspots (e.g., the Cerrado, Patana grasslands, and the Western Ghats), and several authors considered frost to be a (co-)driver of grassland ecosystems in their study areas (Assis *et al.*, 2011; Joshi *et al.*, 2020).

Average annnual frost events (1969 - 2019)

0   ≥ 250

Studies on frost in tropical mid-altitudes:

Effects of frost on woody vegetation:	Lower treelines:	Frost as a co-driver of biodiverse grasslands:
1, 4, 7, 9, 13, 16	2, 3, 5, 8, 11, 12, 15, 17, 18	6, 10, 14
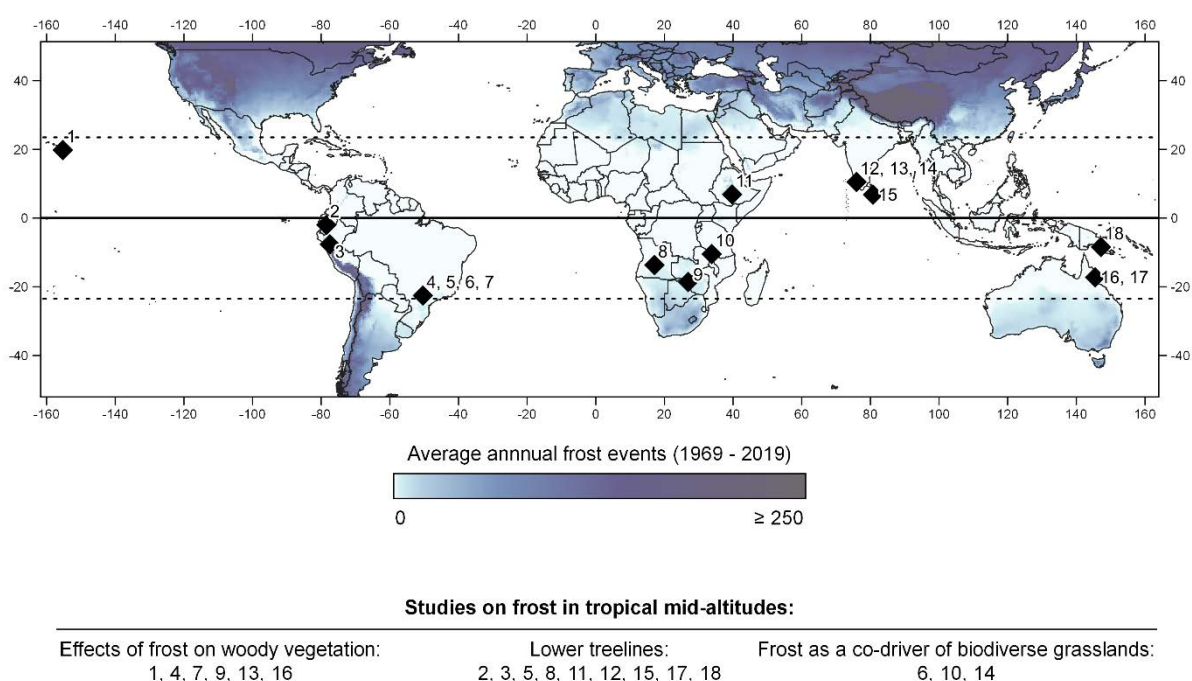
Figure 7.7. Frost related studies from tropical mid-altitudes: a) effects of frost on woody vegetation: [1]Scowcroft & Jeffry (1999), [4]Hoffmann *et al.* (2019), [7]Silberbauer-Gottsberger *et al.* (1977), [9]Holdo (2006), [13]Das *et al.* (2015), [16]Curran *et al.* (2010); b) reports on lower treelines: [2]Bader & Rujten (2008), [3]Young (1993), [5]Brando & Durigan (2005), [8]Finckh *et al.* (2016), [11]Miehe & Miehe (1994), [12]Caner *et al.* (2007), [15]Mueller-Dombois & Perera (1971), [17]Metcalfe & Ford (2008), [18]Wardle (1971); c) frost as a co-driver of biodiverse grasslands: [6]de Assis *et al.* (2011), [14]Joshi *et al.* (2020), [10]Burrows & Willis (2005). The map of annual frost events is based on the average annual number of frost events in 1969 – 2019, calculated from the CRU TS v4.04 dataset (Harris *et al.*, 2020).

Dry-season frost has been neglected as a driver for vegetation patterns or history in the tropics. Annual means do not reflect the frost-influenced climate with extreme daily fluctuations (see **Fig. 7.6**). It is neither easily detectable in data sets based on mean temperature (e.g. ,WorldClim 2; Fick and Hijmans, 2017) nor in global models with 0.5° spatial resolution (Harris *et al.*, 2020), which overrides the micro- and meso-topography of real landscapes. For example, Aleman and Staver (2018), observed the strong spatial segregation of forests and savannas occurring at intermediate

precipitations and climate, but they could not explain the current mesic savanna and forest distributions (e.g., in central Africa).

Thus, our findings have major biogeographic implications. Although the current effects of frosts on vegetation patterns in our study region are substantial, they have been considerably stronger in the past. The Pleistocene glacial maxima had a drier atmosphere and considerably lower global temperatures. Prentice *et al.* (2011) assumed in their study of the Last Glacial Maximum (LGM) a dynamic global vegetation model applying a global mean temperature of 6°C below the current mean. Drier atmospheric conditions facilitated nocturnal outgoing radiation, and lower mean temperatures pushed the ambient temperature closer to the 0°C threshold. The combination of these factors implies a considerable extension of nocturnal frost occurrences into the transitional seasons under the LGM climate for south-central Africa and tropical highlands worldwide, in combination with correspondingly lower minimum temperatures during peak dry season and a considerable spatial expansion of frost-prone areas into lower altitudes.

Recognizing frost as an important environmental constraint for forest growth in tropical mid-altitudes helps to understand the surge of tropical grasslands in south-central Africa since the Pliocene. The continuous Miocene forest belt of today's Zambezian Floristic Region disintegrated with decreasing global temperatures and increasing climate seasonality in the late Miocene (Herbert *et al.*, 2016). Geoxyle taxa evolved parallel to this process (Maurin *et al.*, 2014), avoiding frost damage to buds by relocating them to woody underground organs (e.g., lignotubers, woody rhizomes, xylopodia). The evolutionary success of geoxyles in this region can be explained by their frost-avoidance strategy (Finckh *et al.*, 2016). Dry-season frost regimes under seasonal tropical climates could also explain the convergent evolution of geoxyles in the Zambezian Floristic Region and the Brazilian Cerrado, as well as the rise of endemism-rich, montane grasslands (e.g., in the Indian Ghats as described by Caner *et al.*, 2007 and in central Sri Lanka as described by Mueller-Dombois and Perera, 1971).

Conclusion

Seasonal frost regimes in topographically accentuated landscapes are an important driver of forest–grassland distribution in the highlands of southern Africa. The increasing incidence of frost with growing climate seasonality and decreasing global temperatures during the Pliocene and Pleistocene may account for the fragmentation of the south-central African forest ecosystems since the late Miocene, which could not be adequately explained by increasing aridity and lower atmospheric CO_2 content alone. In other words, increasing seasonal aridity may have tipped a thermic threshold rather than a hygric threshold for tropical forest ecosystems in the African tropics and comparable tropical highlands worldwide.

Data availability

All AWS data are available at www.sassscalweathernet.org. Microclimate data are stored in the SOILTEMP data base (https://soiltemp.weebly.com/). The particular data used for this study is stored on Zenodo.org under https://doi.org/10.5281/zenodo.5515364. The results of the valley depth analysis as well as data on vegetation classification and R-codes for microclimate and vegetation analyses are also stored there. The Landsat 8 Level-1C tile (path/row: 178/70; 2017-08-10T14:49:22z) is available at the USGS Earth Resources Observation and Science (EROS) Center archive (https://earthexplorer.usgs.gov/).

-VIII-

Syzygium guineense
subsp. huillense
(Myrtaceae)

The Tough, the Wet and the Hidden: Evolutionary Strategies of a Polyploid Tropical Tree in a Changing Environment

Paulina Zigelski, Barbara Rudolph, Jens Oldeland, Fernanda Lages, Norbert Jürgens, Manfred Finckh

Abstract

  The Zambezian Floristic Region (ZFR) in south-central Africa experienced major environmental changes in the past and is nowadays home to numerous woody taxa of wet-tropical provenance. Within many taxa, we observe adaptations to multiple habitats, but know little about their environmental drivers. In order to gain knowledge about adaptation and speciation processes in this region, we chose the tree species complex *Syzygium guineense* (Willd.) DC. s. l. as a model. Using microsatellite genotyping and multivariate analysis of functional traits of nine phenotypes occupying various habitat types, we analyzed phenotypic and genetic differentiation with regard to environmental factors. We found polyploidy, weak correlation between genetic and spatial distances and three admixed genetic ancestries. Distinct growth forms and habitats characterize each of them.

  We identified several groups, i.e. ecotypes, which most probably mirror evolutionary strategies to overcome environmental changes happening in the ZFR over the last 10 Ma. Strong environmental filters favored the persistence of conservative ecotypes in refugia, and the evolution of ecotypes adapted to newly emerged habitats with increased disturbance regimes. Polyploidy and phenotypic plasticity possibly promoted these processes, which until now were seldom documented in adaptation to drought stress of tropical tree species. Our findings highlight the value of the Zambezian vegetation mosaic as a unique evolutionary experiment.

Keywords:

Introduction

Climate change and subsequent ecosystem transformations are significant drivers that affect the evolution and ecology of all species on earth. This is particularly relevant to current anthropogenic impacts on the earth's ecosystems (Rosenzweig *et al.*, 2008; Gattuso *et al.*, 2015; Hautier *et al.*, 2015; Boivin *et al.*, 2016; Pecl *et al.*, 2017). In a stable environment and within their range, plant and animal species occupy ecological niches to which they are well adapted and which allow them to persist, compete and interact with other species (Holt, 2009). However, a major shift to an ecosystem, for instance a permanent and directed change in climate and environment, might transform, narrow or eliminate the multidimensional environmental space of ecological niches and thus threaten the survival of the affected species.

Except from going extinct, species were observed to follow certain strategies in reaction to such changes (Aitken *et al.*, 2008). Either, they migrate to favorable sites that provide niches, which sufficiently resemble their ancestral ones, thus conserving their traits and "tracking their habitats" (Eldredge *et al.*, 2005). This strategy ultimately leads to distributional shifts (Davis & Shaw, 2001; McLeman & Smit, 2006; Soberón & Nakamura, 2009) and is often successful, if environmental changes are strong, rapid (at evolutionary timescales) or affect the landscape unevenly (Wiens *et al.*, 2010). Or, species respond to the new selective forces, adapt to new environmental conditions and colonize emerging niches at their ancestral site, thus diverging to new species given enough time and persistent reproductive isolation (Aitken *et al.*, 2008; Hoffmann & Sgrò, 2011). Species of high genetic diversity and phenotypic plasticity are likely to follow the latter pathway, particularly if the environmental change is gradual and affects larger regions (Nicotra *et al.*, 2010; Wiens *et al.*, 2010).

However, before speciation is accomplished and a new species evolves, a taxon has to pass through gradual steps of morphological, (spatial), environmental and genetic differentiation from other conspecific populations (De Queiroz, 2007). During speciation, species might diverge and evolve from ancestor species first by forming populations in different ecological niches, while populations are still compatible (Mallet, 2008; Pfennig *et al.*, 2010). The formation of discernibly adapted types is often reported for widespread species and might also reflect a stage without speciation involved (De Jong, 2005; Beierkuhnlein *et al.*, 2011). Such environmentally induced ecological and morphological diversification within one species is termed polyphenism, and the variants are commonly referred to as ecotypes (Pfennig *et al.*, 2010).

As environmental changes happen continuously all over the world at different spatial and temporal scales, we are constantly witness to evolutionary processes and diverse stages during speciation, e.g. phenotypes, ecotypes or sub-species (Mallet, 2008; Pfennig *et al.*, 2010; Lowry, 2012) as specific responses to environmental conditions and their changes. Studying the interrelations between genetic and environmental or phenotypic differentiation thus contributes to our understanding of speciation, ecosystem functionality, ecological and biodiversity patterns

(Rundell and Price, 2009), particularly if we study complex ecosystems that were not in scientific focus yet.

The Zambezian Floristic Region (ZFR), covering large parts of south-central Africa (White, 1983a; Linder *et al.*, 2005), is understudied in this regard, despite being home to many particular ecosystems that emerged due to climatic changes since the late Miocene, 10 Ma (Cerling *et al.*, 1993). The ZFR is situated in the tropical subhumid summer rainfall region of Angola, Zambia, Congo and neighboring areas between 5° to 20° southern latitude with pronounced precipitation seasonality. The region comprises the western part of the semi-deciduous miombo woodlands and is dominated by trees of the legume subfamily Detarioideae, i.e. species of *Brachystegia, Isoberlinia, Cryptosepalum* and *Julbernardia*. Open grasslands occur at sites that are seasonally inundated (e.g. Dambo ecosystems) or too frost- and fire-prone to support tropical forests (Veldman *et al.*, 2015b; Finckh *et al.*, 2016).

Over most of the Tertiary, these landscapes were dominated by tropical evergreen closed-canopy forests (Axelrod & Raven, 1978; Bonnefille, 2011), which were sustained by humid conditions and mild seasonality (Zachos *et al.*, 2001). However, global climatic changes led to increasing aridity and stronger seasonality towards the end of the Pliocene and further on in the Pleistocene (Trauth *et al.*, 2009; Herbert *et al.*, 2016). As a result, the biomes of south-central Africa shifted latitudinally towards the equator (Bonnefille, 2011). A concomitant drop in atmospheric CO_2 (Cerling *et al.*, 1997), an increased seasonality with cold, dry spells (Demenocal, 1995; Herbert *et al.*, 2016) and flammability of the landscapes (Bond *et al.*, 2003a) in turn disrupted the continuous evergreen forest cover. This facilitated the spread of C4 grasslands (Keeley & Rundel, 2005; Osborne, 2008) and promoted the emergence of today's mosaic landscape of forests, woodlands, and open grasslands.

Due to this palaeo-environmental turmoil, woody plant species of tropical ancestry were eliminated or redistributed (Bond and Keeley, 2005). On the other hand, within many plant families evolved convergently a new life form, the *geoxylic suffrutices* (White, 1976; Zigelski *et al.*, 2019a), as adaptation to new environmental conditions. Sometimes labelled as "underground trees" (White, 1976), this life form is characterized by massive, readily resprouting woody rootstocks (Pausas *et al.*, 2018). They are able to survive adverse aboveground conditions, and have gained recent scientific interest (Maurin *et al.*, 2014; Finckh *et al.*, 2016; Lamont *et al.*, 2017; Meerts, 2017; Zigelski *et al.*, 2019a).

The underlying genetic and phenotypic mechanisms that enable woody plants to meet and cope with changing environments are still unclear. Similarly, their contribution to evolutionary pathways in the ZFR remains yet undisclosed. Such knowledge, though, can be pivotal for conservation strategies in the context of current environmental changes.

We thus chose the widely distributed tropical tree species complex *Syzygium guineense* (Willd.) DC. s. l. (Myrtaceae) as a model "taxon" to link genetic, spatial, phenotypic and environmental patterns with multivariate statistics. The *Syzygium guineense* complex is highly polymorphic and

occurs in different habitats throughout tropical Africa. Hence, its analysis allows us to deduce its evolutionary history, discuss the transition from phenotype to ecotype to species, and draw conclusions on principal evolutionary strategies. In particular, we addressed the following objectives:

I)   Do recognized phenotypes constitute distinct genetic groups?

II)   What is the relative importance of geography, environmental conditions and/or phenotypic response in explaining the pattern of genetic variation?

Materials and methods

Study region and species sampling

The study area comprises the western part of the ZFR. It includes the WWF ecoregions (Olson & Dinerstein, 2002) of Angolan Miombo Woodlands, characterized by an undulating mosaic of wooded ridges, open valleys and linear wetlands. Furthermore, the Western Zambezian Grasslands are part of the study area, located in the Zambezi Graben and characterized by extended open plains that are annually flooded, interspersed with woodland patches on elevated sites. Detarioideae tree species in the woodlands and a diversity of *geoxylic suffrutex* species in the open "grasslands" characterize both ecoregions. Several large river systems (Cuanza, Zambezi, Kwando, Cubango/Okavango and Cunene) drain the study area, extending with their evergreen gallery forests into the neighboring ecoregions of semiarid savannas.

The Myrtaceae species complex *Syzygium guineense* (Willd.) DC. s. l. and the closely related *S. cordatum* Hochst. ex Krauss and *S. benguellense* (Welw. ex Hiern) Engl served as target taxa in this study. The distributional range of *S. guineense* s.l. is much larger than the ZFR itself and stretches from West and Central African rain forests to the Ethiopian highlands in the east and southwards to the major river systems of Cunene, Okavango and Zambezi and the South African KwaZulu-Natal province (Exell *et al.*, 1966; Coates Palgrave, 2002). The phenotypes of this complex in the study area include trees, shrubs and *geoxylic suffrutices* in various habitats including dense and open woodlands, riparian forests, mountainous escarpments and open grasslands (appendix **Figs. S8.1**). For analyzes, we selected 10 individuals per site (=population) belonging to a morphological unit (=phenotype) and we distinguish between nine different phenotypes within the *Syzygium* complex (**Tab. 8.1**). Populations of different phenotypes can occur at the same site.

Populations were sampled in the period 2013–2017 in the Caprivi Strip of Namibia, at the Okavango Panhandle in Botswana, along the upper and middle Zambezi, in the Liuwa Plains and Kafue National Parks in Zambia, and at several locations in south, central, west and east Angola (**Fig. 8.1 and Tab. S8.1**). Seven specimens from herbaria (LUB and HBG) were also included in the genetic analysis. In total, the dataset included 140 successfully genotyped individuals from 76 sites/69 populations (herbarium specimens were not part of populations). One to four individuals represent each population at a given site.

Collections took place at sites with zonal miombo woodlands, open grasslands, rocky escarpments, gallery forests along river systems and the ecotones in between. For each population we collected leaves for genetic analyses of 3 - 5 individuals and recorded a set of characteristic variables for all ten individuals per population (table S1): phenotype, life form, growth height, leaf stiffness, geoxylic habit, observed/estimated inundation, and elevation. Furthermore, the following leaf characteristics of six typical leaves were measured for each individual per population: leaf length and width, and petiole length. From this, we calculated leaf area (0.5 * leaf length * leaf width * π), leaf form ratio (leaf length : leaf width) and leaf petiole ratio (leaf length : petiole length).

Table 1: Overview of defined phenotypes and discernable characteristics. Listed are their taxonomic basis according to Coates Palgrave (2002) and Exell et al. (1966), the respective number of individuals and populations used in the analysis (number of herbarium specimens in brackets), their main habitats, life form and general leaf traits. The phenotype code is always an abbreviation of the corresponding taxon; the "x" indicates deviating appearance.

Phenotype	Corresponding taxon	n (Ind/Pop)	Habitat	Life form	Leaf traits
SB	*Syzygium benguellense* (Welw. ex Hiern) Engl	3/2	river	tree	Soft, oblong lamina; obtuse tip/base; no/short petiole
SC	*Syzygium cordatum* Hochst. ex Krauss	18/7 (1)	river/ wetland	tree	Soft, obovate to round lamina; obtuse tip; cordate base; no petiole
SGB	*Syzygium guineense* ssp *barotsense* F.White	20/9 (1)	river	tree	Soft, elliptic lamina; cuspidate tip; tapering base; long petiole
SGG	*Syzygium guineense* ssp *guineense* Keay	12/8 (1)	forest	tree	Soft, oblong-obovate lamina; acuminate tip; tapering base; variable petiole
SGGx	*Syzygium guineense* ssp *guineense* Keay	10/7	open woodland	small tree/ shrub	Soft to stiff, oblong-obovate lamina; obtuse-acuminate tip; tapering base; variable petiole
SGH	*Syzygium guineense* ssp *huillense* (Hiern) F.White	42/23 (1)	open grassland	geoxyle	Stiff, obovate lamina; obtuse-acuminate tip; (broadly) tapering base; short petiole
SGM	*Syzygium guineense* ssp *macrocarpum* (Engl) F.White	17/9 (1)	miombo woodland	small tree	Soft, obovate-elliptic lamina; cuspidate-acuminate tip; tapering base; long petiole
SGMx	*Syzygium guineense* ssp *macrocarpum* (Engl) F.White	9/4	woodland/ grassland ecotone	geoxyle/ shrub	Stiff to soft, obovate-elliptic lamina; acuminate tip; tapering base; medium petiole
ST	*Syzygium "tundavalense"**	9/2 (3)	Afromontane forest	small tree	Stiff, elliptic lamina; cuspidate-acuminate tip; tapering base; long petiole

*We found no description for a species or subspecies of *Syzygium* that matched this phenotype. Hence it was termed arbitrarily after the site where it was first found (Tundavala, Angola).

Genetic analysis

DNA was extracted from dried leaves following the protocol of Doyle and Dickson (1987), modified as in Dumolin *et al*. (1995). DNA extraction from herbarium specimens was conducted with the EZNA® HP Plant DNA Kit from Omega (Norcross, GA, USA) according to the provided instructions.

For molecular analysis, eight microsatellite (simple sequence repeats: SSR) loci from the related species *Syzygium sayeri* (Hillyer *et al.*, 2007) and 14 SSR loci from *S. paniculatum* (Thurlby *et al.*, 2011) were tested for applicability in the different *Syzygium* phenotypes. Of these, seven were suitable for further analyses. For the detection of the PCR products with the automated sequencer 3500 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA; Hitachi, Tokyo, Japan) the following forward primers were labelled with HEX or 6-FAM: SAY-1E4, SAY-3F10, SAY-6C10, SAY-6NE (Hillyer *et al.*, 2007) and SP38BGT, SP75BGT, SP85.1BGT (Thurlby *et al.*, 2011). The PCR was conducted in a 10 µL reaction volume with the following conditions: 2 mM $MgCl_2$, 1x B Buffer (my-Budget Taq DNA Polymerase Kit, Bio-Budget, Germany), 0.2 mM dNTPs, 0.3 µM of each primer, 0.25 U Taq (my-Budget Taq DNA Polymerase Kit, Bio-Budget) and 5–10 ng DNA template.

The PCR was run in a TGradient (Analytic Jena, Germany) with an initial denaturation (95 °C for 4 min), 35 cycles of denaturation (94 °C for 30 sec), annealing (50 °C for 30 sec), elongation (72 °C for 1 min) and a final elongation (72 °C for 10 min). All PCRs were repeated to verify reproducibility of the PCR products.

To determine fragment lengths, the final products were diluted 1:30 with Hi-Di running buffer (Thermo Fisher Scientific, USA) and analyzed with a 3500 Genetic Analyzer (Applied Biosystems, USA) according to manufacturer's instructions using a GeneScan™ 500 Liz® Size Standard (Thermo Fisher Scientific, USA). The data was subsequently revised and edited manually with GeneMapper v5 software (Applied Biosystems, Inc., Foster City, CA, USA).

Genetic data analysis

Population genetic analysis was conducted with the Bayesian approach implemented in STRUCTURE (Pritchard *et al.*, 2000) under the following conditions. A burn-in period of 30,000 MCMC replicates was followed by 100,000 replicates. Since we consistently observed more than two alleles (maximum four alleles) at a single locus per individual, we had to assume at least tetraploidy. Thus, the simulation was conducted assuming admixture with correlated allele frequencies and tetraploidy. Allowance for unknown allele dosage and for null alleles were implemented following the manual instructions (a row of zeros for recessive alleles). Prior grouping of individuals was not used in the model. The most representative number of genetic clusters (best K) was calculated for K = 1 to K = 10 with ten repeats per K of successful simulations. The results were interpreted using the Evanno method (Evanno *et al.*, 2005) implemented in STRUCTURE Harvester (Earl and von Holdt, 2012) and the K with highest likelihood [LnP(K)] and Delta K [Δ(K)], was chosen for further analysis (**Tab. S8.2** and **Fig. S8.2**).

117

Test for multicollinearity

Based on the genetic characterization, we created a matrix of phenotypic, genetic and environmental parameters for each individual. In this way, we aimed to gain insights into the parameters' interrelations and to identify groups of similar traits and preferences. In order to avoid biased results in the subsequent analyses, we first tested all parameters for multicollinearity using package *mctest* (Imdad & Aslam, 2018). Only significantly independent variables according to the Farrar-Glauber test (Farrar & Glauber, 1967) were kept. For environmental parameter we included inundation, BIO12: mean annual precipitation (MAP) derived from WorldClim 2 (Fick & Hijmans, 2017) and soil types according to the World Reference Base at 250m resolution (Hengl *et al.*, 2017a). Phenotypic parameters in the analyses were phenotype, geoxylic habit, leaf stiffness, mean growth height and leaf area (LA). Genetic characteristics were represented by mean ancestry to the K genetic clusters derived from STRUCTURE analysis (**Tab. S8.1**). Herbarium samples and individuals with missing data were excluded from this matrix, leaving 125 individuals from 69 populations. We conducted all subsequent multivariate analyses at population level to avoid pseudoreplication and overplotting. Genetic ancestries were averaged for each population.

PAM clustering

We aimed to identify biological entities within our sample set that are ecologically, genetically and/or morphologically distinct. Thus, using the PAM clustering algorithm (Kaufman & Rousseeuw, 2009), we conducted a clustering analysis taking genetic (ancestries according to STRUCTURE analysis), environmental (MAP, soil type and inundation) and morphological (phenotype, LA, leaf stiffness, height, geoxylic habit) variables into account, to find the most probable number of groups (k). Based on the Gower distance matrix of our dataset, we tested clustering patterns for k = 1 to k = 50 according to (Kaufman & Rousseeuw, 2009) with packages *cluster* (Maechler *et al.*, 2018) and *tsne* (Donaldson & Donaldson, 2010) in R. As recommended by Kaufman and Rousseeuw (2009), we chose the k (cluster number) scoring the first distinct maximum silhouette width for further analysis, i.e. where the distances of individuals within one cluster are minimal to each compared to individuals from other clusters. However, this was not the global, but the first local maximum. We defined the hence identified and characterized groups as ecotypes and used this categorization for further analyses.

Moran Eigenvector Maps

To test for significant spatial effects in our dataset and to take spatial autocorrelation into account, we created distance-based Moran's Eigenvector Maps (dbMEM) for the spatial distribution of our populations, using package *PCNM* (Legendre *et al.*, 2012) in R. The first five dbMEM eigenfunctions were used as spatial explanatory variables in the following RLQ and fourth corner analyses, as they had the highest positive eigenvalues and significant scores for Moran's I, indicating strong spatial autocorrelation.

RLQ and fourth-corner analyses

RLQ and fourth corner are multivariate analyses (like PCA or CCA) that test for similarity of observations (in this case populations) based on their traits and on their environment. It furthermore allows identifying correlations between trait and environmental variables and thus possible biological responses to environmental conditions. In order to perform RLQ (ordination of observations) and fourth corner (test for significance of environment-trait correlations) analyses, we divided the original dataset (table S1) into three matrices: a matrix of environmental parameters (R); a matrix of morphological/genetic traits (Q); and a symmetric population-by-population matrix (L). The five dbMEM vectors were included in the R-matrix as spatial explanatory variables. The analyses were conducted following the protocol of Dolédec *et al*. (1996) and Dray *et al.* (2014), in R with package *ade4* (Dray & Dufour, 2007). The resulting ordination was plotted in combination with the genetic ancestries from STRUCTURE analysis and the PAM cluster affiliations using *ggplot2* (Wickham, 2016) in R.

Genetic differentiation across phenotypes, ecotypes and distance

We tested the degree of genetic differentiation between phenotypes and ecotypes using F-statistics and distance matrix based permutational multivariate analyses of variance, a refinement of the common Analysis of Molecular Variance (AMOVA, Excoffier *et al*. (1992)). All analyses were done with packages *polysat* (Clark & Jasieniuk, 2011) and *vegan* (Oksanen *et al.*, 2013) in R, which allow for common analyses on polyploidy data. First, individual allele frequencies were computed upon which we calculated pairwise F_{st} (Nei, 1973) between phenotypes and the groups derived from the PAM clustering (=ecotypes). In the following, we used the allele frequencies to create a distance matrix between individuals based on the Bruvo distance metric (Bruvo *et al.*, 2004). The analysis of variance was then conducted with 1000 permutations, with phenotype as group. This kind of test was not applied to ecotypes as groups, as they are partly defined by their genetic pattern, which would lead to circularity. In addition, overall genetic differentiation by spatial distance ("isolation by distance") was tested using the Mantel test with Pearson correlation (Manel *et al.*, 2003) in *ade4* (Dray & Dufour, 2007) in R.

Results

Genetic analysis: STRUCTURE

The raw genotype data showed that most individuals are probably at least tetraploid, as up to four different alleles per locus were frequently detected. Furthermore, we found no evidence of fixed heterozygosity, which would be more consistent with auto- than with allopolyploidy, making at least the majority of phenotypes to autotetraploids: in the phenotypes SC, SGB, SGGx, SGH, SGM, SGMx and ST, the maximum number of different alleles per locus was four, while SB and SGG had up to

three different alleles/locus (see **Tab. 8.1** for abbreviations). In total, we found 93 different alleles for the seven loci.
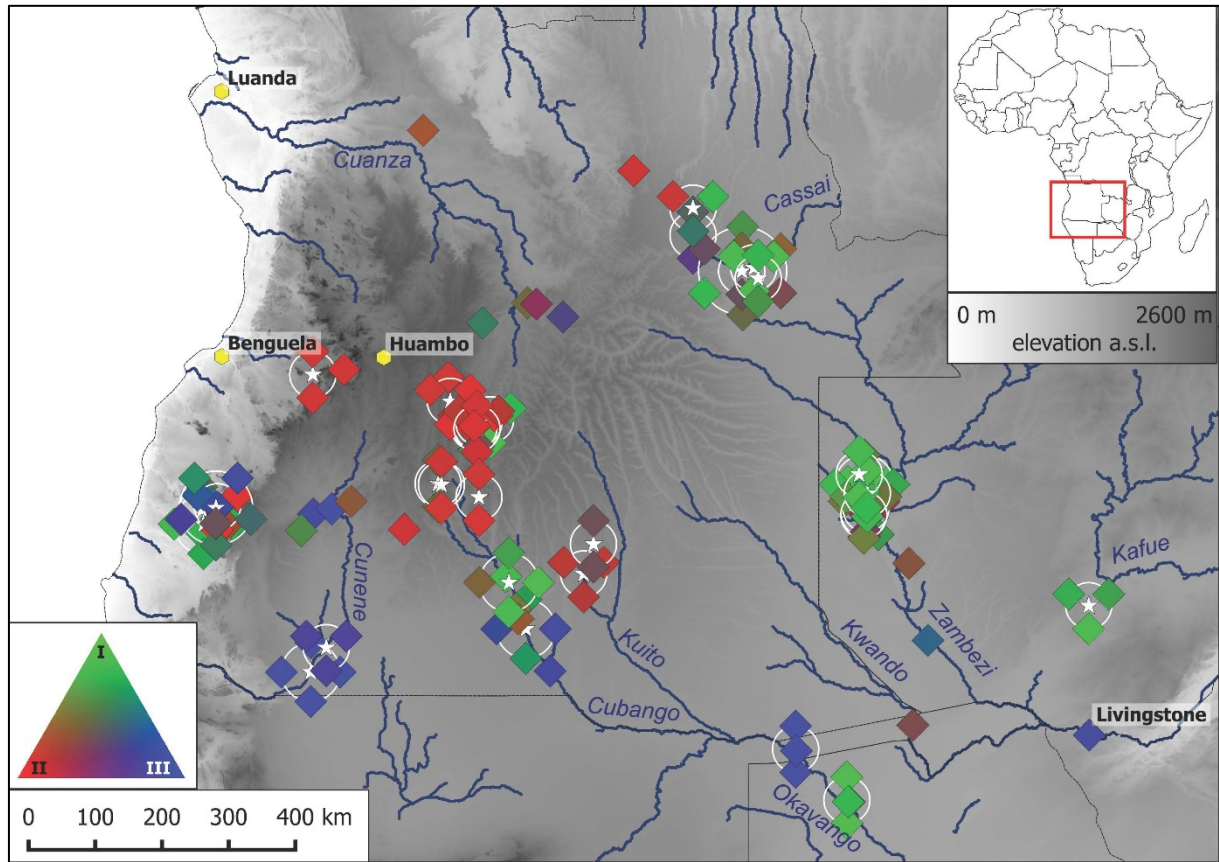
Figure 8.1: Geographic distribution of genetic clusters from STRUCTURE analysis. The 140 successfully genotyped individuals are colored according to their respective affiliations to the three genetic clusters. Sampling points in close proximity are scattered around their placement center to allow visibility of all points.

The STRUCTURE analysis identified three genetic clusters as the first distinct optimum of the delta K metric, and a high degree of admixture between the phenotypes. The highest likelihood (LnP(K)) was also found for K = 3. A second optimum was found for nine clusters, though this was due to failed detection of genetic structuring (each individual had the same share of each cluster), leading to seemingly high likelihood and probability (**Tab. S8.2**, **Fig. S8.2**). The three genetic clusters had overlapping geographic distributions (**Fig. 8.1**). Individuals with high cluster I ancestry (green) occurred throughout the region, with the strongest signals in the extended grasslands of the Zambezi Graben and linear grasslands in the Angolan highlands and along major rivers. Cluster II associated individuals (red) showed a strong focus in the miombo woodlands of south-central Angola, but occurred to a weaker degree throughout the region. The signal for cluster III (blue) was strongest in individuals growing along rivers at the southern boundary of the study area, but also occurred at rivers and in mountainous areas further north.

We found associations between the phenotypes and specific genetic clusters (**Fig. 8.2a**). Phenotype SGH was associated with cluster I, some individuals showing up to 83.5 % ancestry but on average remain at 59.3 %. Another strong ancestry signal was detected in the phenotypes SGM and SGMx, whose individuals belong on average to 75.7 % (SGM) / 79.7 % (SGMx) to cluster II with

maximum 85.7 %. Phenotype SGB was represented strongest in cluster III (maximum 84.7 %, average 68.1 %). The other phenotypes showed a higher degree of genetic admixture: phenotypes SB, SC and SGGx displayed similar average ancestries of 42 % - 49 % from cluster I, 28 % - 35 % from cluster II and 21 % - 23 % from cluster III, whereas phenotype SGG on average associated 28.4 % to cluster I, 40.6 % to cluster II and 31.0 % to cluster III. Phenotype ST affiliated 32.9 % with cluster I, 19.9 % with cluster II and 47.2 % with cluster III.
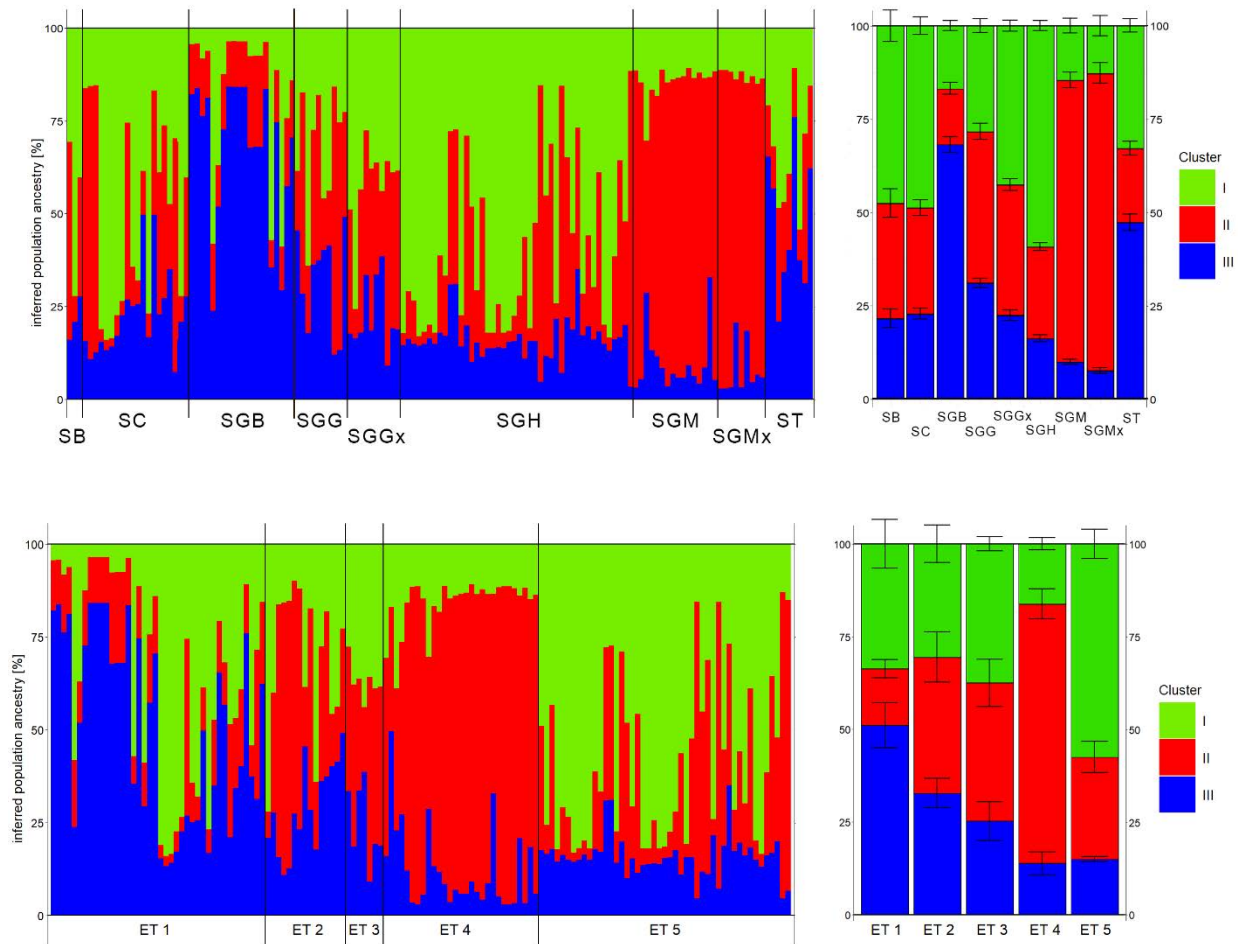
Figure 8.2: Results from STRUCTURE analysis with the best fit of three genetic clusters. A) Individual genetic pattern grouped by the nine phenotypes, and their averaged affiliations. B) Individual genetic pattern grouped by the five ecotypes, and their averaged affiliations.

PAM clustering

The PAM clustering analysis revealed a global, but not very distinct maximum silhouette width at k = 23 (k_{23} = 0.341, Δk_{23} = 0.006). However, the silhouette width reached a comparable local and distinct maximum at k = 5 (k_5 = 0.307, Δk_5 = 0.033), giving strong support for five groups. The respectively associated traits and environmental factors for each of the five identified groups are listed in **Tab. 8.2** and their genetic pattern shown in **Fig. 8.2b**.

For k = 5, some populations of different phenotypes were joined to one group. However, those within one group combined phenotypes were ecologically, genetically and partly spatially similar, indicating that these associations represent distinct ecotypes within the *Syzygium* complex. The

first group (=ecotype ET 1) for example was characterized by riparian trees, growing in seasonally flooded areas or along rivers, particularly the major river systems at higher latitudes (**Fig. S8.3a**).

Table 8.2: Grouping of populations according to the PAM clustering analysis. The five PAM clusters are recognized as distinct ecotypes (see text) and named accordingly (ET = ecotype). For each ecotype, the mean values and the standard deviation is given for the numeric parameters used in the analysis (though longitude / latitude were not implemented in the clustering analysis), and the three most frequent categories and their percentage is given for the categorical variables used in the analysis. I, II and III correspond to genetic clusters I, II and III from STRUCTURE analysis. Mean annual precipitation = MAP, seasonally flooded = seas. flooded. For detailed information on soil types please refer to World Reference Base for Soil Resources (IUSS Working Group, 2006).

Ecotype	N	Phenotype (%)	Latitude	Longitude	Leaf area [cm²]	Height [m]	I	II	III	MAP [mm]
ET 1	16	SGB / SC / ST (56:31:13)	-16.21° ± 1.78°	18.06° ± 4.01°	37.41 ± 15.53	6.25 ± 2.44	0.34 ± 0.26	0.15 ± 0.1	0.51 ± 0.24	720.13 ± 234.09
ET 2	9	SGG / SB / SC (78:11:11)	-14.44° ± 1.00°	20.07° ± 3.46°	32.35 ± 11.07	10 ± 2.69	0.31 ± 0.15	0.37 ± 0.2	0.33 ± 0.12	949.33 ± 206.11
ET 3	5	SGGx (100)	-11.84° ± 1.52°	19.76° ± 1.82°	60.74 ± 13.89	5.6 ± 1.14	0.38 ± 0.04	0.37 ± 0.14	0.25 ± 0.12	1156.8 ± 162.04
ET 4	16	SGM / SGMx / SC (56:19:13)	-13.13° ± 1.33°	17.06° ± 1.94°	65.08 ± 34.54	4.45 ± 2.35	0.16 ± 0.06	0.7 ± 0.16	0.14 ± 0.13	1154.19 ± 119.22
ET 5	23	SGH / SGGx / SGMx (87:9:4)	-14.30° ± 1.55°	20.42° ± 2.94°	51.19 ± 17.75	0.66 ± 0.82	0.57 ± 0.19	0.28 ± 0.2	0.15 ± 0.03	991.52 ± 160.33

Ecotype	Soils (%)	Inundation (%)	Geoxyle (%)	Leaf stiffness (%)
ET 1	haplic and ferralic Areno-, haplic Calci- and Luvisols (31:19:13:13)	slow river, seas. flooded, dry (56:25:13)	no geoxyle (100)	soft, stiff (88:12)
ET 2	haplic Podzols, ferralic Areno-, calcic Luvi-, haplic Arenosols (56:22:11:11)	dry, fast river, seas. flooded (78:11:11)	no geoxyle (100)	soft (100)
ET 3	haplic and acric Ferral-, ferralic Arenosols (60:20:20)	dry, fast river, seas. flooded (40:40:20)	unknown (100)	stiff (100)
ET 4	haplic Ferral-, ferralic Areno-, Acric Ferralsols (50:25:19)	dry, slow and fast river (81:13:6)	no geoxyle, geoxyle, unknown (75:19:6)	soft, stiff (94:6)
ET 5	haplic Ferral- and Arenosols and Podzols (30:26:26)	dry, seas. flooded (57:43)	geoxyle, unknown (91:9)	stiff (100)

Furthermore, it included the populations from Afromontane forests. While the genetic ancestry was quite admixed, the third genetic cluster however showed the biggest share. The second group, ET 2, constituted rather tall, small-leaved trees from dense or riparian forests with an even share of ancestry between all genetic clusters (**Fig. S8.3b**). Small trees and shrubs from open woodlands in the central/northern part of the study area, with occasional association to water, dominate the third group ET 3 (**Fig. S8.3c**) It shows no distinct genetic ancestry. Contrariwise, small trees and shrubs from ferralic miombo forests in the northwestern part of the study area were subsumed in the fourth group, ET 4, and had a clear different genetic signature to cluster II (**Fig. S8.3d**). The fifth group lastly, ET 5, encompassed all obligate suffrutex populations from the whole study area, together with two low growing tree populations from the Liuwa plains and the Angolan Escarpment (**Fig. S8.3e**).

RLQ and fourth-corner analyses

RLQ ordination displays the interrelations and similarity of populations with respect to spatial distribution, phenotypic traits, genetic structure and environmental factors (**Fig. 8.3**). The first axis of the RLQ represented 47.9 % of the total variance and was particularly correlated with ancestry from cluster I and II, phenotypes SGM(x) and SGH, seasonal flooding and slow running rivers. The second axis covered 20.8 % of the total variance and was particularly correlated with ancestry from cluster II and III, phenotypes SGM(x) and SGB, slow running rivers and dry conditions (see **Tab. 8.3** for complete overview). The spatial explanatory variables derived from dbMEM analysis (MEM1 – MEM5) were partly significant for the ordination of the populations; to a moderate degree, MEM1 had influence on the first, and MEM3 – MEM5 on the second axis. This indicates that spatial distance plays a minor role in the differentiation between populations and mirrors the genetic isolation by distance identified by the Mantel test (see below).

Moreover, the dbMEM variables were associated with – and reflected the spatial distribution of – certain phenotypes, environmental conditions and traits. More precisely, MEM1 was positively correlated to SGG and negatively to SGM and cluster II ancestry. MEM2 was positively correlated to populations of unknown geoxylic habit and MEM3 was positively correlated to SGMx and geoxylic habit, negatively to ST, no geoxylic habit and cluster III ancestry. Lastly, MEM4 was positively correlated to SC and cluster III ancestry, and negatively to SB and cluster II ancestry. For the complete list and test results, see **Tab. 8.3**.

Overall, the populations aggregated loosely together in a triangle shape where each corner was dominated by one of the genetic clusters evident from STRUCTURE analysis (clusters I-III) (**Fig. 8.3**). Additionally, each corner also represents a different life form (suffrutex, shrub, tree) and habitat preferences (grassland, woodland, rivers). The population aggregations in the RLQ plot mirrored the ecotype assignment from the PAM cluster analysis. This ecotype affiliation had a strong effect on the ordination, as populations of the same ecotype grouped close to each other, but overlapped and merged in contact zones.
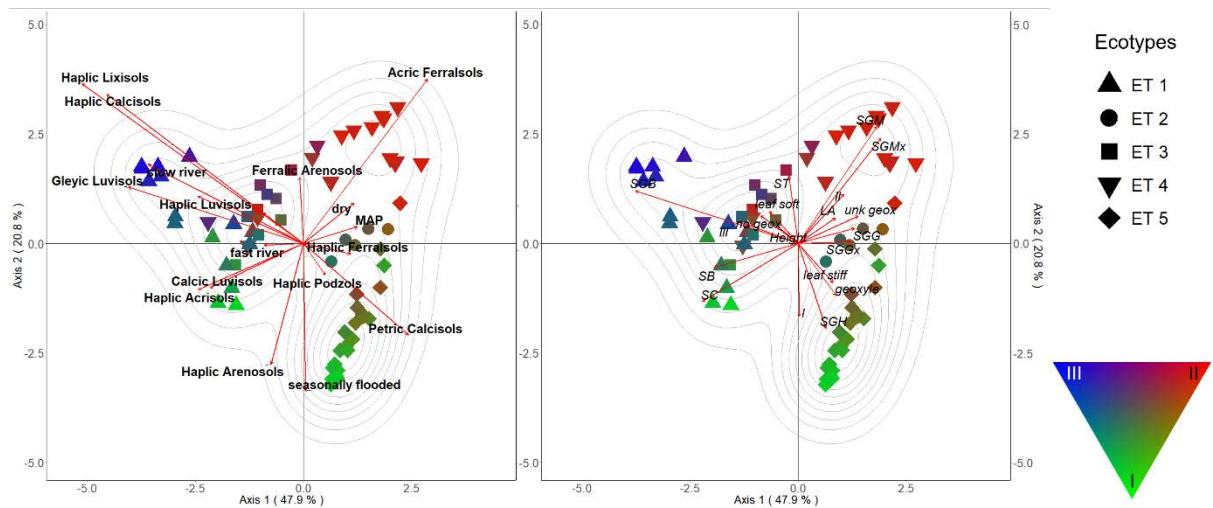
Figure 8.3: Ordination of populations in the first two dimensions according to RLQ analysis. Left plot: environmental variables (matrix R), right plot: phenotypic and genetic (clusters I, II, III) variables (matrix Q). The arrows indicate direction and strength of variable correlations; they are scaled three times to improve visibility. Though the spatial variables (Moran Eigenvectors MEM1 – MEM5) influence the populations' ordination, their arrows are removed from the plot to improve visibility; their significance and correlations' strength can be inferred from table 3. The populations are colored according to their ancestry from the three genetic clusters and shaped according to the five groups (=ecotypes) from PAM clustering.

Table 8.3: Results from RLQ and fourth corner analysis. Variables that significantly influence ordination of populations (Axis 1 and 2), significantly correlate to the genetic variables (clusters I-III) and significant spatial correlations (MEM1-MEM5) are listed. If categorical, the respective significant categories are given. For comparison between continuous variables, Pearson correlation coefficient (r) is calculated, between continuous and categorical variables, the F-test is applied and estimates are given, and between categorical variables Chi² test is conducted. Positive correlation = pos., negative correlation = neg., mean annual precipitation = MAP, leaf area = LA, seasonal = seas., unknown = unk. For detailed information on soil types please refer to World Reference Base for Soil Resources (IUSS Working Group, 2006).

Significant, correlated variables		Categories	Test	Estimate	Adj. p-value
axis 1 (47.9 %)	phenotype	pos.: SGM(x) / neg.: SGH	F	4.854	0.001
	leaf stiffness	pos.: soft / neg.: stiff	F	6.653	0.021
	geoxyle	pos.: no geoxyle, neg.: geoxyle	F	3.804	0.044
	I		r	-0.619	< 0.001
	II		r	0.417	0.001
	inundation	pos.: slow river / neg.: seas. flooded	F	7.768	0.004
	MEM1		r	-0.270	0.049
axis 2 (20.8 %)	phenotype	pos.: SGM(x), SGGx / neg.: SGB, SC	F	36.429	< 0.001
	LA		r	0.412	0.001
	leaf stiffness	pos.: stiff / neg.: soft	F	9.279	0.008
	geoxyle	pos.: (unk.) geoxyle / neg.: no geoxyle	F	8.390	0.002
	II		r	0.504	< 0.001
	III		r	-0.649	< 0.001
	soil	pos.: acric and haplic Ferralsols / neg.: gleyic Luvi-, haplic Lixi- and Calcisols	F	9.374	0.004
	MAP		r	0.525	0.001

Table 8.3 continued

	inundation	pos.: dry / neg.: slow river	F	22.600	0.001
	MEM3		r	0.357	0.010
	MEM4		r	-0.357	0.010
	MEM5		r	0.281	0.049
cluster I	soil	pos.: haplic Areno-, calcic Luvisols / neg.: haplic Calci- and Lixisols	F	3.948	0.032
	inundation	pos.: seas. flooded / neg.: slow river	F	9.733	< 0.001
cluster II	soil	pos.: acric Ferral-, calcic Petrisols / neg.: gleyic Luvi-, haplic Lixisols	F	3.756	0.043
	MAP		r	0.374	0.002
	inundation	pos.: dry / neg.: seas. flooded	F	7.461	0.001
	MEM1		r	-0.274	0.023
	MEM4		r	-0.356	0.003
cluster III	soil	pos.: gleyic Luvi-, haplic Calci- and Lixisols /neg.: acric Ferralsols	F	6.978	0.004
	MAP		r	-0.345	0.005
	inundation	pos.: slow river / neg.: dry, seas. flooded	F	13.696	< 0.001
	MEM3		r	-0.289	0.015
	MEM4		r	0.303	0.015
Soil	phenotype	SB: calcic and haplic Luvisols			
		SC: haplic Acri-, Areno- and Luvisols			
		SGB: gleyic Luvi-, haplic Calci-, Lixi- and Luvisols			
		SGG: ferralic Arenosols, haplic Podzols			
		SGGx: acric Ferralsols	Chi²	138.950	0.008
		SGH: haplic Areno-, petric Calcisols			
		SGM: acric Ferralsols			
		SGMx: acric, haplic Ferralsols			
		ST: ferralic Arenosols			
MAP	phenotype	Neg.: SB, SC, SGB, ST / pos.: SGG(x), SGH SGM(x)	F	5.256	< 0.001
	leaf area		r	0.301	0.012
Inundation	phenotype	SB: slow river			
		SC: fast river			
		SGB: slow river			
		SGG: dry			
		SGGx: fast river	Chi²	83.642	< 0.001
		SGH: seas. flooded			
		SGM: dry			
		SGMx: dry			
		ST: dry			
	leaf area	pos.: dry / neg.: rest	F	3.649	0.020
	leaf texture	stiff: dry, seas. flooded / soft: fast, slow river	Chi²	12.900	0.003
	geoxyle	geoxyle.: dry, seas. flooded / no geoxyle.: fast, slow river / unk. geoxyle.: dry, fast river	Chi²	20.580	0.002

Table 8.3 continued

MEM1	phenotype	pos.: SGG / neg.: SGM	F	2.356	0.024
MEM2	geoxyle	pos.: unk. geoxyle	F	3.273	0.042
MEM3	geoxyle	pos.: geoxyle / neg.: no geoxyle	F	3.265	0.042
	phenotype	pos.: SGMx / neg.: ST	F	5.086	0.001
MEM4	phenotype	pos.: SC, neg.: SB	F	3.238	0.007

Genetic differentiation across phenotypes, ecotypes and distance

Unsurprisingly, considering the high degree of admixture, the genetic differentiation was quite low. Globally, we found a differentiation degree of F_{st_all} = 0.082 over the entire samples set with the *polysat* analysis in R. With regard to the three genetic clusters identified by STRUCTURE analysis, cluster I showed a differentiation of F_{K_I} = 0.046 from a hypothetical ancestral population, cluster II showed F_{K_II} = 0.043 and cluster III showed F_{K_III} = 0.050. Similar low values were found in the pairwise comparison between phenotypes and ecotypes, respectively, based on similarity in allele frequencies (see **Tab. 8.4**). Here, the highest degree of differentiation was found for phenotype ST, particularly with regard to SB (F_{st_ST-SB} = 0.149) and SGGx ($F_{st\_ST-SGGx}$ = 0.109), while the rest ranged from 0.011 to 0.093. The values between ecotypes were even lower, with the highest F_{st_3-5} = 0.045 between ET 3 and ET 5 and the rest ranging from 0.017 to 0.034. Overall, as evident from permutational tests of variance based on allele frequency similarity, the genetic pattern was found to differ significantly between phenotypes (F = 6.671, R^2 = 0.289, p < 0.001). To a lesser degree, but still significant, the Mantel test detected weak genetic differentiation with spatial distance (r = 0.090, p = 0.012). To avoid circularity his test was not applied to ecotypes as they are partly defined by their genetic pattern.

Table 4: Overview of pairwise F_{st} statistics between phenotypes and ecotypes within the *Syzygium* complex. The global F_{st} over the entire sample set is F_{st} = 0.082. The rate of genetic differentiation was based on 1000 permutations of dissimilarity calculations from individual allele frequencies.

	SB	SC	SGG	SGGx	SGH	SGM	SGMx	ST
SGB	0.058	0.058	0.063	0.053	0.043	0.054	0.055	0.058
SB		0.036	0.067	0.069	0.022	0.052	0.080	0.149
SC			0.061	0.019	0.020	0.029	0.041	0.093
SGG				0.048	0.032	0.047	0.060	0.091
SGGx					0.011	0.030	0.057	0.109
SGH						0.023	0.026	0.051
SGM							0.014	0.072
SGMx								0.081

	ET 2	ET 3	ET 4	ET 5
ET 1	0.029	0.034	0.031	0.028
ET 2		0.025	0.026	0.030
ET 3			0.027	0.045
ET 4				0.017

Discussion

Do phenotypes constitute distinct genetic groups?

Our results show that the nine morphologically defined phenotypes of the *Syzygium guineense* complex do not constitute nine distinct genetic groups, but are mostly specific admixtures between the three recognized genetic ancestries. Only three phenotypes (SGH, SGM(x), SGB) have an obviously higher affiliation towards a single genetic cluster. Furthermore, based on a combination of ecological, genetic, and phenotypic data, our findings indicate the presence of five distinct ecotypes within the complex that combine ecologically similar phenotypes. However, also from this perspective we encounter a high degree of genetic admixture and again three ecotypes (ET 1, ET 4, ET 5) with an evident association towards single genetic clusters. The remaining ecotypes ET 2 and ET 3 are genetically and ecologically not as distinctly defined, which, with regard to the overall weak genetic differentiation, might mark them as artefacts from the clustering analysis. We will thus focus our discussion on the three genetically supported types.

The low genetic differentiation between the groups, no matter whether eco- or phenotypes, stands in contrast to the strong phenotypic differentiation. The weak genetic pattern might in part result from limited sample size, null alleles, autopolyploidy (Parisod *et al.*, 2010) and limited number plus poor cross-species amplification of the SSR loci used in this study (optimized for *Syzygium paniculatum* and *S. sayeri*) (Chapuis & Estoup, 2006). However, it is also likely that recent evolution and active gene flow between ecotypes are responsible.

Although we do not provide a dated reconstruction of the evolution of the *Syzygium* complex with this study, the morphological similarity, the close genetic relatedness and the admixture point to a rather recent emergence of its phenotypes. Dated phylogenies of sympatric *geoxylic suffrutex* species from south-central Africa show that this life form emerged more than 10 Ma and reached a divergence and radiation peak approx. 2.3 Ma (Maurin *et al.*, 2014). This period coincides with major environmental changes in the ZFR, as the former wet-tropical forests gave way to deciduous dry tropical forests (miombo) and spreading grasslands (Cerling *et al.*, 1997; Osborne, 2008; Bonnefille, 2011); a consequence of the climatic changes since late Miocene (Herbert *et al.*, 2016). *Syzygium guineense* and *S. cordatum* supposedly diverged approx. 9 Ma and 7.8 Ma, respectively (Thornhill *et al.*, 2015), implying that the *S. guineense s.l.* complex started to radiate in our study area within the last 10 Myr. Thus, our results indicate that the ecotypes identified in our analyses should be regarded as evolutionary responses to changing environments in the ZFR during late Miocene, Pliocene and Pleistocene.

Strikingly, we found different types of genetic patterns within pheno- and ecotypes (see **Fig. 8.2** and **Tab. 8.2**). For one, ET 5 represents morphological similarity and low genetic admixture over a wide geographical range. On the other hand, ET 4 equally shows low genetic admixture, but exhibits remarkable phenotypic plasticity at local scale (phenotypes SGM/SGMx). While the first case points to a stable environment, favoring narrow phenotypic responses with fixed genotypes (DeWitt *et al.*, 1998), the second case is an example of phenotypic flexibility in small scale heterogeneous and

disturbance driven environments (Alpert & Simms, 2002; Gratani, 2014). Such cases of high phenotypic flexibility in plants due to instable environments are well known in literature, for instance for *Polygonum persicaria* (Sultan & Bazzaz, 1993), *Populus* spp. (Wu and Stettler, 1998) or the Hawaiian Myrtaceae *Metrosideros polymorpha* (Aradhya *et al.*, 1993; Cordell *et al.*, 1998; James *et al.*, 2004).

Despite the fact that *Syzygium benguellense* and *S. cordatum* are commonly regarded as congeneric tree species (Exell *et al.*, 1966; Coates Palgrave, 2002), they are genetically remarkably close to the other *S. guineense* types and well embedded within the species complex. This hints at active gene flow, not only among the riparian types, but also with the surrounding terrestrial ones, which casts doubt on their taxonomic status, making them no true species (De Queiroz, 2007). However, given the small sample size in this study (SB: 3 individuals, SC: 18 individuals), further research is needed to resolve this question, particularly since other genetic markers (ITS, *matK*, *ndhF*) indeed differentiate *S. guineense* and *S. cordatum* (Thornhill *et al.*, 2015). Yet, the GenBank sequences of *S. guineense* used by Thornhill *et al.* are not specified to subspecies/phenotype level; hence, their sequences might stem from e.g. SGM or SGB (which in our analysis differ genetically from SC).

What is the relative importance of geography, environmental conditions and/or phenotypic responses in explaining the pattern of genetic variation?

It is evident from the RLQ and fourth corner analyses (**Fig. 8.3**, **Tab. 8.3**) that ancestry from each genetic cluster is correlated with specific sets of environmental conditions, which we consider as relevant filters for (incipient) genetic and (maintaining) phenotypic differentiation. In the following section, we discuss the interplay and relative importance of geographical and environmental factors, phenotypic responses and genetic ancestries that might have influenced the emergence of different types and the overall pattern of genetic variation.

Although cluster I ancestry was found in every individual in varying degrees, it was most strongly associated to the obligate geoxylic suffrutices from ecotype ET 5 / phenotype SGH , growing on (alluvial) sandy soils (see **Fig. 8.3e**). It is thus associated with, and differentiation maybe driven by, strong environmental stresses like waterlogging, frost and fire in the open grasslands which are unfavorable for trees (Cole, 1963; Bond & Keeley, 2005; Schneibel *et al.*, 2013; Finckh *et al.*, 2016). By hiding their buds underground, this life form thus developed the capacity to recover rapidly from complete seasonal aboveground dieback (White, 1976; Zigelski *et al.*, 2019a). The annual dieback however limits their growth height strongly, though the leathery leaves indicate adaptation to both thermal stresses (Medina, 1983). For instance, SGMx populations from ET 4 with comparable morphology, but soft leaves (cluster II) occur at less frost exposed sites than ET 5 with leathery leaves (cluster I), whose traits prevent frost damage more effectively (Fitter & Hay, 2012; Sakai & Larcher, 2012). Next to recurrent fire events, these frosts could have driven this growth forms' evolution, as studies on climatic conditions in Africa in the Pleistocene indicate even

stronger frost regimes due to lower temperatures during dry spells and global glaciation events (Schefuß *et al.*, 2003; Powers *et al.*, 2005; Prentice *et al.*, 2011).

Cluster II ancestry is strongest in ecotype ET 4 / phenotype SGM(x), which occur on ferralic soils and share adjoining habitats with ET 5 in the western miombo region (**Figs. S8.3d, S8.3e**). The disturbance regime in those open woodlands and forest-grassland ecotones is similar to the ones in ET 5's habitats with recurrent frost and fire events (Schneibel *et al.*, 2013; Finckh *et al.*, 2016). Ecotype ET 4, however, shows a different phenotypic response. These small trees and shrubs with cluster II ancestry react with decreasing growth height, increasing stem number and increasing geoxylic habit towards the open grasslands (own observations; Revermann *et al.*, 2013), thus showing a phenotypic gradient ranging from small multistemmed trees to facultative geoxylic suffrutices. In comparison, the narrow phenotypic range of other ecotypes might mirror a lower disturbance frequency in their relatively stable habitats, which offsets the need to retain the costly phenotypic flexibility (DeWitt *et al.*, 1998).

Our findings indicate furthermore that populations with ancestries from clusters I and II are less differentiated than those from cluster III, i.e. that there is more genetic exchange. This can be explained by more extant contact zones between populations and ecotypes with ancestry from cluster I or II, as both groups prefer and share terrestrial habitats (**Tab. 8.3, Fig. 8.3**). The central Angolan Plateau or the Liuwa Plains in Western Zambia for instance, harbor multiple ecotypes with cluster I and II association in close proximity to each other due to small-scale heterogeneous landscapes (Cole, 1963), and genetic exchange seem to be favored in such contact zones (Jiggins & Mallet, 2000).

Ancestry from cluster III on the other hand is focused in ecotype ET 1, which comprises trees with strong water association. Occupying refugial niches in extrazonal forests (i.e. gallery forests) along major river systems or seasonally flooded wetlands, ET 1 is able to spread furthest south of all *Syzygium* ecotypes into arid regions (**Fig. S8.3a**). This leads to less, narrow and linear contact zones with other ecotypes, and might explain the stronger genetic differentiation. Similar to the study of Johansson *et al.* (1996), the spatial and genetic pattern of ET 1 hint at dispersal and gene flow along rivers as main vectors. The course and direction of the rivers in the Kalahari region changed several times over the Pleistocene and during the last millennia (Moore & Larkin, 2001). Even today, in years with high precipitation, ephemeral channels connect the Zambezi and Kwando river systems to the endorheic Okavango Delta (Burrough *et al.*, 2009), providing temporary routes of dispersal and genetic exchange. Since ET 1 commonly grows with branches drooping above the water and their fleshy, edible fruits are able to float, this is a plausible mechanism for long distance downstream dispersal towards the Delta (Barrat-Segretain, 1996).

Another explanation for the southern distribution of this ecotype and genetic signature is drawn by Aide and Rivera (1998) and Meave et al., (1991; 1994). They showed that gallery forests and wetlands could function as environmentally buffered refugia for tropical tree species within more arid and seasonal environments. Year-round water supply and microclimate of gallery forests

generally prevent drought stress and temperature extremes. This ecotype thus seems to adopt a niche conservative evolutionary strategy (Wiens *et al.*, 2010) after the environmental changes in Southern Africa.

Strikingly, ancestry from each genetic cluster is particularly associated with specific soil and inundation conditions, making these factors differentiating environmental filters. MAP and MEM variables (spatial distribution) furthermore influence ancestry from clusters II and III. As cluster I ancestry was found all over the sampling range, it is not surprising that no spatial structure could be identified. The geographic focus of cluster II ancestry was in the northern and western part of the sampling range, because there ferralic soils and drier (no inundation) soil conditions prevail (Hengl *et al.*, 2017a). Cluster III ancestry on the other hand is focused in the southern part of the sampling range and discussed above. The weak genetic differentiation is therefore not only consequence of ecological divergence, but also of genetic isolation by distance (Wright, 1943), as indicated by the Mantel test. However, one needs to keep in mind that our study area represents only a part of the entire geographical and environmental range of *Syzygium guineense* s.l. (Exell *et al.*, 1966; Coates Palgrave, 2002), and that genetic patterns at larger spatial scales might remain undetected.

Incipient genetic differentiation in multiple directions might have also been promoted by the polyploidy of the *Syzygium guineense* complex. Our results indicate an autopolyploid (autotetraploid) nature of the complex, rather than an allopolyploid, since we found no fixed heterozygosity. Several studies show polyploidy to be advantageous in the face of challenging environments as it enhances phenotypic flexibility (Parisod *et al.*, 2010; te Beest *et al.*, 2011; Hahn *et al.*, 2012; Wei *et al.*, 2018), which in this study is demonstrated by the gradual phenotypic transition within ET 4, coupled with the same genetic ancestry. Furthermore, investigation of the exact ploidy levels of the *Syzygium* populations and deeper tests of gene flow would provide interesting objectives for further research. It would for instance clarify whether polyploidizations occur in contact zones because of hybridization (Petit *et al.*, 1999; Seehausen, 2004), whether there are different ploidy levels within the *Syzygium guineense* complex (cytotypes like in *Centaurea maculosa* (Treier *et al.*, 2009) or *Solidago altissima* (Halverson *et al.*, 2008)) and whether directions of gene flow among ecotypes are discernible.

Polyploidy within the genus *Syzygium* is well known, though mostly from Southeast Asia and Australia (Fjeldsaå & Lovett, 1994; Thurlby *et al.*, 2011; Lai *et al.*, 2015). However, polyploidy in tropical trees in general, particularly in African species, has rarely been documented (Baum & Oginuma, 1994; Tosso *et al.*, 2016), though polyploidy might have facilitated habitat shifts after environmental changes also in other species, e.g. *Afzelia* (Donkpegan *et al.*, 2017). Lacking awareness for tropical polyploidy might result from fewer occurrences at lower latitudes (Dynesius & Jansson, 2000), or lower frequencies in woody species in general (Otto & Whitton, 2000). On the other side, however, Bawa (1973) reports that the percentage of polyploid tree species in a Costa

131

Rican lowland tropical community lies between 50% and 70%. Thus, our results draw attention to the still rather unnoticed polyploid proportion of African woody species, and the role that polyploidy might have played in adaptation processes, though more research is needed with regard to ploidy level in the pheno-/ecotypes.

Conclusions

Our phylogeographic study of the *Syzygium guineense* complex indicate the formation of multiple ecological groups with different adaptation pathways in a heterogeneous environment that emerged after past climatic changes in the region. We found the strongest ecological and genetic support for three evolutionary strategies within this tropical species complex: 1) The retreat to wet refugial sites (analogous to Duminil *et al.*, 2015), 2) the occupation of high-disturbance habitats that require phenotypic plasticity and toughness, and 3) the avoidance and survival of lethal disturbances by hiding underground. It is striking, how these three evolutionary strategies emerged, since the link between identified genetic patterns and pheno- or ecotypes is weak and not throughout consistent.

Currently, our findings indicate still active gene flow and very weak genetic differentiation between the pheno- and ecotypes, despite their wide morphological, ecological and spatial range. As the ZFR comprises a high diversity of tropical tree taxa with closely related suffrutex species (White, 1976, 1983a; Maurin *et al.*, 2014; Moura *et al.*, 2017; Revermann *et al.*, 2017; Zigelski *et al.*, 2019a), which were subject to these environmental changes and evolutionary pressures, we expect to find convergent (as well as more unique) ecological adaptations and evolutionary pathways in other taxa. This emphasizes the relevance of the ZFR as an evolutionary laboratory.

Furthermore, we have presented a striking example of the difficulty of classifying (sub-)species based on traits of morphology and habit alone, as open gene flow between these discrete pheno- and ecotypes challenges the classical species concept. Moreover, we demonstrate that the taxonomic status of two congeneric species, *S. benguellense* and *S. cordatum*, needs to be carefully checked, as we were not able to confirm genetic distinctiveness from *S. guineense* for them. With this study, we thus hope to promote awareness of evolutionary processes in dynamic landscapes and of the role of polyploidy. Finally, we hope to encourage further ecological and evolutionary research of this unique evolutionary setting in order to better understand and support sustainable management of ecosystems within the Zambezian Floristic Region.

Annona stenophylla
subsp. nana
(Annonaceae)

Functional traits and symbiotic associations of geoxyles and trees explain the dominance of detarioid legumes in miombo ecosystems

Amândio L. Gomes, Rasmus Revermann, **Paulina Meller**, Francisco M. P. Gonçalves, Marcos P. M. Aidar, Fernanda Lages and Manfred Finckh

Summary

> The miombo region in Africa is covered by a mosaic of woodlands and geoxylic grasslands and is subject to disturbances such as fires, frost and drought, and low nutrient availability. The dominance of Fabaceae Detarioideae species in miombo ecosystems is remarkable but little understood. We therefore compared plant functional traits (PFTs) of common woody species of the Angolan plateau, grouped by life form (trees, geoxyles), lineage (Fabaceae: Detarioideae, non-Detarioideae) and symbiont association (ectomycorrhiza, rhizobia).

> PFTs reflect group-specific adaptations to prevalent environmental conditions. To analyse the impact of environmental drivers, we selected PFTs reflecting ecophysiological aspects of leaf morphology, nutrient content and water transport. Traits were measured following standardized protocols.

> We found differences in key PFTs between trees and geoxyles reflecting both life formspecific adaptations to environmental conditions and lineage-specific strategies to cope with environmental stresses. We interpret higher leaf thickness and higher wood density of geoxyles as responses to harsher open environments. Fabaceae in general and ectomycorrhizal species showed better nutrient status.

> Symbiotic associations of detarioid legumes with ectomycorrhiza show specific advantages for phosphorous uptake as compared to Rhizobia-associated Fabaceae and to non-Fabaceae and thus may be crucial for the stunning dominance of Detarioideae in miombo landscapes.

Introduction

The miombo ecoregion is one of the main biomes of south-central Africa covering more than 3.6 million km² across 11 countries including Angola (Chidumayo, 1995; Frost, 1996). Miombo ecosystems are typically dominated by woody plants from the genera *Brachystegia*, *Julbernardia*, *Isoberlinia* and *Cryptosepalum* (Frost, 1996; Timberlake & Chidumayo, 2011), belonging to the legume subfamily Detarioideae (Azani *et al.*, 2017). In Angola, miombo woodlands correspond to c. 47% of the total land area (Barbosa, 1970) and are the main vegetation type, covering the landscape of the Central Plateau. Generally, miombo woodlands form mosaics with open habitats along the valleys (Stellmes *et al.*, 2013b). These open habitats are codominated by dwarf shrubs with massive underground woody structures (geoxylic suffrutices; White, 1976; Zigelski *et al.*, 2019a; hereafter termed geoxyles) together with tall C4 grasses. These geoxylic grasslands are locally known as Anharas or Chanas.

Due to their ecological and socioeconomic importance (Campbell, 1996; Syampungani *et al.*, 2009; Timberlake & Chidumayo, 2011; Sanfilippo, 2014) miombo woodlands have been subject of studies in many countries in the eastern miombo region (Williams *et al.*, 2008; Shirima *et al.*, 2011; Kalaba *et al.*, 2012; Jew *et al.*, 2016). In Angola, however, miombo woodlands have been less well-studied (e.g. Sanfilippo, 2014; Revermann *et al.*, 2016, 2018a; Gonçalves *et al.*, 2017).

The need to study the ecophysiology of miombo woodlands as a base for its sustainable management has been emphasized for more than two decades (Chidumayo, 1995; Campbell, 1996). Human population growth accompanied by land use change and intensification makes it urgent to better understand the stresscoping mechanisms of miombo vegetation. Miombo is subject to many environmental stresses such as generally low nutrient availability (Chidumayo, 1994; Frost, 1996), and fire (Ryan & Williams, 2011), frost (Finckh *et al.*, 2016) and water stress (Vinya *et al.*, 2012) in the dry season. Leaf shedding (Frost, 1996) by woody plants and underground allocation of assimilates and biomass by geoxyles (White, 1976; Zigelski *et al.*, 2019a) are conspicuous responses to these stresses. Nitrogen-fixing root nodules and mycorrhizal associations are less obvious and remain understudied in the western miombo region, although they are known to improve the ecophysiological fitness of plants in challenging environments (Malloch *et al.*, 1980; Dakora & Phillips, 2002; Tedersoo Leho *et al.*, 2020).

Plant functional traits (PFTs) have been used as an approach to study ecophysiological responses of plants to a broad range of environmental factors which allows a better understanding of functional groups associated with resource use, life strategies and ecosystem functioning (Reich *et al.*, 2003; Violle *et al.*, 2007; Garnier & Navas, 2012; Pérez-Harguindeguy *et al.*, 2013). So far, some baseline studies on functional traits from savanna and forest ecosystems have included miombo ecosystems (Chidumayo, 1994; Hoffmann *et al.*, 2005; Poorter & Bongers, 2006; Vinya *et al.*, 2012). However, studies comparing traits from tree species in miombo woodlands with geoxyle species from the neighbouring geoxylic grasslands are still scarce (Meerts, 2017; Gomes *et al.*, 2019).

Of specific interest in this context is the dominance of the legume subfamily Detarioideae in African tropical and subtropical forests (de la Estrella *et al.*, 2017) (comprising miombo woodlands and associated geoxylic grasslands). Detarioid legumes are not associated with nitrogen-fixing Rhizobia (as is the case in most Fabaceae) but many genera have ectomycorrhizal (ECM) symbionts (de la Estrella *et al.*, 2017). Corrales *et al.* (2018) suggest that ECM associations on nutrient-poor tropical soils optimize nutrient supply and thus might be pivotal for the dominance of ECM-associated taxa in many tropical forest ecosystems, especially among the families Dipterocarpaceae (Asia) and Myrtaceae (Australia). However, Corrales *et al.* (2018) indicate that grassland ecosystems have been poorly studied in relation to ECM occurrence and species composition. So far, no analysis has been made on how detarioid and nondetarioid legumes perform comparatively under woodland vs grassland conditions.

Thus, to better understand functional adaptations of woody taxa in grassland vs woodland habitats, we compare PFTs of geoxyles and trees co-occurring in contiguous miombo landscapes and discuss the role of environmental factors for the differences in PFTs. Then we investigate how far the differences in PFTs are influenced by lineage-specific symbiotic interactions in order to better understand why detarioid legumes are such a dominant element in miombo woodland as well as associated grassland habitats.

Materials and Methods

Research site

The study was conducted in the Cusseque area of the Chitembo Municipality, located in Bié Province, Angola (**Fig. 9.1**). The landscape of the study area is dominated by miombo woodlands on the hills and open geoxylic grassland in the valleys. Predominant soils are either sandy (Arenosols) or ferralitic (Plinthosols), characteristically very acid (average pH = 3.3) and with low plant-available phosphorous (average 9.3–10.1 mg kg^{-1}) (Gröngröft *et al.*, 2013).

The study area has a subhumid summer rainfall climate with a pronounced wet season lasting from October to April. Mean annual precipitation is about 987 mm. Mean annual temperature is 20.4°C (Weber, 2013), with maximum temperatures above 40°C and minima below -7°C. Night frosts occur frequently in the valleys during the dry season, with highest frequency in June and July (Finckh *et al.*, 2016).

Apart from frost, dry season fire is the main disturbance factor for the open habitats in the area, occurring from May to September with a peak in July (Schneibel *et al.*, 2013). These fires affect more than 70% of all geoxylic grasslands in the Okavango Basin annually, whereas for comparison only about 10% of the surface of dense miombo woodlands is affected (Stellmes *et al.*, 2013a). Almost all fires in the study area are set by local people to clear grasslands for hunting and woodlands for agriculture (Schneibel *et al.*, 2017).
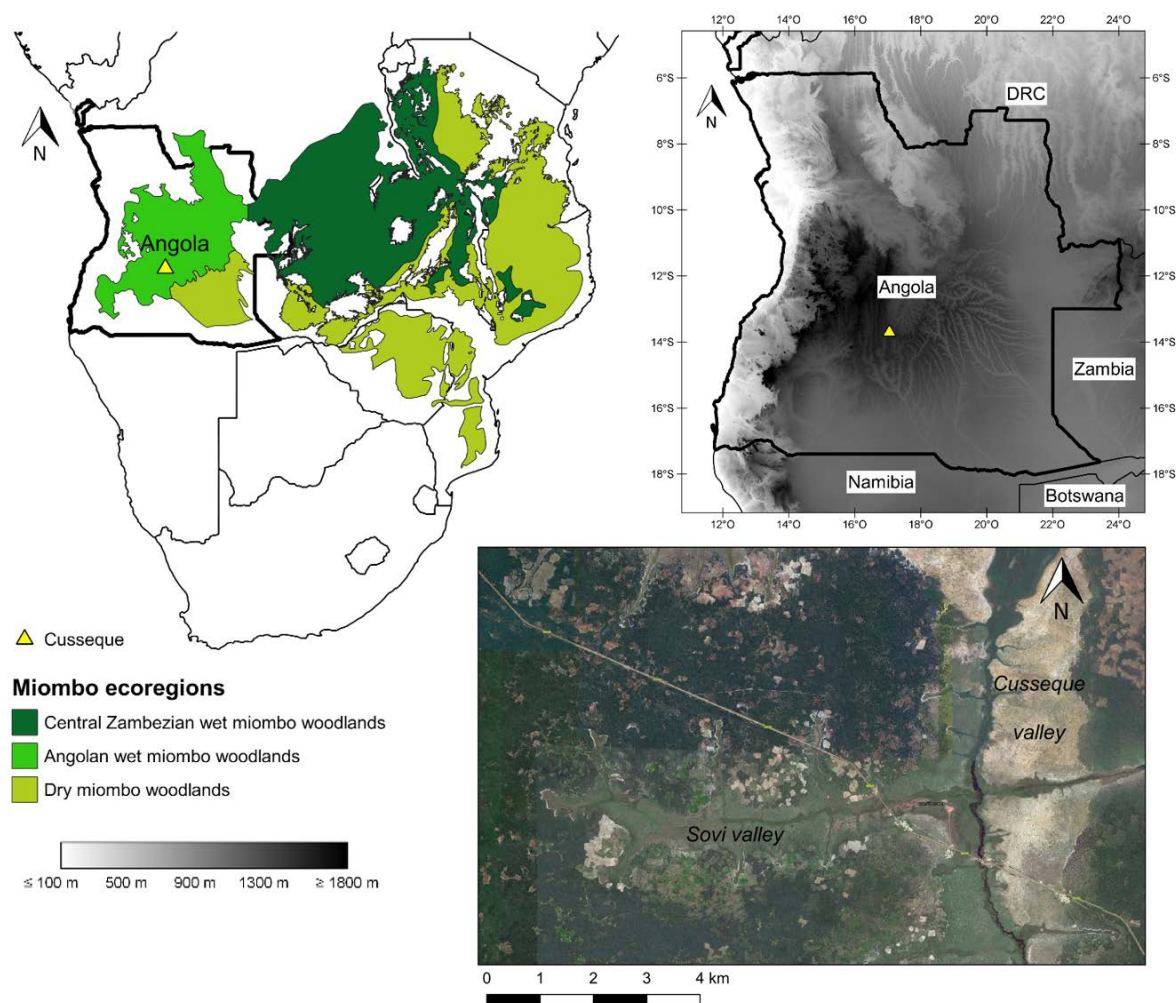
Fig. 9.1: Location of the research site Chitembo. Left: the miombo ecoregions in Africa (based on Olson & Dinerstein, 2002). Right: location in the upper Cubango catchment, Angola. The occurrence of open geoxylic grasslands on ferralitic soils (light green colour) and sandy deposits (white) is a characteristic feature in the valleys, contrasting with the woodlands on the hills (dark green).

Sample collection

We sampled 14 tree species from woodland habitats (nine Fabaceae and five non-Fabaceae) and 12 geoxyle species from open habitats (three Fabaceae and nine non-Fabaceae), all being very common in the area (Revermann *et al.*, 2017). An overview of the sampled species is given in Supporting Information Table S1. Samples were collected at the end of February and early March 2014 during the growing season and advanced wet season (Weber, 2013; Revermann & Finckh, 2013). At this time of the year the plants are fully developed. Five individuals from each tree and geoxyle species were sampled, whereby several sun-exposed, fully expanded leaves that showed no symptoms of pathogen/herbivore attack were chosen.

Plant functional type (PFT) measurements

We selected PFTs known to show responses to a broad range of environmental factors. Links of the selected PFTs to ecophysiological mechanisms are well reported in the literature (Kattge *et al.*, 2011; Singh & Verma, 2020). For all species, we measured specific leaf area (SLA), leaf thickness

(LT), leaf area (LA), leaf dry matter content (LDMC), wood density (WD), leaf nutrient content (carbon (LC), nitrogen (LN), phosphorus (LP), calcium (LCa), magnesium (LMg), potassium (LK)), C : N and N : P ratios, and leaf water potential (LWP). Trait measurements were made following standardized protocols (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013; Müller, 2017).

SLA and LA

For each species, 10 leaves were collected from each of the five individuals (totalling 50 leaves per species). Every leaf (excluding petioles) was scanned with a portable scanner to determine LA. Subsequently, the leaves were placed in a paper envelope and oven dried for 48 h at 70°C until constant weight was achieved. Then we determined the leaf dry mass (LDM) using a high-precision Kern 770 digital scale. SLA was calculated dividing LA by LDM. LA for the scanned images was determined using XNVIEWMP software (https://www.xnview.com/en/xnviewmp/). For compound leaves we used only the leaflets, excluding petiole and/or rachis.

LT

Here, the same leaves were used as for the SLA determination. The measurements were made using a digital calliper at an intermediate position between the leaf margin and the midrib for each leaf. These individual measurements were then averaged to calculate species-mean values.

LDMC

Because water-saturated fresh leaf mass was not measured in the field, LDMC was estimated indirectly from LDMC $\approx$ 1/ (SLA × LT) (Pérez-Harguindeguy *et al.*, 2013). Before calculations, values of LT were divided by 10 to achieve the same units as in SLA (cm).

WD

For geoxyles we collected woody samples (diameter $\geq$ 2 cm) by digging up woody parts located below ground. For related tree species we collected branches of the same diameter. To measure wood density we used the volume displacement method (Osazuwa-Peters & Zanne, 2011). After drying the woody segment in an oven at 103°C for at least 72 h, we measured the weight and calculated WD (ratio of the dry mass and the fresh volume). Values were averaged per species.

LN and LC

The same leaf samples used for SLA and LT were analysed for all leaf nutrient contents. Dried samples were ground finely with a disc mill (from Retsch-solutions) and kept dry in an exsiccator. Then, 100–200 mg of ground material was used for analysis in the Elementar C/N Analyzer Vario Max Cube. Samples were burned at 900°C in the presence of O_2 and the released NO_x gases were led through a column containing copper, zinc and tungsten, reducing them to N_2, which was quantified with a detector (Dumas Combustion Method) (Müller, 2017). The released CO_2 was quantified similarly. The measured carbon and nitrogen values were calculated to give the C/N percentage of the respective samples, according to the calibration standards of known C/N content that were also combusted. The C : N ratio of each species was determined by dividing LC by LN.

LP, LCa, LMg and LK

About 250 mg of dry matter, finely ground, was digested with 8 ml of concentrated HNO_3 plus 800 µl H_2O_2 in a tightly closed Teflon tube in a microwave (1600 W) during 15 min of temperature ramp to 200°C and cooked for a further 15 min at 200°C under pressure. The resulting product was diluted in 50 ml of distilled water. Before measurement with an inductively coupled plasma–optical emission spectrometer (ICP-OES, Spectro Arcos, Kleve, Germany), all samples were centrifuged to precipitate all particles. Before each run, a calibration was conducted with solutions of known concentration (0.0, 0.5, 1.0, 5.0, 10.0, 50.0 mg P/L) and a linear regression was fitted between P concentration and signal intensity.

To infer a robust estimate of total P concentration, five wavelengths (177.4, 178.3, 213.6, 214.9 and 253.6 nm) were used, while concentrations of Ca/K/Mg were deduced from signals at 422.6, 766.4 and 279.5 nm, respectively. Furthermore, the spectra were examined thoroughly to detect any interfering signals or background/underground disturbances, in which case the errors were corrected and the concentrations were recalculated. The concentrations inferred from signals of all element-specific wavelengths were averaged.

Leaf water potential (LWP)

LWP measurements were made under field conditions using a pressure Pump-Up Chamber Instrument (PMS Instrument Co. USA; methodology according to Scholander *et al.* (1965)), a standard method used for plant water status measurements (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013). Measurements were made in the rainy (end of March) and dry seasons (early June) twice a day, at predawn (5 h) and midday (12 h). All measurements were made within 1 h after starting operation. Five leaves from five individuals per species (totalling 25 leaves) were successively cut and placed inside the chamber, with the cut end protruding from the seal. Once the chambers had been hermetically closed, pressure was gradually applied pumping the chamber. Once a water film appeared, pumping was stopped and the pressure indicated on the display was recorded. It was not possible to measure LWP of Combretum platypetalum in the dry season as it is leafless at this time of year. For this reason, we excluded the species when analysing LWP. Mean LWP was considered the mean of the two seasons (rainy and dry).

Data analysis

Comparisons of all PFTs within and between groups were made, using one-way ANOVA (t-test). Principal components analysis (PCA) was used to analyse multivariate associations of the PFTs based on the scaled covariance matrix of variables. In particular, we investigated whether the spectra of trait-based plant strategies differed between life forms (tree/geoxyle) and symbiont type (Rhizobia yes/no; ECM yes/no).

Missing values for wood density in *Rhus exelliana* (due to the excessively soft wood of the rhizome) and for LWP in *C. platypetalum* (due to early leaf shedding) were imputed beforehand

using imputePCA in the R package missMDA (Josse & Husson, 2016). All statistical analyses were carried out using STATISTICA (Version 7) and the packages FactoMineR (Lê *et al.*, 2008; Husson, 2010) and factoextra (Kassambara & Mundt, 2017) in R.

Results

Principal component analysis

The first six components of the PCA sufficiently explain the variance in the data (85.3%), with the first two covering almost 50% (**Fig. 9.2**). The first component shows a strong positive correlation with SLA, LP and LN and a negative correlation with C : N ratio. Tree species are separated from geoxyle species, as well as Fabaceae from non-Fabaceae and ECM species from non-ECM species. The second component correlates with LDMC, and reflects the well-known antagonism between LMg and LK. Geoxyles spread more across the first components than trees, indicating a higher variance across PFTs. WD and LA showed no clear pattern in this analysis.
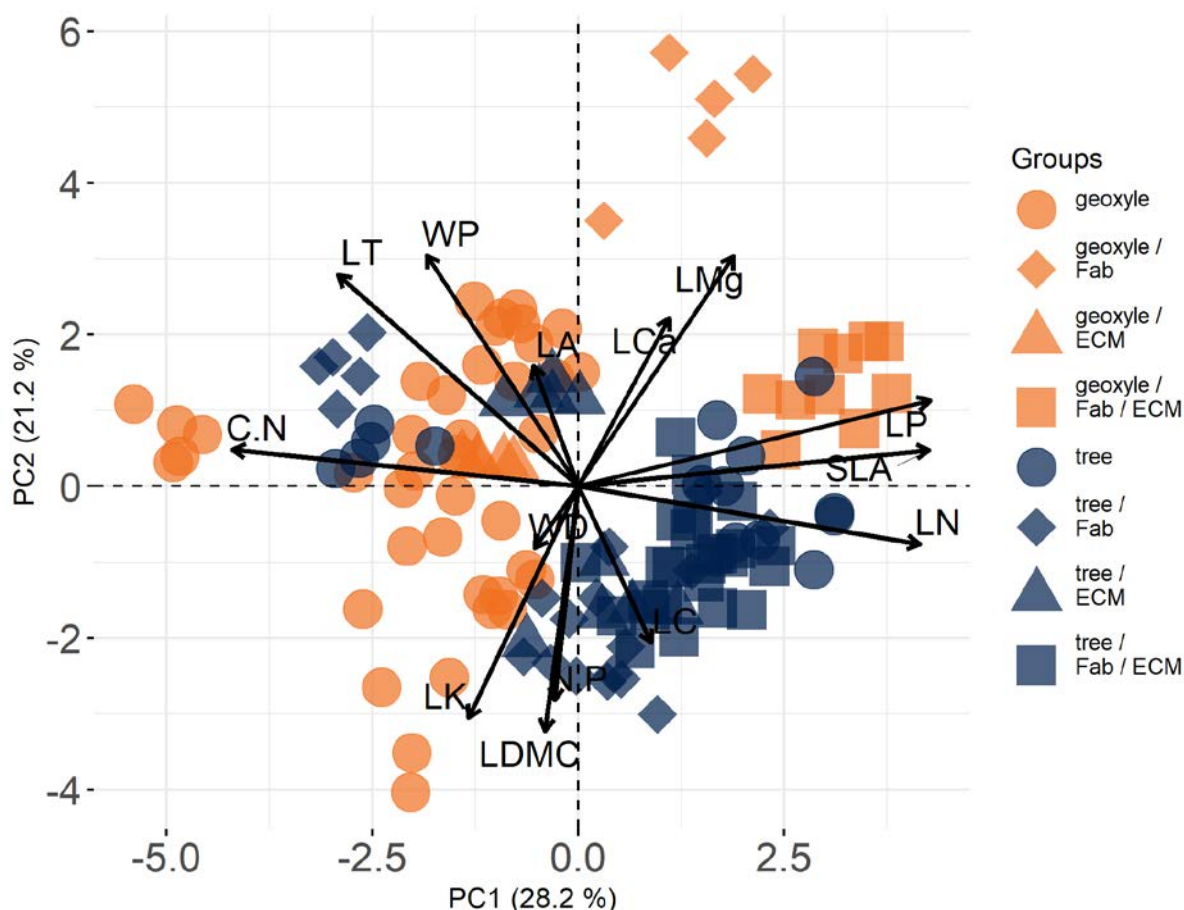
Fig. 9.2: Principal component analysis (PCA) showing correlation of traits and species dispersion in relation to life form, belonging to Fabaceae and symbiotic status. Abbreviations: SLA, specific leaf area; LT, leaf thickness; LA, leaf area; LDMC, leaf dry matter content; WD, wood density; LN, leaf nitrogen; LC, leaf carbon; LP, leaf phosphorus; LMg, leaf magnesium; LCa, leaf calcium; LK, leaf potassium; C : N, carbon to nitrogen ratio; N : P, nitrogen to phosphorus ratio; WP, water potential. ECM, ectomycorrhizal species; Fab, Fabaceae.

Within-life-form variation

We found highly significant differences for most PFTs within the life forms (**Tab. 9.1**). For geoxyles, all species differed significantly from each other in all PFTs, while for trees all except LMg differed between all species. The highest trait variance within life forms was found for WP, LT and C : N ratio (both), and LA plus LMg (geoxyles). For species-specific details in the analysed traits, see **Tab. S9.2** (geoxyles) and **Tab. S9.3** (trees).

Table 9.1: Mean and standard error of all plant functional traits, including results of one-way ANOVA between geoxyles and trees and within each group.

Trait	Mean ± SE		ANOVA between		ANOVA within			
	Geoxyles	Trees			Geoxyles		Trees	
			F	*P*	*F*	*P*	*F*	*P*
SLA (cm²/g)	74.33 ± 2.42	83.27 ± 1.77	9.16	***	36.64	***	14.86	***
LT (mm)	0.35 ± 0.01	0.28 ± 0.01	27.48	**	143.40	***	89.51	***
LA (cm²)	95.05 ± 6.94	118.38 ± 7.46	5.13	***	89.75	***	32.15	***
LDMC (mg/g)	0.43 ± 0.016	0.46 ± 0.01	2.23	ns	19.05	***	12.67	***
WD (g/cm³)	0.62 ± 0.02	0.56 ± 0.01	13.68	***	3.13	***	12.01	***
LN (%)	1.51 ± 0.06	1.97 ± 0.07	26.04	***	35.60	***	35.44	***
LC (%)	49.57 ± 0.35	51.03 ± 0.47	6.00	**	8.88	***	15.58	***
LP (mg/g)	0.94 ± 0.05	1.12 ± 0.04	8.45	***	27.53	***	23.70	***
LCa (mg/g)	5.99 ± 0.41	5.06 ± 0.24	3.27	ns	25.33	***	7.10	***
LMg (mg/g)	1.96 ± 0.35	0.26 ± 0.05	26.59	***	57.07	***	0.94	ns
LK (mg/g¹)	7.48 ± 0.47	10.21 ± 0.09	38.02	***	56.30	***	15.58	***
C : N ratio	36.14 ± 1.92	28.24 ± 1.12	16.48	***	53.70	***	62.69	***
N : P ratio	17.05 ± 0.65	18.08 ± 0.5	1.60	ns	4.13	***	21.97	***
WP (bar)	−7.21 ± 0.48	−9.29 ± 0.5	8.66	***	366.15	***	245.34	***

- SLA, specific leaf area; LT, leaf thickness; LA, leaf area; LDMC, leaf dry matter content; WD, wood density; LN, leaf nitrogen content; LC, leaf carbon content; LP, leaf phosphorus content; LCa, leaf calcium content; LMg, leaf magnesium content; LK, leaf potassium content; C : N, carbon to nitrogen ratio; N : P, nitrogen to phosphorus ratio; LWP, leaf water potential.
- ns, Not significant; **, significant; ***, highly significant ($P < 0.05$).

Between-group variation

Comparison between trees and geoxyles

One-way ANOVA (**Tab. 9.1**) showed significant differences between geoxyles and trees for most PFTs, except for LDMC, LCa and N : P ratio. On average, SLA, LA, LN, LC, LP, LK and WP were higher in trees than in geoxyles, while LT, WD, LMg and C : N ratio were higher in geoxyles than in trees.

Comparison between Fabaceae and non-Fabaceae

Separating Fabaceae species from non-Fabaceae species in both life forms, one-way ANOVA (**Tab. S9. 4**) showed significant differences in many PFTs. Within geoxyles, SLA, LN, LP, LCa and LMg were higher for Fabaceae species than for non-Fabaceae species, while LK, and C : N and N : P ratios were higher for non-Fabaceae species. Within trees, SLA, LDMC, LN, LC, LP, LK and N : P ratio were higher for Fabaceae species than for non-Fabaceae species, while LT, LA, LCa and C : N ratio were higher for non- Fabaceae species (**Fig. 9.3**).
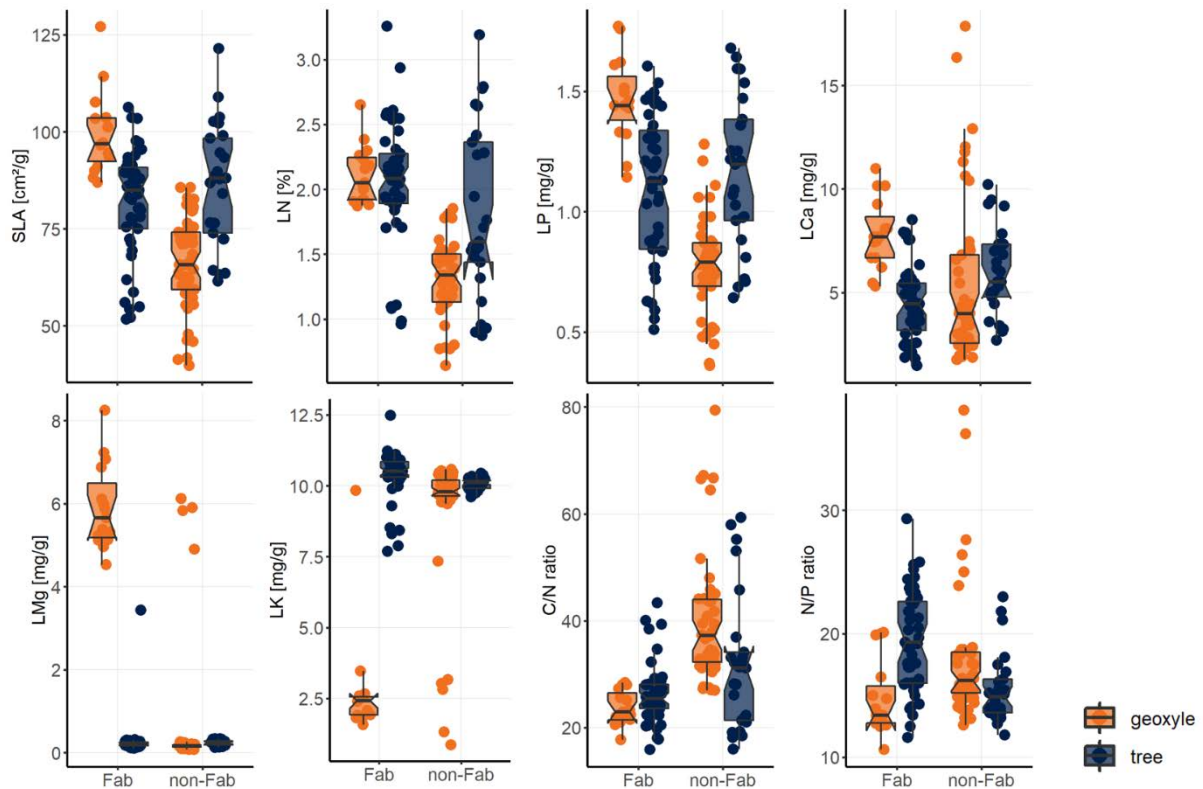
Fig. 9.3: Plant functional traits (PFTs) that differ significantly between geoxyles and trees with regard to lineage (Fabaceae (Fab)/non-Fabaceae (non-Fab)) (Supporting Information Table S4). Jittered points indicate variance of the data and nonoverlapping notches show significant differences. Horizontal lines indicate the scale of values adopted for each PFT. Blue circles indicate trees and orange circles indicate geoxyles. SLA, specific leaf area; LN, leaf nitrogen; LP, leaf phosphorus; LMg, leaf magnesium; LCa, leaf calcium; LK, leaf potassium; C : N, carbon to nitrogen ratio; N : P, nitrogen to phosphorus ratio.

Comparison between ECM-associated and non-ECM-associated species

To investigate the effect of ectomycorrhizal associations, we separated geoxyles and trees into ectomycorrhizal (ECM) species from species without this association (non-ECM) to analyse its influence on trait variation (**Tab. S9.5**). Regardless of the life form, again SLA and LP were significantly higher in ECM-associated species. The differences in other traits varied between life forms, but those traits that were significant relate to a better nutritional status of ECM-associated species. Geoxyles differ in more traits between groups, reflecting the higher variance already encountered in the PCA (**Fig. 9.2**).

In a separate consideration, we looked for the influence of ectomycorrhiza within the dominant plant family of the miombo region. We compared how detarioid species and non-detarioid Fabaceae species (regardless of the life form) perform with regard to the most important variables of the PCA (**Fig. 9.4**; **Tab. 9.2**). Here, one-way ANOVA showed significantly higher LN and N : P ratio for nondetarioid species, while SLA and LP were the opposite. There were no significant differences in C : N ratio between detarioid and nondetarioid species.
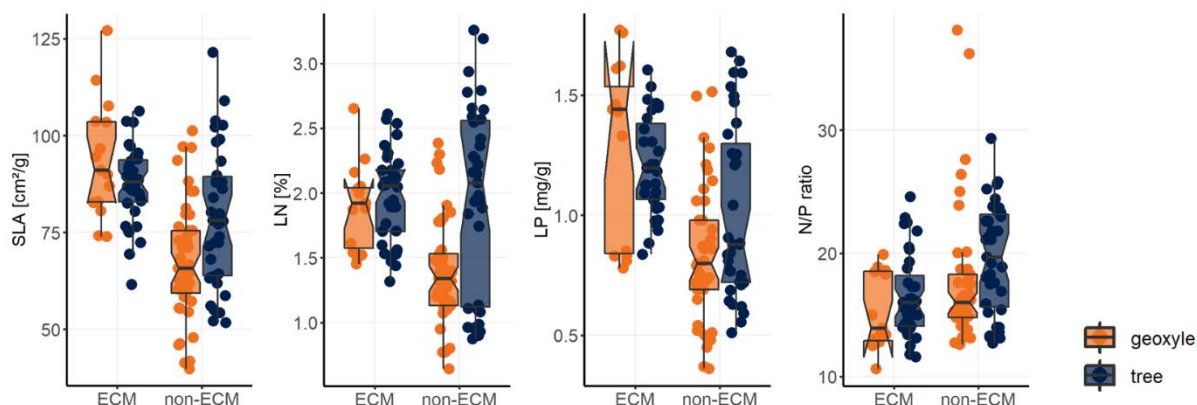
Figure 9.4: Plant functional traits (PFTs) that differ significantly between geoxyles and trees with regard to symbiotic type (ectomycorrhiza (ECM)/nonectomycorrhiza (non-EMC)) (Supporting Information Table S5). Jittered points indicate variance of the data and nonoverlapping notches show significant differences. Horizontal lines indicate the scale of values adopted for each PFT. Blue circles indicate trees and orange circles indicate geoxyles. SLA, specific leaf area; LN, leaf nitrogen; LP, leaf phosphorus; N : P, nitrogen to phosphorus ratio.

Table 9.2. One-way ANOVA comparing Detarioideae (Det) and non-Detarioideae (n-Det) legume species regarding specific leaf area (SLA), leaf nitrogen (LN) and leaf phosphorus (LP) contents, and carbon to nitrogen (C : N) and nitrogen to phosphorus (N : P) ratios.

	Mean ± SE		One-way ANOVA	
	Det	n-Det	*F*	*P*
SLA (cm²/g)	92.93 ± 1.92	85.63 ± 2.75	34.10	***
LN (%)	2.12 ± 0.04	2.35 ± 0.09	7.43	***
LP (mg/g)	1.34 ± 0.04	1.13 ± 0.06	9.92	***
C : N ratio	24.66 ± 0.52	22.75 ± 0.86	3.99	ns
N : P ratio	15.65 ± 0.57	21.11 ± 0.77	34.10	***

- Significant differences (*P* < 0.05) are marked with asterisks; ns, not significant.

Discussion

What drives the functional differences between geoxyles and trees?

Apart from the large differences in height, the morphology of trees and geoxyles is strikingly similar. Reproductive traits do not show substantial differences while vegetative traits of geoxyles are restricted to a part of the phenetic space of trees (Meerts, 2017). However, until now the specific ecophysiological adaptations of these life forms have rarely been analysed. In this study, we show that they comprise distinct combinations of functional traits reflecting different ecophysiological strategies. We often observe trade-offs between two strategies, namely higher WD of geoxyles which balances survival investment (high WD; Loehle, 1988; King *et al.*, 2006) against hydraulic conductivity (low WD; Borchert, 1994). Lower SLA and higher LT for geoxyles indicate that the lower xylem volume in geoxyle stems is associated with a lower volumetric flow rate of water. Two explanations for this spring to mind. Vinya *et al.* (2012) indicate coordination between branch hydraulic properties and leaf functional traits in miombo woodland trees. A lower leaf area ratio to sapwood area (Huber value) in comparison with trees may simply result in reduced needs for high volumetric flow rates. However, we are not aware of any comparative study on Huber values comparing trees with geoxyles. Alternatively, a relationship of lower xylem vulnerability to cavitation, associated with higher WD (Barotto *et al.*, 2018), also seems plausible. This would be in line with the fact that the frost-prone geoxyle habitats have also promoted strategies towards higher drought tolerance with increment on WD and mycorrhizal colonization (Midgley *et al.*, 2010; Brunner *et al.*, 2015; Volaire, 2018; Rodriguez-Zaccaro & Groover, 2019).

Another ecophysiological distinction is apparent in that geoxyles had higher magnesium (LMg) and lower potassium (LK) than trees and vice versa, representing the trade-off between investment in photosynthesis and adaptation to water stress (Hugouvieux *et al.*, 2002; Tůma *et al.*, 2004; Lisar *et al.*, 2012). Geoxyles optimize photosynthesis and relative growth rate. Because geoxyles are increasingly covered by tall C4 grasses from mid-December onward (Zigelski *et al.*, 2019a), rapid growth with incipient vegetation period is beneficial. By allocating carbohydrates belowground to storage, geoxyles are able to cope with reduced assimilation in the later rainy season and during the dry season, and to resprout rapidly afterwards (Pausas *et al.*, 2018).

Strikingly, LDMC did not differ between life forms. Used as an indicator of plants' resource use strategies, it represents a trade-off between rapid assimilation/growth (high LDMC) and efficient resource conservation (low LDMC) (Wilson *et al.*, 1999; Garnier *et al.*, 2001; Díaz *et al.*, 2004). Furthermore, LDMC is a reliable predictor of total aboveground net primary production (aNPP; Smart *et al.*, 2017) and the similarity of LDMC between life forms suggests a comparable productivity of geoxylic grasslands and woodlands, but with different strategies of biomass allocation. 'Underground forests' (White, 1976) are thus not only similar in terms of dominant genera (e.g. *Brachystegia*, *Cryptosepalum*), but also show similar productivity to aboveground forests.

Ecophysiological differentiations between geoxles and trees are thus driven by different stress and disturbance regimes in their respective environments. Nutrient limitation, however, affects all life forms in the miombo region regardless, as shown, for example, by the N : P ratio, indicating consistently P-limited systems (Aerts & Chapin, 1999; Güsewell & Koerselman, 2002). In the following we discuss the role of symbiotic interactions to cope with this deficiency.

How are functional differences influenced by lineages with different symbiotic associations?

For several traits, we find lineage-specific differences that show Fabaceae to have more favourable trait values. This is caused by their ability to fix nitrogen via microbial root symbionts, which directly affects important traits. SLA, for example, is strongly linked to growth rate and resource use by plants (Vendramini *et al.*, 2002) and is vital for resource capture, usage and availability (Grime *et al.*, 1997). Nitrogen directly affects vegetative growth and determines photosynthetic ability (Waite & Sack, 2010; Blonder *et al.*, 2011). Fabaceae are among the plants with highest LN and have in general low C : N ratios (McKey, 1994; Miller, 2000; Colgan *et al.*, 2015). This is in line with the negative correlation we found between C : N ratio and SLA, LN and LP. Besides, when environmental conditions are favourable, Fabaceae have a higher photosynthetic rate than most other plant families (Tuohy *et al.*, 1991; McKey, 1994). Often, they increase their competitive ability by allocating resources to storage organs (Pérez-Harguindeguy *et al.*, 2013). Furthermore, low C : N ratios in Fabaceae allow for high decomposition rates and, thus, for rapid nutrient turnover (Lewis *et al.*, 2005).

Why are Detarioideae so dominant in miombo ecosystems?

We compared several groups in our study, but wish to draw particular attention to the comparison between Detariodeae (ECM) and non-Detariodeae in the nutrient analyses (**Tabs. 9.2**, **S9.4**, **S9.5**). Leaf phosphorous content (LP) was significantly higher in trees than in geoxyles, in Fabaceae than in non-Fabaceae, and in ECM than in non-ECM species. Phosphorus is essential for plant growth and reproduction (White & Hammond, 2008), but limited in the soils of the study area (Gröngröft *et al.*, 2013; our own measurements). Besides ECM, plants adapt to low phosphorous availability through conservative use in tissues, such as redeployment (Hedin, 2004; McGroddy *et al.*, 2004; Güsewell, 2005; Minden & Kleyer, 2014) and changes in biomass allocation (Hermans *et al.*, 2006) within the organism during ontogeny.

The dominant genera of the miombo are detarioid with ECM (Högberg, 1982). They are thereby enabled to take up P directly from organic matter (Högberg & Nylund, 1981; Högberg & Piearce, 1986; Frost, 1996; Hall *et al.*, 2020) and to stimulate biological N-fixation (Tiessen, 2008). By contrast, nondetarioid legumes have to invest fixed nitrogen into phosphatase production to cope with phosphorous-limitation (Houlton *et al.*, 2008). Lower LP in geoxyles compared to trees may partly be biased by the lower proportion of detarioid geoxyles (25% of species) compared to trees (64%) in our analysis. Yet, we also find lower LP in geoxyles compared to trees among non-

Fabaceae, indicating that this pattern also reflects less soil organic matter in geoxylic grasslands due to their much higher fire frequency compared to woodlands (Stellmes *et al.*, 2013a).

Conclusions

Our study found significant differences between geoxyles and trees co-occurring in contiguous areas of the Angolan Central Plateau for almost all analysed traits. These differences reflect adaptations to the disturbance regime and environmental stresses of their respective habitats. Each group developed a wide range of responses to cope with these local environmental conditions, particularly through changes in biomass allocation (below- or aboveground), ecophysiological strategy and leaf/wood morphology. Lineage-specific symbiotic interactions such as ECM or rhizobia, which improve nutrient uptake, dominate the pattern of variation in most traits. Strikingly, key traits such as specific leaf area, nitrogen and phosphorus content were dominated by detarioid Fabaceae. ECM associations provide even better nutrient provision than rhizobia for both tree and geoxyle species. The striking dominance of detarioid species in both grasslands and woodlands of the miombo is linked to their symbionts, which provide advantageous ecophysiological adaptations to nutrient-deficient soils and environmental stresses. With our study, we provide new insights into little-studied, fundamental aspects of biogeochemical cycles in the miombo region.

Acknowledgements

-X-

Leptactina prostrata
(Rubiaceae)

General Discussion

Regarding geoxyles, there have been many knowledge gaps and simplified narratives that prevented a comprehensive understanding of this life form. In the previous chapters, I thus aimed to provide a clearer picture of many aspects of this complex life form, though it is still non-exhaustive. Nevertheless, in the following I can synthesize new findings on the diversity and distribution patterns of geoxyles, on their biogeographical origin, on the role of environmental factors for their evolution and distribution, and on the evolutionary pathways and differentiations that enabled species to become geoxylic.

(1) How diverse are geoxyles and where do they occur?

Previous compilations of geoxyle species native to Africa differ greatly in their number, depending on the depicted region. White (1976) was the first to assemble a list, he counted 102 geoxyles (strict sense, with tree relatives) for the Zambezian Floristic Region (ZFR), and 7 for the Sudanian Floristic Region. Maurin *et al.* (2014) counted 266 geoxyles s.s. for southern Africa, including parts of the ZFR. In this work, I identified 198 geoxyles s.s. for the western ZFR (**chapter III**), and 279 geoxyles s.l. for Angola alone, 132 of which endemic to the country (47.3%) (**chapter IV**).

The extent of geoxyle diversity in the entire ZFR is even greater. According to my own compilations from Angola and Zambia, combined with a search for species described with keywords like "woody rootstock", "woody rhizome", "geoxylic suffrutex" in the Flora Zambesiaca via JSTOR Global Plants (https://plants.jstor.org/), at least 699 geoxyle species s.l. in 176 genera occur in the ZFR. Of these, at least 345 species are endemic to the ZFR (49.4%), i.e. do not occur outside the boundaries of the ZFR (**Fig. 10.1**), as confirmed by occurrence records retrieved from GBIF (https://www.gbif.org/). In total, the ZFR harbours around 8500 different plant species, of which 54%, i.e. 4590 species, are endemic to the region (White 1993). This means that geoxyles make out 7.5% of all endemic species in the ZFR (345 out of 4590), and 8.2% of the overall species (699 out of 8500).

The main geoxyle family by far in the ZFR is Fabaceae, with around 200 species, followed by Asteraceae (around 100 species), Rubiaceae (around 70 species), Euphorbiaceae (around 40 species), and Lamiaceae (around 30 species). There are 65 plant families with geoxyles in the ZFR, but mostly in low numbers, e.g. 45 families contribute only 1 to 4 species each to the ZFR geoxyle species pool. The Cerrado in Brazil is a known hotspot for geoxyles, with environmental conditions comparable to the ZFR (Pennington & Hughes, 2014). Moreover, the Cerrado is in general a biodiversity hotspot with around 10,000 different plant species (Myers *et al.*, 2000), making it the most species rich savanna worldwide (Ratter *et al.*, 1997; Simon *et al.*, 2009). However, the number of geoxyles is lower compared to the ZFR, with around 500 species (5%) (Aline Bombo, personal communication). Contrariwise, the dominant families are similar, albeit in different order: Asteraceae, followed by Fabaceae, Amaranthaceae, Lamiaceae, Myrtaceae and Euphorbiaceae (Ratter *et al.*, 1997; Filgueiras, 2002; Aline Bombo, personal communication). These similar

findings in the Cerrado and in the ZFR confirm the integral role of geoxyles for the plant diversity and functioning of savanna ecosystems worldwide (Pennington & Hughes, 2014).

These findings also raise the question, why the ZFR is so rich in geoxyle species, and I will approach this in the following. On the one hand, the ZFR is surrounded by different phytochoria that constitute a various array of different biomes (White, 1993). Not all of them have contributed geoxyle species to the Zambezian species pool, but some of them have done so greatly (**chapter V**). The details will be illustrated and discussed in the next subchapter, here it is simply important to note that the high geoxyle species richness within the ZFR is facilitated by multiple origins from outside of the ZFR.
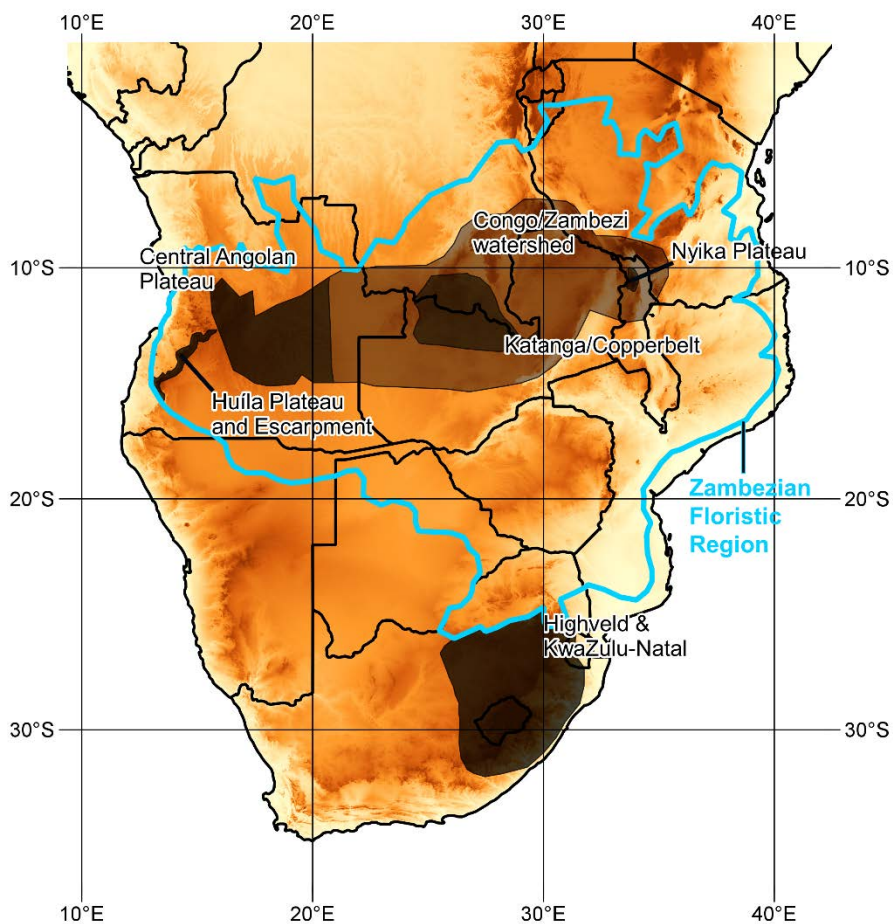
Figure 10.1: Sub-centres of geoxyle diversity and endemism within and adjacent to the Zambezian Floristic Region (ZFR). Linder (2001) identified two centres of plant endemism in the ZFR: The Huíla Plateau and the Zambezi/Congo watershed (light grey). For the latter, he stated that it might extend far into Angola, and comprise several distinct centres of endemism. For geoxyles, this is certainly true, as each of the dark highlighted areas, and even the light grey one, is characterized by distinct geoxyle communities.

On the other hand, while geoxyles generally occur in open areas of reduced tree cover, I observed that the pattern of geoxyle diversity is not homogeneous throughout the ZFR. Tropical grasslands and savannas make out a substantial area within the ZFR (see **chapter II**). However, not all open, grassy areas are kept open by the same environmental drivers, so that locally, plant communities might have to adapt to very specific conditions. While fire is commonly regarded as the main driver of grassy biomes in Africa (Bond & Keeley, 2005; Staver *et al.*, 2011; Archibald *et al.*, 2019), locally,

other drivers can play a critical role (Burtt Davy, 1922; White, 1976; Finckh *et al.*, 2016; Botha *et al.*, 2020). Endemic plant communities can emerge, if the area is isolated enough, and if those drivers are long enough in place to promote speciation, i.e. hundreds to thousands of generations (Keppel *et al.*, 2018). With regard to geoxyles, I identified several such local sub- centres of endemism within the ZFR (**Fig. 10.1**), which in part correspond to the centres of diversity and endemism recognized by Linder (2001).

Each of these sub-centres has a specific set of long-term stable environmental conditions, therefore serving as refugia during times of climatic fluctuations in the Pliocene and Pleistocene. Angola has at least three sub-centres of geoxyle diversity and endemism, with distinct geoxyle communities in each: The Huíla Plateau and Escarpment in the southwest is probably the richest, or at least best studied and easily recognizable (Linder, 2001). It constitutes Afromontane grasslands, forming a narrow high-altitude band that is geographically separated from other Afromontane regions. The only shallowly covered bedrock, frequent anthropogenic fires, and grazing by livestock promoted a tipping towards open grasslands, from the original mosaic of Afromontane forests and grasslands. The conditions seems to have been long enough in place to promote a high diversity and endemism of geoxyles (**chapters IV, V**; Goyder & Goncalves 2019).

In eastern Angola, plains covered by deep and nutrient-leeched Kalahari sands are home to other geoxyle communities, and different endemic plants. This sub-centre of endemism extends further into Zambia and DR Congo up to the borders of Malawi and Tanzania, and corresponds to the diversity and endemism center of the Congo/Zambezi watershed by Linder (2001). Ironically, Linder remarked that the high species diversity and endemism is somewhat surprising, as there are no iconic landforms, but only miombo woodlands. However, the deep Kalahari sands themselves promote a high plant diversity (Lock, 1998), and within the Congo/Zambezi watershed, as defined by Linder, I identified at least two subcentres with rather special environmental conditions. These two, the Katanga/Copperbelt region and the Nyika Plateau, will be discussed below.

The central Angolan Plateau (Bié plateau, Huambo plateau) with its many valley systems is not formerly recognized as separate centre of endmism by Linder (2001), although he admits that the centre of endemism of the Congo/Zambezi watershed might extend further west into Angola, including the central Plateau. Linder also states that the widely extended Congo/Zambezi centre of endemism might in fact be subdivided into several sub-centres with distinct endemic plant communities. My findings show that this is true, at least for geoxyles. The high geoxyle diversity and distinctness on the central Angolan Plateau has several reasons. On the one hand, due to its higher altitude, it is prone to frequent nocturnal frosts, which is a specific environmental stress to which geoxylicity is an apt answer (Finckh *et al.*, 2016; Botha *et al.*, 2020). On the other hand, it comprises a mosaic of distinct geoxyle communities, growing on a mosaic of different substrates (Revermann *et al.*, 2017; Gomes *et al.*, 2021). While the bedrock of the plateau is granite, covered by ferralithic soils, the numerous valley systems which intersect the bedrock are often filled with alluvial and aeolian Kalahari sands (Gröngröft *et al.*, 2013).

Outside of Angola, the Zambian Copperbelt and Congolese Katanga region comprise a sub-centre of endemism within the ZFR that is strongly driven by edaphic factors. From a matrix of wet miombo woodlands rise numerous hills and rocky outcrops of high copper and cobalt content, covered with azonal grassland vegetation (Malaisse *et al.*, 2016). Most of the plants growing there are metallophytes, i.e. they tolerate the high heavy metal concentrations in the ground, or are even dependent on them to grow and proliferate. Approximately 600 plant species occur in the Katanga region, of which about 60 are dependent on copper- and/or cobalt-rich soils, and 32 are strictly endemic to Katanga (Faucon *et al.*, 2010). A considerable share of the Katanga flora is herbaceous and/or geoxylic. Even if the proportion of strict endemics in Katanga is low compared to other metalliferous habitats (Faucon *et al.*, 2010), this site nevertheless adds a substantial share of metal-tolerant geoxyles to the species pool, that occur nowhere else in the ZFR.

The Nyika plateau in northern Malawi is an Afromontane region with considerable plant diversity and endemism (Willis *et al.*, 2001), about 1891 species in total (Burrows & Willis, 2005). The plateau and its foothills are therefore enclosed and protected in the Nyika National Park. Miombo woodlands cover the foothills of the plateau, and evergreen forests occur locally in gorges, landslips and near water bodies. The top of the plateau however is covered by montane grasslands, and they constitute a big part of the plateaus' plant diversity. This is evident from the fact that all the 21 genera with highest species numbers in the Nyika flora are associated partly or entirely with grasslands (Burrows & Willis, 2005). Furthermore, 130 species, 10 of which endemic to Nyika plateau, can be considered as geoxylic in the broad sense, because they are described as having woody rootstocks, rhizomes or tubers. Fire is common on the plateau, with the park management executing controlled burning of the grasslands approximately every three years (Burrows & Willis, 2005). However, due to its high altitude of up to 2600 m, the plateau also receives several frost nights per years, which might have had a far greater impact on the vegetation structure than fires (**chapter VII**).

Geoxyle diversity does not only result from multiple local centres of endemism, but also from multiple lifeforms of origin. About half of the 279 geoxyle species that occur in Angola have close tree relatives (141 species) (**chapter IV**), the remaining are closely allied to perennial herbs, or lianas and vines. In general, geoxyles with particularly massive underground structures, for instance *Brachystegia russelliae* or *Syzygium guineense* subsp *huillense*, evolved with high certainty from tree species (**chapter VIII**). Geoxyles with more unobtrusive underground structures ("small woody rootstock"), stem with some certainty from lineages of perennial herbs. Here, Asteraceae with their xylopodia are a good example, in the Miombo as well as in the Cerrado (Appezzato-da-Glória *et al.*, 2008). These species can be regarded as "secondary geoxyle species", because they acquired their woodiness only subsequently. The "primary geoxyles" have always been woody in the first place, stemming from trees. Several geoxyles evolved in lineages composed of lianas and vines, for instance *Landolphia* (Apocynaceae), or *Ampelocissos* (Vitaceae). Since lianas and vines are a characteristic element of tropical forests, they too were exposed to changing climate and

environment in the late Miocene (Axelrod & Raven, 1978). It is therefore not surprising that some species followed analogous evolutionary pathways, and relocated their stems belowground. Accordingly, all liana-related geoxyle species, which were part of this study, have long woody rhizomes that wind their way through underground trees, horizontally through the soil.

The striking species diversity of geoxyles is not directly translated to functional belowground diversity. Although there are different types of underground storage organs (USOs) and belowground bud banks (BBBs), they are quite redundant functionally (**chapter V**). The three main functions of the geoxyles' belowground organs can be summarized to a) storage of reserves, b) resprouting after disturbance [using a)], and c) clonal propagation [using a) and b)] (Pausas *et al.*, 2018; Ott *et al.*, 2019). All geoxyles do have the means for a) and b) (by definition), and a large share of geoxyles is able to do c) (**chapter V**). Often, these three principles are realized in dozens of co-occurring geoxyle species within one grassland site (**chapter VI**), so there is either more to it or the type of the belowground organ is not relevant for species diversity, and functionally redundant (Loreau, 2000, 2004). Conversely, functionally redundant species communities promote stable ecosystems, which are more resilient to disturbances and changes (Buisson *et al.*, 2019; Biggs *et al.*, 2020).

The assumption of redundancy is supported by the finding that geoxyles within a genus (sometimes also within a family) mostly share the same BBB type (**chapter V**). Lineage-specific BBB types, together with the multitude of lineages from which geoxyles evolved, point towards an inherited predisposition, of lineages to certain belowground forms and functional types. The belowground functional diversity in geoxyles is therefore owed to their origin from different families and life forms.

(2) What is the biogeographical origin of geoxyles?

Because geoxyles form a very heterogeneous group, it is not surprising to discover that they have multiple origins (**chapter V**). One of the main biomes of origin are wet-tropical forests, which until the middle to late Miocene, right before the spreading of tropical grasslands, extended into the area of todays' ZFR (Axelrod & Raven, 1978). The gradual receding of wet-tropical forests thus likely left many species behind that were able to adapt increasingly to the conditions in the newly emerging grasslands. The evolution from tree to geoxyle was facilitated by selected trait shifts, i.e. environmental conditions selected for individuals with increasingly belowground biomass allocation (Giroldo *et al.*, 2017). Accordingly, many of the geoxyles with this wet-tropical forest background are geoxyles in the strict sense, i.e. originating from tree species, and belong to families that are closely associated with such forests (**chapter V**). The most prominent example is the Rubiaceae family, followed by Fabaceae, which comprise most geoxyles species. But there are also many smaller tropical families with geoxyle species, like Anisophyllaceae (*Anisophylla fruticulosa*), Chrysobalanaceae (*Parinari capensis*) or Annonaceae (*Annona stenophylla* subsp. *nana*).

A similar pattern was discovered for the Cerrado in Brazil, a large fire-dependent neotropical savanna and biodiversity hotspot, also for geoxyles. Analogous to African savannas, the Cerrado emerged in the late Miocene (less than 10 Ma), when C4 grasslands replaced retreating wet-tropical forests (Cerling *et al.*, 1997; Pennington & Hughes, 2014). These tropical and very species-rich forests still surround most of the Cerrado, and have contributed greatly to the Cerrados' biodiversity (Simon & Pennington, 2012). Like in Africa, many phylogenetically unrelated forest lineages adapted convergently to the new conditions, acquiring the geoxylic habit, among others (Simon *et al.*, 2009). Examples for Cerrado geoxyles with close rainforest tree relatives are numerous, for instance species pairs like the geoxyle *Andira humilis* and the tree *Andira macrothyrsa* (Fabaceae) (Pennington, 2003); geoxyle *Jacaranda decurrens* and tree *Jacaranda caucana* (Bignoniaceae) (Gentry, 1992); or geoxyle *Parinari obtusifolia* and tree *Parinari campestris* (Chrysobalanaceae) (Prance, 2021).

A substantial share of geoxyles is derived from savanna lineages (**chapter V**), however, most stem from the south-hemispheric savanna (Zambezian), not the north-hemispheric one (Sudanian). The Sudanian Floristic Region is similar in extent, ecology and vegetation structure to the ZFR, but much poorer in species. They are recognized by White (1983) as different phytochoria because they harbour distinct plant species pools that are mostly endemic to their respective floristic region and overlap only little. This is certainly true for geoxyles, as there are only few shared species (e.g. *Combretum sericeum*), some species endemic to the Sudanian floristic region (e.g. *Cochlospermum tinctorium*), and much more geoxyle species endemic to the ZFR (see **chapters III** and **IV**).

It is striking that so few species are common between the Zambezian and the Sudanian despite the superficial similarity of both floristic regions. Asséde *et al.* (2020) give reasonable explanations that focus on the different geomorphological pasts and surrounding biomes of the two regions. The

key for the greater plant diversity and distinctiveness in the ZFR was the uplift of the African plateau during the Miocene, from 20 Ma (Partridge & Maud, 1987), which resulted in much higher altitude and tectonic activity in the ZFR, compared to the Sudanian Floristic Region. In consequence, the ZFR lies on average 1000 m higher, has a richer lithography, and more heterogenous soils, particularly in the east (see **Figs. 2.8, 2.9**). The higher altitude of the ZFR also allows for occasional to frequent frost events in the dry season, which do not occur in the Sudanian Floristic Region (Assédé *et al.*, 2020), except during the last glacial maxima (Anhuf, 2000; Prentice *et al.*, 2011). This emphasizes the potential role that frost has played in geoxyle evolution and diversification (**chapters V, VII**). Assédé et al (2020) also illustrate that the past positions, extents and surrounding biomes of both Floristic Regions changed markedly during the last 25 my. But while the extent of the ZFR, i.e. the south-hemispheric savanna-woodlands, grew in favour of central African rainforest, the Sudanian Floristic Region, i.e. the north-hemispheric savanna-woodlands, lost most of its extent to the emerging Sahara and Sahel. Since this happened before the major peak of geoxyle evolution in the late Pliocene and early Pleistocene (Maurin *et al.*, 2014), it is plausible that the missing frost driver, less substrate diversity, and less "evolutionary area" resulted in an overall much poorer geoxyle diversity in the Sudanian Floristic Region.

Some geoxyles, or more precisely, their precursors, entered the ZFR from the fynbos biome of the Cape Floristic Region. The Cape itself represents a biodiversity hotspot with an extraordinary species-richness (9000 species) and endemism (67%) relative to the small area (90,000 km²) (Linder, 2003). The fynbos is a mediterranean type biome, meaning that most of the precipitation falls in winter, opposed to summer rainfall in the ZFR. Lightning-caused fires are likely and have long been present in the biome (Manry & Knight, 1986). Correspondingly, the dominant plant lifeform are fire-tolerant, sclerophyllous shrubs (Linder, 2005). As Lamont *et al.* (2017) have shown for the shrublands (winter rainfall) and grasslands/savannas (summer rainfall) of South Africa, lightning-induced fires are common in both biomes. Frost is present and locally even severe, but less significant for geoxyle evolution than in the ZFR (Davies *et al.*, 2016a), at least for the genus *Protea* (Lamont *et al.*, 2017). *Protea*, together with another typical Cape genus, *Thesium*, migrated from fire-adapted fynbos shrublands to frost- and fire-prone C4 grasslands in the ZFR, and developed several geoxylic species. *Protea* is a well-studied genus that was able to switch between biomes in the past, as Lamont *et al.* (2013) have shown: When C4 grasslands emerged adjacent to the fynbos shrublands in South Africa in the late Miocene (7-19 Ma), they offered a different, more frequent fire regime, because grasses constitute a faster regenerating fuel than shrubs, which take four to six years (Kruger & Bigalke, 1984). To survive under this different fire regime, directional selection promoted the shift from serotiny to non-serotiny (Lamont *et al.*, 2020), from small and sclerophyllous to large and weak leaves, and from nonsprouting to resprouting from belowground lignotubers in *Protea*. These new traits allowed the genus to spread north from the Cape Floristic Region, and to establish in frost-prone grasslands, too (Finckh *et al.*, 2016). Geoxyles

that originate from the Cape are therefore truly fire-evolved geoxyles, characterized by lignotubers or xylopodia (Pausas *et al.*, 2018), and rather stemming from shrubs than from trees.

Beside the fynbos biome, the grassland biome, including Highveld and adjacent areas in KwaZulu-Natal in South Africa, also contributes and shares several geoxyles species to the ZFR, and forms itself a geoxyle hotspot adjacent to the ZFR (**Fig. 10.1**). Like the Nyika Plateau, this highland is part of the Afromontane Archipelago, a phytochorion on its own that stretches mostly along Eastern Africa (White, 1993). Palaeoecological studies have shown that the Afromontane grasslands of South Africa are natural, i.e. not formed by anthropogenic deforestation, and existed throughout the Quaternary (Meadows & Linder, 1993). According to White (1976), the Afromontane region in South Africa is poor in geoxyle species counting only six species, however, this is only true when the focus lies on geoxyles s.s., with tree relatives. Burtt Davy (1922) for instance recognizes 16 geoxyles s.s. for the Highveld, and Mucina *et al.* (2006) state that the region is rich in endemics, many of those with large belowground storage organs (which also includes non-woody species). Being a high altitude, frost-effected grassland that probably has been in place for at least the glacial periods in the Pleistocene (Bond *et al.*, 2003b; Prentice *et al.*, 2011), and the close proximity to the ZFR via the Afromontane archipelago, surely facilitated many species migrations to and from the grassland biome in South Africa.

For both the Cerrado and the ZFR, surrounding biomes have been important contributors to their respective species richness. Moreover, it was an important event for both that the positions and extents of the surrounding biomes as well as of themselves changed repeatedly during the last 25 my (Axelrod & Raven, 1978; Cerling *et al.*, 1997). This way, species were confronted with new conditions and either had to retreat to refugia (following their biome), or adapt to the new conditions (changing the biome), or go extinct (Aitken *et al.*, 2008). The extent of the third option is unknown, but enough species adapted to the new conditions to make their new biomes a geoxyle diversity hotspot. But, this also emphasizes that the biogeographical origin of geoxyles is relative, as the position of the shifting biomes depend on the time of observation.

(3) Which environmental factors have driven the evolution of the geoxylic life form?

Fire

Early on scientists considered various environmental drivers for the evolution of geoxyles, Burtt Davy (1922) for instance discussed the potential of dry season frosts and drought for geoxyle evolution. Contrariwise, White (1976) compared effects by frost, fire, and edaphic conditions, concluding that the latter promoted the geoxylic habit, simultaneously providing exaptations to fire and frost as well. Today however, the dominant narrative is that fire was the driver of geoxyle evolution, e.g. by Maurin *et al.* (2014) or Lamont *et al.* (2017). For this argument to be true, fire regimes at the onset of geoxyle evolution would have to be frequent enough that the acquisition of geoxyle traits (dwarf habit, belowground storage organs and bud banks, resprouting ability) would be beneficial. When looking at the geoxyle hotspots of today, i.e. Cerrado, ZFR and South Africa, they are indeed regions of highest fire frequency, burning often once a year (Bowman *et al.*, 2009).

However, nearly all these fire are anthropogenic, and geoxyles settled grasslands millions of years before humans did. Prehuman, natural fire frequencies, i.e. caused by lightning, are hard to reconstruct precisely, but fossilized charcoal deposits indicate the presence of fire from the late Miocene onwards, parallel to C4 grassland expansion ca 8 Ma (Keeley & Rundel, 2005). But fire frequencies or return intervals are not available for this time. More reliable estimates of fire frequency cover the last one million years (Bird & Cali, 1998; Archibald *et al.*, 2012; Daniau *et al.*, 2013). Those studies indicate fire frequencies increased markedly in Africa, ca 400,000 – 200,000 years ago, when humans learned to use fire as a land management tool. Before that, non-anthropogenic fire frequencies have been considerably lower (Saarnak, 2001). Most geoxyles s.s. evolved in this period of non-anthropogenic fire regimes, in the last 5 My (Maurin *et al.,* 2014).

There are studies that nowadays link lightning and burning frequency, or identify the amount of fires started by lightning in better-studied, fire prone regions, some of which are home to geoxyles. For instance, in the Fynbos biome, lightning density amounts to 0.74 ± 0.81 strikes per km² and year (Manry & Knight, 1986). This relates to a long natural fire return interval of (6-) 15 – 20 (-40) years, which is needed by the shrubby vegetation to recover from seeds and bud banks (Kruger, 1979; Bond, 1980; van Wilgen, 1981). In the sourveld grassland biome (=Highveld) of South Africa, lightning density is higher with 7.28 ± 2.50 strikes per km² and year (Manry & Knight, 1986). Correspondingly, the vegetation is adapted to frequent burning and benefits from fires every 1 – 3 years, as dead grass biomass accumulates quickly, shadowing out itself and other plants (Scott, 1966; Uys *et al.*, 2004). In the Cerrado, up to 20 strikes per km² per year have been counted, particularly in mountain ranges, causing 36 wildfires in the Cerrado from 2015 to 2019 (Schumacher *et al.*, 2022).

However, lightning data and studies from the ZFR indicate that longterm summer lightning density is lower (8.7 – 12.8 strikes per km² and year), compared to the grassland biome in South Africa

(12.8 – 21 strikes per km² and year) (Roy & Balling, 2014). Moreover, Archibald *et al.* (2009) show that in Africa south of the equator, lightning density and fire activity overlap only little, and it varies depending on the vegetation type. The critical time is the transition from dry to wet season, when vegetation is dry and flammable after the dry season, and first thunderstorms of the wet season have started. In the ZFR this is typically in October. In this month, about 1 - 2 strikes per km² hit woodlands and woodland mosaics, which is the vegetation type corresponding to the ZFR (Archibald *et al.*, 2009). Overall, around 15 strikes per km² were recorded in 2003 for woodlands and woodland mosaics, which comes close to the Cerrado (Schumacher *et al.*, 2022). What is more important to note is that although a natural, lightning-caused fire regime might be sufficiently frequent to be correlated with the spread of C4 grasslands (Bond & Keeley, 2005; Keeley & Rundel, 2005), the seasonality of fire was quite different to todays' (Saarnak, 2001; Van Wilgen *et al.*, 2008; Archibald *et al.*, 2012).

If geoxyles in the ZFR evolved and adapted in response to natural fires, they would have to benefit from an irregular fire regime happening in the late dry/early wet season. But as White (1976) already pointed out, that is not the case. Geoxyles depent on a headstart in resprouting and flowering on grasses (Trapnell, 1959; Fidelis & Blanco, 2014), and show decreased fitness under late burning (**chapters III, VI**). The situation might be different for South African biomes, because climate allows for some lightning and subsequent fires in the dry season (Manry & Knight, 1986). The genus *Protea* is a good example here, because it originates from the Cape Flora and undoubtedly diversified and spread in response to natural fire (Valente *et al.*, 2010; Lamont *et al.*, 2013, 2017). But *Protea* is only one genus out of 176 genera with geoxyles s.l. (see **chapter X.1**). In the ZFR, the geoxylic lifeform is thus unlikely a response to lightning-caused fires alone.

There is further evidence pointing to other drivers of geoxyle evolution. The subcentres of diversity and endemism in the ZFR (see **chapter X.1**) are not or only partly marked as fire-affected by Archibald *et al.* (2009), probably because the fire-prone areas are too small-scale. But being small-scale also means that it is more unlikely to be struck by lightning, and that grasslands are too discontinuous to support widespread fires. Moreover, geoxyle species with xylopodia and lignotuber, underground storage organs that are clearly a response to fire (Fidelis *et al.*, 2014; Pausas *et al.*, 2018), are rare in Angola. They make out less than 10% of the species pool (**chapter V**), although the sampled grasslands are burned annualy. Similarly, no xylopodia or lignotuber have been found in forb species near the Kruger National Park in South Africa, an arid savanna of high fire frequency (Bombo *et al.*, 2021), although here, the low precipitation might hinder establishment of geoxyles (**chapter IV**). Furthermore, xylopodia are assumed to be rare in African ecosystems (White, 1976; Robbrecht, 1988). In contrast, xylopodia are the dominant belowground organ in regularly burned Brazilian Campos grasslands (Fidelis *et al.*, 2014), and lignotubers are common in fire-affected Mediterranean shrublands (Paula *et al.*, 2016) and Australian eucalypts (Carr *et al.*, 1982).

Frost

If fire is not the primary driver of geoxyle evolution in the ZFR, what is? A definite answer is difficult to give, but at least locally, frost in the dry season seems to have played an important role, as Burtt Davy already recognized in 1922. The characteristics of geoxyles, i.e. dwarf habit, resprouting ability, belowground bud banks and storage organs, are advantageous against both fire and frost events (**chapters VI, VII**). Therefore, geoxyles that evolved in response to mid-dry season frost in the Pliocene and Pleistocene would have exaptations that allowed them to thrive and spread under the subsequent anthropogenic fire regimes in sub-saharan Africa (Finckh *et al.*, 2016). Several points support this theory. First, tropical grasslands, particularly at higher altitude, don't need fire to stay open and prevent tree encroachment; frost does that, too (**chapter VI, VII**; Botha *et al.*, 2020; Joshi *et al.*, 2020). Second, in these regions, frost has been in place far longer and at reliably higher frequencies than fire, and has probably been more severe in the past (Prentice *et al.*, 2011; Finckh *et al.*, 2016). Third, regions that are particularly rich in geoxyles in terms of abundance, diversity and endemism, are also particularly frost-affected, e.g. the Angolan Plateau (**chapter IV**) or the Nyika Plateau (Burrows & Willis, 2005).

The severity and frequency of frost events in afrotropical ecosystems depend on altitude, topography, seasonality and type of vegetation cover. Frosts occur almost exclusively during the night and in the dry season in the Afrotropics, because after sunset there is no source of warmth, and low air humidity offers no thermal isolation against outgoing longwave radiation. This is particularly pronounced at higher altitudes (> 1500 m a.s.l.), as overall temperatures are lower there, and in areas of marked topography, where cold air can pool in valleys and depressions (Clements *et al.*, 2003; Bojórquez *et al.*, 2019; Duker *et al.*, 2020).

Frosts occur, because the warmth of the sun that is stored in the ground during the day quickly radiates back into clear, low humidity skies once the sun has set, and temperatures keep dropping until the sun rises again (**Fig. 7.6**). At ground level, this happens more slowly, if the ground is covered with dense vegetation (woodlands or forests), and more rapidly and strongly, if the ground is bare or only covered by a herbaceous layer (grasslands). Lowest temperatures are reached atop the vegetation, where thermal radiation leaves the biosphere and enters the atmosphere (Leuning, 1988; Ball *et al.*, 1997).

In woodlands and forests this mean that the tree canopies are affected, which often causes them to loose their leaves, as they are deciduous. In grasslands however, this affects and controls the whole community of grasses, tree seedlings and saplings, herbs, and geoxyles. Particularly plants of tropical origin are sensitive to chilling or freezing temperatures, and quickly die back after frost (Sakai & Larcher, 2012). Most plants in the ZFR are tropical, and perennial, i.e. they have buds either protected underground (thermally isolated by soil), or protected by bark or old leaf sheaths (thermally isolated by plant tissues), so they can recover quickly after topkill. Tree seedlings, however, often have had no time to develop shoot or bud protection before frosts hit them, so that they don't establish easily at frost-prone sites (Botha *et al.*, 2020; Joshi *et al.*, 2020). The frost

regime as it is today, with up to 40 frost nights per dry season in central Angola (**Fig. 2.5; chapter VII**), or over 50 frost nights in the Afromontane regions in South Africa (**Fig. 2.5**; Finckh *et al.*, 2016), therefore plays a significant role in shaping afrotropical ecosystems (Holdo, 2006; Wakeling *et al.*, 2012; Botha *et al.*, 2020), and geoxyle hotspots. Frost in the dry season is known also from the Cerrado, but seems to occur at a much lower frequency than in Africa (Brando & Durigan, 2005; Hoffmann *et al.*, 2019), at least today.

However, it is not sufficient to look at frost events nowadays, rather one has to look at the climatic conditions from the late Miocene onwards, when geoxyles evolved. It was during this time that the atmosphere cooled down globally, and aridity and seasonality became widespread in Africa (Demenocal, 1995; Herbert *et al.*, 2016; Saarinen *et al.*, 2020). Under these conditions not only flammable C4 grasslands could emerge and spread (Keeley & Rundel, 2005), but also (mega)herbivores that feed on those grasses (Janis *et al.*, 2004; Janis, 2008). Moreover, as described above, the seasonality and open environment greatly promoted the occurrence of frosts. The glacial cycles during the Pleistocene (2.58 – 0.01 Ma), which is also the time when most geoxyles evolved from trees (Maurin *et al.,* 2014), lead to mean temperatures that were up to 6°C lower than today during times of glacial maxima (Prentice *et al.*, 2011). As I showed in **chapter VII**, behind such a mean annual temperature are even lower local, nocturnal minima that are defined topographically (valleys, depressions). This means that during glacial maxima, frost seasons have been longer, and their severity and frequency much higher than today. Glacial periods in the northern hemisphere and seasonal and cool conditions in south hemispheric Africa are both caused by precession maxima, i.e. a "wobbling" of the earth axis which leads to a shifting Intertropical Convergence Zone (ITCZ). Interestingly, these glacial periods also coincide with maxima in fire frequency in southern Africa in the last 170,000 years (Daniau *et al.*, 2013). This is not surprising, because biomass killed by frost provides good fuel for subsequent fires, again showing the close link between frost and fire (Davies *et al.*, 2016a; Botha *et al.*, 2020).

Herbivory

As Davies *et al.* (2016a) pointed out rightly, frost alone cannot explain the evolution of geoxyles, because frost kills sensitive biomass, but it doesn't remove it, so that the light-demanding geoxyles would quickly become overshadowed by moribund biomass. As a driver, frost works only if it is coupled with an agent that consumes the biomass, which can either be fire (Bond & Keeley, 2005), or herbivores, including mammals (Staver *et al.*, 2021) and termites (Okullo & Moe, 2012). Studies have shown that herbivores reduce grass biomass and favour forb communities, partly because many forbs/geoxyles are unpalatable or even toxic to mammalian herbivores (Siebert & Dreber, 2019). While the extent of herbivory by termites probably didn't change much in the last few million years, mammalian herbivory did so greatly. Karp *et al.* (2021) have shown that in savannas and grasslands of America and Australia, fire activity has been much lower right before the extinction of the (mega)herbivores at the end of the Pleistocene, than afterwards. Africa in contrast, where

most of the (mega)fauna from 12,000 years ago still exists (Faith, 2014), retained a stable fire activity. This is not contradictive however, because the time frame of Karp *et al.*'s (2021) study is not relevant for geoxyle evolution. Going further back in time, Staver *et al,* (2021) show that grazer diversity and thereby abundance has been much higher in the past, particularly around 0.5 – 2.5 Ma, coinciding with the main phase of geoxyle s.s. evolution (Maurin *et al.*, 2014). It is therefore very likely that grass biomass and competition was lower, and fire activity as well, as discussed above.

It is also possible that in the past, mixed feeder herbivores fed directly on those geoxyles that were not unpalatable or toxic to them. For instance, it has been observed in the Cangandala National Park in Angola that Sable antelopes feed on newly resprouting geoxyles in the dry season (Amândio Gomes, personal communication). Staver *et al.* (2021) show that the richness and abundance of mixed feeders and grazers alternated over time in Africa (Faith *et al.*, 2019), and that mixed feeders were more abundant before and after the peak in grazer richness, i.e. before 2.5 Ma and after 0.5 Ma. Given that mixed feeders can use more then one food resource, they benefit from the asynchronous availability of resprouting geoxyles or forbs in the dry season, and later on grasses in the rainy season (Staver & Hempson, 2020). This poses a selective pressure on palatable geoxyle precursors to reduce aboveground, and increase belowground biomass and resprouting ability, concomittently to a reduced competition by grasses.

So far I have shown how mammalian herbivores can influence vegetation structure of grasslands and savannas, whereby this herbivore type especially affects more arid savannas, e.g. in southern or east Africa (Hempson *et al.*, 2015). Strikingly, abundance of mammalian herbivores is higher in those savannas on nutrient-rich soils, which are less productive because of lower rainfall, but of higher forage quality, and less so in the high-productive but dystrophic, wet savannas of central Africa (Hopcraft *et al.*, 2010; Fynn *et al.*, 2015; Staver *et al.*, 2021), where geoxyles thrive. In the wetter systems, however, other herbivores play a significant role, especially invertebrate herbivores, i.e. termites and grasshoppers. They complement vertebrate herbivores in that their consumption activity alternates seasonally to that of vertebrate herbivores, and in the wet season, invertebrate herbivory even exceeds that of vertebrates (Okullo & Moe, 2012; Davies *et al.*, 2016b). Moreover, in systems where populations of mammalian herbivores are low, as in most of the ZFR, invertebrates assume the role of the primary plant biomass consumers (Davies *et al.*, 2016b). Termites are one of the main invertebrate herbivores, and because they feed particularly on dead biomass, they are perfect in removing frost-killed biomass (Andersen & Lonsdale, 1990).

In Africa, several termite species are known to be important dead biomass (grass) harvesters, most of them belonging to the genera *Trinervitermes* and *Hodotermes*, together with fungus-growing species of the genera *Macrotermes* and *Odontotermes* (Andersen & Lonsdale, 1990). Those termite species can reach high mount densities per hectar, ranging from 0 to 1300 (mean: 230), depending on locality. However, these numbers should be cautiously regarded as maxima at particularly favourable sites; realistic numbers likely range below 100 mounds per hectar in

savannas and grasslands, because not all are inhabited and active at a given time (Benzie, 1986). Consumption rates of termites in Africa vary depending on the locality of the grassland or savanna, and may range around 20.2 kg grass per ha per year in Kruger National Park (Meyer, 2003), South Africa, 81 kg grass per ha per year in a southern Guinean savanna, Nigera (Ohiagu, 1979), or 27.8 g mixed litter per m² per year (= 278 kg per ha per year) in Tsavo National Park, Kenya (Buxton, 1981). Termites thereby consume up to 30% of the annual litter production (Dangerfield & Schuurman, 2000).

Edaphic factors

For completeness, I will briefly discuss edaphic drivers of open grassy biomes, and how these might have affected geoxyle evolution. In his landmark review on geoxyles, White (1976) postulated that geoxyles are mostly restricted to, and therefore dependent on, grasslands within the past or present extent of Kalahari sands in south-hemispheric Africa. Thus, he assumed the geoxylic lifeform to be strongly correlated to the soil conditions there. Conditions encompass a striking nutrient-scarcity, and seasonally changing water tables, alternating between very dry and hard to waterlogged and anaerobic. Supposedly, these seasonally changing conditions prevent tree growth and at best allow only for the growth of dwarf or underground trees (White, 1976; Tinley, 1982). However, my findings do not indicate that geoxyles are strongly correlated to such edaphic grasslands and waterlogged soils, particularly since I show that geoxyles are very abundant, diverse and endemic at sites that are sloped, well-drained and prone to other environmental drivers (see **chapters III, IV, V, VII**). If anything, geoxyles occur at the periphery of seasonally waterlogged grasslands (Zigelski *et al.*, 2018).

The important observation that is being made here, however, is that waterlogged areas provide sites absent of trees, a longterm open environment with niche opportunities for evolving species. Such sites might therefore have been one of the first places to be colonized by evolving geoxyles, but not because of the (nearly) waterlogged nature of those sites, but because of their openness, which probably allowed for frost occurrences since the Miocene cooling (**chapter VII**; Herbert *et al.*, 2016). Moreover, geoxyle species with lineage-dependent inclination or tolerance towards more anaerobic, waterlogged soils, like *Syzygium guineense* subsp. *huillense*, profit especially from such environments and are able to spread widely along drainage lines and dambos (**chapter VIII**; Matayaya *et al.*, 2017). Seasonally waterlogged soils, though very patchy and small-scale, also occur in the Cerrado, and seem to support some geoxyle species as well (Batalha *et al.*, 2005; Cianciaruso *et al.*, 2005).

Another important aspect of Kalaharis sands, and most soils in south-central Africa in general, is their low nutrient-content, locally often coupled with high concentrations of metals like aluminium, iron, copper or cobalt. Generally, both geoxyles and trees occur on similarly nutrient-poor and metal-rich soils (**chapter VIII**; Gröngröft *et al.*, 2013; Gomes *et al.*, 2019, 2021), edaphic conditions are thus unlikely the direct driver behind geoxyle evolution (Lamont *et al.*, 2017). However, specific soils and soil heterogeneity are known to favour speciation processes, leading locally to high

diversity and endemism (Cowling *et al.*, 1996; Barthlott *et al.*, 2005; Hulshof & Spasojevic, 2020), as already described in **chapter X.1**. In principle, plants begin to tolerate, then to specialize for specific edaphic environment, before they radiate within it and lastly become too specialized and incompetetive to survive outside the specific edaphic environment (Anacker, 2014). Most geoxyles in Africa have not reached this final stage, perhaps except a few endemics from Katanga (Faucon *et al.*, 2010) or the Huíla Plateau (Goyder & Gonçalves, 2019). Edaphically controlled grasslands with an endemic flora adapted to high metal concentrations also occur in Brazilian savannas, and similar to the ZFR, the flora is dominated by shrubs, subshrubs and herbs (Filgueiras, 2002). However, all those patterns in both Africa and South America indicate that soil conditions are not the principal driver of geoxyle evolution, but rather of open habitats, which are a necessity for geoxyles.

(4) Which ecological, genetic, and functional differentiations went along during geoxyle evolution?

One of the remarkable facts of geoxyles s.s. is that they are so strikingly similar to their tree relatives, apart from the growth height. Both in the ZFR and in the Cerrado, many morphological traits, e.g. leaf size, do not differ between congeneric trees and geoxyles (Meerts, 2017; Giroldo *et al.*, 2017; Gomes *et al.*, 2019). As I have shown and discussed in the previous chapters (**V**, **VIII** and **IX**), trees or lianas becoming geoxylic requires a number of adaptations, most apparently developing a dwarf habit, re-allocating woody axes (biomass) from above- to belowground, storing and protecting reserves and buds in specialized belowground organs, and being able to reach sexual maturity in this state (Giroldo *et al.*, 2017). An opposed development took place in geoxyle species that evolved from perennial herbs. Here, no aboveground woody biomass needed to be relocated, instead, the rootstocks became increasingly long-lived, massive and woody in response to frequent disturbances, with Asteraceae being a good example (Appezzato-da-Glória *et al.*, 2008; da Silva *et al.*, 2014).

More differentiations become evident if we investigate ecological, genetic and functional patterns. Ecologically, trees and geoxyles differ strongly, this was already discussed in depth (**chapters VIII, X.3**). In contrast, genetic analyses are mostly restricted to dated phylogenies showing when congeneric tree and geoxyle species diverged (e.g. Simon *et al.*, 2009; Maurin *et al.*, 2014), but except from **chapter VIII** there is no study showing the possible genetic mechanisms behind. I have shown that phenotypic plasticity, likely caused by polyploidy, enabled at least one widespread geoxyle (*Syzygium guineense* subsp. *huillense*) to adapt to grassland environments. Several studies show that polyploidy is advantageous in challenging environments (with a high disturbance regime), as it enhances phenotypic flexibility (Parisod *et al.*, 2010; te Beest *et al.*, 2011; Hahn *et al.*, 2012; Wei *et al.*, 2018). However, the presence of polyploidy in tropical woody taxa is poorly studied, though definitively present and supposedly quite high (Bawa, 1973; Baum & Oginuma, 1994; Tosso *et al.*, 2016). Polyploidization can happen within one generation, often as a response to frequent environmental disturbances, and may thereby instantly create a new, reproductively isolated species (Aradhya *et al.*, 1993; Parisod *et al.*, 2010; Hahn *et al.*, 2012). It is therefore likely that evolution of the geoxylic lifeform was facilitated by polyploidy and/or phenotypic plasticity in other species as well.

Along the same line, Giroldo *et al.* (2017) linked the multiple independent origins of geoxyles with the relative ease with which the switch from tree to geoxyle happened. This indicates that genetic changes were easily acquired, rather being based on different gene regulations than on actual structural mutations (Simon & Pennington, 2012). As an example, Giroldo *et al.* (2017) give the down-regulation of the gibberellin pathways, which is known to induce dwarf growth and concomitant flowering at smaller stem sizes (Davies, 2004; Gupta & Chakrabarty, 2013). This is supported by my finding that genetic differentiation is weak between tree and geoxyle, and genetic

exchange is still happening between eco-morphologically differentiated (sub-)species (**chapter VIII**). Genetic differentiation thus seems to be a long-term and still ongoing process.

Despite changing habitat and thereby environmental conditions during their evolution, geoxyles are conservative in many ecophysiological traits (**chapter IX**). Most notably, geoxyles have the same symbiotic associations as their respective tree relatives, i.e. ectomycorrhizal symbiosis is dependent on the lineage, not on the habitat or lifeform. Analogously, leaf dry matter content, a direct proxy for net primary productivity (Smart *et al.*, 2017), indicates comparable productivity by geoxyles in grasslands and trees in woodlands, the only difference being *where* the biomass is allocated.

However, functional analysis also revealed ecophysiological trade-offs between geoxles and trees, driven by different stressors in their respective environments, and relating to the different life strategies of geoxyles and trees (**chapter IX**). Geoxyles developed a higher wood density than trees, which reflects a higher investment in survival and persistence (belowground) (Loehle, 1988; King *et al.*, 2006), compared to the hydraulic conductivity enabled by lower wood density, which is needed by high-growing trees (Borchert, 1994). This is supported by the fact that the frost-prone habitats promote strategies towards higher drought tolerance by increased wood density and mycorrhizal colonization (Midgley *et al.*, 2010; Brunner *et al.*, 2015; Volaire, 2018; Rodriguez-Zaccaro & Groover, 2019).

Another ecophysiological adaptation during geoxyle evolution is evident from the trade-off between investment in photosynthesis (higher magnesium content in leaves), and adaptation to water stress (higher potassium content in leaves) (Hugouvieux *et al.*, 2002; Tůma *et al.*, 2004; Lisar *et al.*, 2012). Geoxyles need to resprout quickly before grasses overshadow them in the rainy season (**chapters III, VI**). Accordingly, they needed to optimize photosynthesis to store sufficient reserves belowground in the short time period of low competition for light (**chapter IX**).

In conclusion, geoxyle evolution required specific adaptations to new environments, which were ecological, genetic and functional in nature. Nevertheless, many original traits remained conserved in the manifold geoxyle lineages, which contributed markedly to the high functional and morphological heterogeneity of the geoxyle lifeform (**chapters V, X.1**; Losos, 2008; Giroldo *et al.*, 2017). This partial niche conservatism in geoxyles therefore represents an example of "easy to evolve and (partly) easy to move" (Edwards & Donoghue, 2013). During the environmental changes in the last millions of years, many species in and around the ZFR, and in the Cerrado likely as well, came in contact with the inherent evolutionary potential. As a result, a multitude of species evolved into geoxyles, crossed biome and lifeform boundaries, and partly radiated and speciated further on, thereby forming this rich, heterogeneous lifeform with analogous adaptations to their new environment.

Open questions and outlook

With this work I provide answers for some of the questions regarding geoxyle diversity, distribution, ecology and evolution. Simultaneously, I also raise many new questions and issues that need to be addressed by coming research. In particular, studies on geoxyles are needed that go beyond analyses in single biomes and on single continents. An intercontinental or global comparison on geoxyle diversity, functionality and ecology would strengthen the fragmentary knowledge we have so far. This is particularly true because the research focus on geoxyles differ, e.g. between the Cerrado and the ZFR, or geoxyles have been neglected and overlooked in other important tropical grassy biomes, e.g. in India (Nerlekar *et al.*, 2022). By adopting and complementing the different lines of research we would gain a much deeper understanding of this life form, and on a global scale.

Pending research questions that have not been adressed yet include animal-geoxyle-interactions like herbivory, pollination, or seed-dispersal. Other aspects like population structure, growth rate, germination success, or propagation mode are untouched as well. Such knowledge, however, is needed if geoxyle grasslands should be managed sustainably. Given the increasing pressure by land use change and/or intensification on geoxyle grasslands, we have to put more effort into understanding how these anthropogenic disturbances affect geoxyle species. The aim should be to learn how geoxyle grasslands can be managed to both accommodate the needs of people, and preserve the diversity and functioning of the grasslands. Ploughing a geoxyle grassland with tractors, as it is increasingly done on the Angolan Plateau, surely is not a sustainable practice.

References

Abreu RCR, Hoffmann WA, Vasconcelos HL, Pilon NA, Rossatto DR, Durigan G. 2017. The biodiversity cost of carbon sequestration in tropical savanna. *Science Advances* 3: e1701284. https://doi.org/10.1126/sciadv.1701284

Aerts R, Chapin FS. 1999. The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation of Processes and Patterns. In: Fitter AH, Raffaelli DG, eds. Advances in Ecological Research. Academic Press, 1–67.

Aide TM, Rivera E. 1998. Geographic patterns of genetic diversity in Poulsenia armata (Moraceae): implications for the theory of Pleistocene refugia and the importance of riparian forest. *Journal of Biogeography* 25: 695–705. https://doi.org/10.1046/j.1365-2699.1998.2540695.x

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38: 541–545. https://doi.org/10.1111/ecog.01132

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1: 95–111. https://doi.org/10.1111/j.1752-4571.2007.00013.x

Aleman JC, Staver AC. 2018. Spatial patterns in the global distributions of savanna and forest. *Global Ecology and Biogeography* 27: 792–803. https://doi.org/10.1111geb.12739

Allaire J, Ellis P, Gandrud C, Kuo K, Lewis B, Owen J, Russell K, Rogers J, Sese C, Yetman C, *et al.* 2017. Package networkD3. *D3 JavaScript Network Graphs from R*. https://CRAN.R-project.org/package=networkD3

Allen DJ, Ort DR. 2001. Impacts of chilling temperatures on photosynthesis in warm-climate plants. *Trends in Plant Science* 6: 36–42. https://doi.org/10.1016/S1360-1385(00)01808-2

Alpert P, Simms EL. 2002. The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evolutionary Ecology* 16: 285–297. https://doi.org/10.1023/A:1019684612767

Alves JV, Silva NG, Fernandes AJ, Guimaraes AR. 2013. Longevity of the Brazilian underground tree Jacaranda decurrens Cham. *Anais da Academia Brasileira de Ciências* 85: 671–678. https://doi.org/10.1590/S0001-37652013005000038

Anacker BL. 2014. The nature of serpentine endemism. *American Journal of Botany* 101: 219–224. https://doi.org/10.3732/ajb.1300349

Andela N, Morton DC, Giglio L, Chen Y, van der Werf GR, Kasibhatla PS, DeFries RS, Collatz GJ, Hantson S, Kloster S. 2017. A human-driven decline in global burned area. *Science* 356: 1356–1362. https://doi.org/10.1126/science.aal4108

Andersen AN, Lonsdale WM. 1990. Herbivory by Insects in Australian Tropical Savannas: A Review. *Journal of Biogeography* 17: 433–444. https://doi.org/10.2307/2845374

ANGOP. 2017. Cameia prepara mais de mil hectares para cultivar arroz. *Agência Angola Press*. http://www.angop.ao/angola/pt_pt/noticias/economia/2017/6/28/Moxico-Cameia-prepara-mais-mil-hectares-para-cultivar-arroz.be825477-10c7-472d-b6e3-cb1ed5d25974.html

Anhuf D. 2000. Vegetation History and Climate Changes in Africa North and South of the Equator (10° S to 10° N) During the Last Glacial Maximum. In: Smolka P, Volkheimer W, (eds.) *Southern Hemisphere Paleo- and Neoclimates: Key Sites, Methods, Data and Models*. Berlin, Heidelberg: Springer, 225–248. https://doi.org/10.1007/978-3-642-59694-0_15

Appezzato-da-Glória B, Cury G, Soares MKM, Rocha R, Hayashi AH. 2008. Underground systems of Asteraceae species from the Brazilian Cerrado. *the Journal of the torrey botanical society* 135: 103–113. https://doi.org/10.3159/07-RA-043.1

Aradhya K, Mueller-Dombois D, Ranker T. 1993. Genetic structure and differentiation in Metrosideros polymorpha (Myrtaceae) along altitudinal gradients in Maui, Hawaii. *Genetics Research* 61: 159–170. https://doi.org/10.1017/S0016672300031335

Araújo MB, Peterson AT. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93: 1527–1539. https://doi.org/ 10.1890/11-1930.1

Archibald S. 2016. Managing the human component of fire regimes: lessons from Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371(1696): 20150346. https://doi.org/10.1098/rstb.2015.0346

Archibald S, Bond WJ, Hoffmann W, Lehmann C, Staver C, Stevens N. 2019. Distribution and determinants of savannas. In: Scogings, P & Sankaran, M (eds.), *Savanna woody plants and large herbivores*: 1–24. https://doi.org/10.1002/9781119081111.ch1

Archibald S, Hempson GP. 2016. Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371(1703): 20150309. https://doi.org/10.1098/rstb.2015.0309

Archibald S, Roy DP, Van Wilgen BW, Scholes RJ. 2009. What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biology* 15: 613–630. https://doi.org/10.1111/j.1365-2486.2008.01754.x

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**: 861–878. https://doi.org/10.1071/WF10008

Archibald S, Staver AC, Levin SA. 2012. Evolution of human-driven fire regimes in Africa. *Proceedings of the National Academy of Sciences* **109**: 847–852. https://doi.org/10.1073/pnas.1118648109

Asner GP, Levick SR, Kennedy-Bowdoin T, Knapp DE, Emerson R, Jacobson J, Colgan MS, Martin RE. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences* **106**: 4947-4952. https://doi.org/10.1073/pnas.0810637106

Assédé ESP, Azihou AF, Geldenhuys CJ, Chirwa PW, Biaou SSH. 2020. Sudanian versus Zambezian woodlands of Africa: Composition, ecology, biogeography and use. *Acta Oecologica* **107**: 103599. https://doi.org/10.1016/j.actao.2020.103599

Assis ACC, Coelho RM, Silva Pinheiro E, Durigan G. 2011. Water availability determines physiognomic gradient in an area of low-fertility soils under Cerrado vegetation. *Plant Ecology* **212**: 1135–1147. https://doi.org/10.1007/s11258-010-9893-8

Aubréville A. 1953. Les expériences de reconstitution de la savane boisée en Côte d'Ivoire. Bois et Forêts des Tropiques **32**: 4-10.

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

Axelrod DI, Raven PH. 1978. Late Cretaceous and Tertiary vegetation history of Africa. In: Werger MJA (eds.), *Biogeography and ecology of southern Africa*. Monographiae Biologicae, vol **31**. Springer, Dordrecht. Pages 77–130. https://doi.org/10.1007/978-94-009-9951-0_5

Azani N, Babineau M, Bailey CD, Banks H, Barbosa AR, Pinto RB, Boatwright JS, Borges LM, Brown GK, Bruneau A, *et al*. 2017. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny: The Legume Phylogeny Working Group (LPWG). *TAXON* **66**: 44–77. https://doi.org/10.12705/661.3

Bader MY, Ruijten JJA. 2008. A topography-based model of forest cover at the alpine tree line in the tropical Andes. *Journal of Biogeography* **35**: 711–723. https://doi.org/10.1111/j.1365-2699.2007.01818.x

Ball MC, Egerton JJG, Leuning R, Cunningham RB, Dunne P. 1997. Microclimate above grass adversely affects spring growth of seedling snow gum (Eucalyptus pauciflora). *Plant, Cell & Environment* **20**: 155–166. https://doi.org/10.1046/j.1365-3040.1997.d01-61.x

Barbosa LAG. 1970. Carta fitogeográfica de Angola. Instituto de Investigação Científica de Angola, Luanda, Angola.

Barotto AJ, Monteoliva S, Gyenge J, Martinez-Meier A, Fernandez ME. 2018. Functional relationships between wood structure and vulnerability to xylem cavitation in races of Eucalyptus globulus differing in wood density. *Tree Physiology* **38**: 243–251. https://doi.org/10.1093/treephys/tpx138

Barrat-Segretain M. 1996. Strategies of reproduction, dispersion, and competition in river plants: a review. *Vegetatio* **123**: 13–37.

Barreda VD, Palazzesi L, Tellería MC, Olivero EB, Raine JI, Forest F. 2015. Early evolution of the angiosperm clade Asteraceae in the Cretaceous of Antarctica. *Proceedings of the National Academy of Sciences* **112**: 10989–10994. https://doi.org/10.2307/26464104

Barthlott W, Mutke J, Rafiqpoor D, Kier G, Kreft H. 2005. Global centers of vascular plant diversity. *Nova Acta Leopoldina* **92**: 61–83.

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**: 76–79. https://doi.org/10.1126/science.aax0848

Batalha MA, Cianciaruso MV, Silva IA, Delitti WBC. 2005. Hyperseasonal cerrado, a new Brazilian vegetation form. *Brazilian Journal of Biology* **65**: 735–738. https://doi.org/10.1590/S1519-69842005000400021

Baum DA, Oginuma K. 1994. A review of chromosome numbers in Bombacaceae with new counts for Adansonia. *Taxon*: 11–20. https://doi.org/10.2307/1223456

Bawa KS. 1973. Chromosome numbers of tree species of a lowland tropical community. *Journal of the Arnold Arboretum* **54**: 422–434.

te Beest M, Le Roux JJ, Richardson DM, Brysting AK, Suda J, Kubešová M, Pyšek P. 2011. The more the better? The role of polyploidy in facilitating plant invasions. *Annals of Botany* **109**: 19–45. https://doi.org/10.1093/aob/mcr277

Beierkuhnlein C, Thiel D, Jentsch A, Willner E, Kreyling J. 2011. Ecotypes of European grass species respond differently to warming and extreme drought: Grass ecotypes and drought. *Journal of Ecology* **99**: 703–713. https://doi.org/10.1111/j.1365-2745.2011.01809.x

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal statistical society: series B (Methodological)* **57**: 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Benzie JA. 1986. The distribution, abundance, and the effects of fire on mound building termites (Trinervitermes and Cubitermes spp., Isoptera: Termitidae) in northern guinea savanna West Africa. *Oecologia* **70**: 559–567. https://doi.org/10.1007/BF00379904

References

Biggs CR, Yeager LA, Bolser DG, Bonsell C, Dichiera AM, Hou Z, Keyser SR, Khursigara AJ, Lu K, Muth AF, *et al.* 2020. Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. *Ecosphere* **11**: e03184. https://doi.org/10.1002/ecs2.3184

Bird MI, Cali JA. 1998. A million-year record of fire in sub-Saharan Africa. *Nature* **394**: 767–769. https://doi.org/10.1038/29507

Blonder B, Violle C, Bentley LP, Enquist BJ. 2011. Venation networks and the origin of the leaf economics spectrum. *Ecology Letters* **14**: 91–100. https://doi.org/10.1111/j.1461-0248.2010.01554.x

Boivin NL, Zeder MA, Fuller DQ, Crowther A, Larson G, Erlandson JM, Denham T, Petraglia MD. 2016. Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Sciences* **113**: 6388–6396. https://doi.org/10.1073/pnas.1525200113

Bojórquez A, Álvarez-Yépiz JC, Búrquez A, Martínez-Yrízar A. 2019. Understanding and predicting frost-induced tropical tree mortality patterns. *Global change biology* **25**: 3817–3828. https://doi.org/10.1111/gcb.14775

Bombo A, Siebert F, Fidelis A. 2021. Fire and herbivory shape belowground bud banks in a semi-arid African savanna. *African Journal of Range & Forage Science*: 1–11. https://doi.org/10.2989/10220119.2021.1982004

Bond W. 1980. Fire and Senescent Fynbos in the Swartberg, Southern Cape. *South African Forestry Journal* **114**: 68–71. https://doi.org/10.1080/00382167.1980.9629837

Bond WJ. 2008. What limits trees in C4 grasslands and savannas? *Annual review of ecology, evolution, and systematics* **39**: 641–659. https://doi.org/10.1146/annurev.ecolsys.39.110707.173411

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

Bond WJ, Keeley JE. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in ecology & evolution* **20**: 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Bond WJ, Midgley JJ. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution* **16**: 45–51. https://doi.org/10.1016/s0169-5347(00)02033-4

Bond WJ, Midgley GF, Woodward FI. 2003a. The importance of low atmospheric CO2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**: 973–982. https://doi.org/10.1046/j.1365-2486.2003.00577.x

Bond WJ, Midgley GF, Woodward FI. 2003b. What controls South African vegetation — climate or fire? *Special Issue — Acocks' Veld Types* **69**: 79–91. https://doi.org/10.1016/S0254-6299(15)30362-8

Bond WJ, Stevens N, Midgley GF, Lehmann CE. 2019. The trouble with trees: afforestation plans for Africa. *Trends in ecology & evolution* **34**: 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*. Springer, pages 125–184. https://doi.org/10.1007/978-3-642-05383-2_5

Borchert R. 1994. Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees. *Ecology* **75**: 1437–1449. https://doi.org/10.2307/1937467

Botha M, Archibald S, Greve M. 2020. What drives grassland-forest boundaries? Assessing fire and frost effects on tree seedling survival and architecture. *Ecology and evolution* **10**: 10719–10734. https://doi.org/10.1002/ece3.6730

Bowman DM, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, D'Antonio CM, DeFries RS, Doyle JC, Harrison SP. 2009. Fire in the Earth system. *science* **324**: 481–484. https://doi.org/10.1126/science.1163886

Brando PM, Durigan G. 2005. Changes in cerrado vegetation after disturbance by frost (São Paulo State, Brazil). *Plant Ecology* **175**: 205–215. https://doi.org/10.1007/s11258-005-0014-z

Brenan JP. 1978. Some aspects of the phytogeography of tropical Africa. *Annals of the Missouri Botanical Garden*: 437–478.

Briske DD. 1996. Strategies of Plant Survival in Grazed Systems : A Functional Interpretation. In: The Ecology and Management of Grazing Systems. Wallingford U.K.: CAB International, 37–67.

Brookman-Amissah J, Hall JB, Swaine MD, Attakorah JY. 1980. A re-assessment of a fire protection experiment in north-eastern Ghana savanna. *Journal of Applied Ecology* **17**: 85–99. https://doi.org/10.2307/2402965

Brooks RR, Brooks RR, Malaisse F, Empain A. 1985. *The heavy metal tolerant flora of southcentral Africa*. CRC Press.

Brown MB, Forsythe AB. 1974. Robust tests for the equality of variances. *Journal of the American Statistical Association* **69**: 364–367.

Brunner I, Herzog C, Dawes MA, Arend M, Sperisen C. 2015. How tree roots respond to drought. *Frontiers in Plant Science* **6**: 547. https://doi.org/10.3389/fpls.2015.00547

Bruvo R, Michiels NK, D'Souza TG, Schulenburg H. 2004. A simple method for the calculation of microsatellite genotype distances irrespective of ploidy level. *Molecular ecology* **13**: 2101–2106. https://doi.org/10.1111/j.1365-294x.2004.02209.x

Buisson E, Le Stradic S, Silveira FAO, Durigan G, Overbeck GE, Fidelis A, Fernandes GW, Bond WJ, Hermann J-M, Mahy G, *et al.* 2019. Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. *Biological Reviews* **94**: 590–609. https://doi.org/10.1111/brv.12470

Burrough SL, Thomas DS, Bailey RM. 2009. Mega-Lake in the Kalahari: a Late Pleistocene record of the Palaeolake Makgadikgadi system. *Quaternary Science Reviews* **28**: 1392–1411. https://doi.org/10.1016/j.quascirev.2009.02.007

Burrows JE, Willis CK. 2005. *Plants of the Nyika Plateau: an account of the vegetation of the Nyika National Parks of Malawi and Zambia*. Pretoria: Southern African Botanical Diversity Network (SABONET).

Burtt Davy J. 1922. The suffrutescent habit as an adaptation to environment. *Journal of Ecology* **10**: 211–219.

Buxton RD. 1981. Termites and the Turnover of Dead Wood in an Arid Tropical Environment. *Oecologia* **51**: 379–384.

Campbell BM. 1996. *The Miombo in transition: woodlands and welfare in Africa*. Bogor, Indonesia: CIFOR.

Caner L, Lo Seen D, Gunnell Y, Ramesh BR, Bourgeon G, G. 2007. Spatial heterogeneity of land cover response to climatic change in the Nilgiri highlands (southern India) since the Last Glacial Maximum. *The Holocene* **17**: 195–205. https://doi.org/10.1177/2F0959683607075833

Carr DJ, Carr SGM, Jahnke R. 1982. The Eucalypt Lignotuber: a Position-dependent Organ. *Annals of Botany* **50**: 481–489. https://doi.org/10.1093/oxfordjournals.aob.a086388

Catarino S, Romeiras MM, Figueira R, Aubard V, Silva J, Pereira J. 2020. Spatial and temporal trends of burnt area in Angola: implications for natural vegetation and protected area management. *Diversity* **12**: 307. https://doi.org/10.3390/d12080307

Cerling TE, Harris JM, MacFadden BJ, Leakey MG, others. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**: 153. https://doi.org/10.1038/38229

Cerling TE, Wang Y, Quade J. 1993. Expansion of C4 ecosystems as an indicator of global ecological change in the late Miocene. *Nature* **361**: 344–345. https://doi.org/10.1038/361344a0

Chapuis M-P, Estoup A. 2006. Microsatellite null alleles and estimation of population differentiation. *Molecular biology and evolution* **24**: 621–631. https://doi.org/10.1093/molbev/msl191

Charles-Dominique T, Davies TJ, Hempson GP, Bezeng BS, Daru BH, Kabongo RM, Maurin O, Muasya AM, Van der Bank M, Bond WJ. 2016. Spiny plants, mammal browsers, and the origin of African savannas. *Proceedings of the National Academy of Sciences* **113**: E5572–E5579. https://doi.org/10.1073/pnas.1607493113

Chidumayo EN. 1994. Phenology and nutrition of miombo woodland trees in Zambia. *Trees* **9**: 67–72. https://doi.org/10.1007/BF00202124

Chidumayo EN. 1995. *Handbook of miombo ecology and management*. Stockholm, Sweden: Stockholm Environmental Institute.

Chidumayo EN. 1997. Effects of accidental and prescribed fires on miombo woodland, Zambia. *The Commonwealth Forestry Review* **76**: 268–272.

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

Cianciaruso MV, Batalha MA, da Silva IA. 2005. Seasonal variation of a hyperseasonal cerrado in Emas National Park, central Brazil. *Flora-Morphology, Distribution, Functional Ecology of Plants* **200**: 345–353. https://doi.org/10.1016/j.flora.2005.02.001

Clark LV, Jasieniuk M. 2011. POLYSAT: an R package for polyploid microsatellite analysis. *Molecular Ecology Resources* **11**: 562–566. https://doi.org/10.1111/j.1755-0998.2011.02985.x

Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* **197**: 19–35. https://doi.org/10.1111/nph.12001

Clayton WD, Cope TA. 1980. The chorology of Old World species of Gramineae. *Kew Bulletin*: 135–171.

Clements CB, Whiteman CD, Horel JD. 2003. Cold-Air-Pool Structure and Evolution in a Mountain Basin: Peter Sinks, Utah. *Journal of Applied Meteorology* **12**: 752–768. https://doi.org/10.1175/1520-0450(2003)042<0752:CSAEIA>2.0.CO;2

Coates Palgrave K. 2002. *Trees of southern Africa. New edition revised and updated by Meg Coates Palgrave.* Cape Town Struik 1212.

Cole MM. 1963. Vegetation and geomorphology in Northern Rhodesia: an aspect of the distribution of the savanna of central Africa. *The Geographical Journal* **129**: 290–305.

Colgan MS, Martin RE, Baldeck CA, Asner GP. 2015. Tree Foliar Chemistry in an African Savanna and Its Relation to Life History Strategies and Environmental Filters. *PLOS ONE* **10**: e0124078. https://doi.org/10.1371/journal.pone.0124078

Congalton RG. 1991. A Review Of Assessing The Accuracy Of Classifications Of Remotely Sensed Data. *Remote Sensing Of Environment* **37**: 35–46. https://doi.org/10.1016/0034-4257(91)90048-B

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302–1310. https://doi.org/10.1126/science.199.4335.1302

Conrad O. 2012. Module Valley Depth. *SAGA Tool Library Documentation* **2**.

Conrad O, Bechtel B, Bock M, Dietrich H, Fischer E, Gerlitz L, Böhner J. 2015. System for Automated Geoscientific Analyses (SAGA) v. *2.1.4. Geoscientific Model Development* **8**: 1991–2007. https://doi.org/10.5194/gmd-8-1991-2015

Coop JD, Givnish TJ. 2007. Gradient analysis of reversed treelines and grasslands of the Valles Caldera, New Mexico. *Journal of Vegetation Science* **18**: 43–54. https://doi.org/10.1111/j.1654-1103.2007.tb02514.x

Cordell S, Goldstein G, Mueller-Dombois D, Webb D, Vitousek P. 1998. Physiological and morphological variation in Metrosideros polymorpha, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. *Oecologia* **113**: 188–196. https://doi.org/10.1007/s004420050367

Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, Ter Steege H, Morgan HD, Van Der Heijden MGA. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian journal of Botany* **51**: 335–380. https://doi.org/10.1071/BT02124

Corrales A, Henkel TW, Smith ME. 2018. Ectomycorrhizal associations in the tropics – biogeography, diversity patterns and ecosystem roles. *New Phytologist* **220**: 1076–1091. https://doi.org/10.1111/nph.15151

Cover T, Hart P. 1967. Nearest neighbor pattern classification. *IEEE transactions on information theory* **13**: 21–27. https://doi.org/10.1109/TIT.1967.1053964

Cowling RM, Rundel PW, Lamont BB, Kalin Arroyo M, Arianoutsou M. 1996. Plant diversity in mediterranean-climate regions. *Trends in Ecology & Evolution* **11**: 362–366. https://doi.org/10.1016/0169-5347(96)10044-6

Creel S, Dröge E, M'soka J, Smit D, Becker M, Christianson D, Schuette P. 2017. The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey. *Ecology* **98**: 2081–2092. https://doi.org/10.1002/ecy.1885

Dakora FD, Phillips DA. 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant and Soil* **245**: 35–47. https://doi.org/10.1023/A:1020809400075

Dangerfield JM, Schuurman G. 2000. Foraging by fungus-growing termites (Isoptera: Termitidae, Macrotermitinae) in the Okavango Delta, Botswana. *Journal of Tropical Ecology* **16**: 717–731. https://doi.org/10.1017/S026646740000167X

Daniau A-L, Sánchez Goñi MF, Martinez P, Urrego DH, Bout-Roumazeilles V, Desprat S, Marlon JR. 2013. Orbital-scale climate forcing of grassland burning in southern Africa. *Proceedings of the National Academy of Sciences* **110**: 5069. https://doi.org/10.1073/pnas.1214292110

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

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

Das A, Nagendra H, Anand M, Bunyan M. 2015. Topographic and bioclimatic determinants of the occurrence of forest and grassland in tropical montane forest-grassland mosaics of the Western Ghats, India. *PLoS ONE* **10**: 0130566. https://doi.org/10.1371/journal.pone.0130566

Davies PJ. 2004. *Plant hormones: biosynthesis, signal transduction, action!* Springer Science & Business Media.

Davies TJ, Daru BH, van der Bank M, Maurin O, Bond WJ. 2016a. Multiple routes underground? Frost alone cannot explain the evolution of underground trees. *New Phytologist* **209**: 910–912. https://doi.org/10.1111/nph.13795

Davies AB, van Rensburg BJ, Robertson MP, Levick SR, Asner GP, Parr CL. 2016b. Seasonal variation in the relative dominance of herbivore guilds in an African savanna. *Ecology* **97**: 1618–1624. https://doi.org/10.1890/15-1905.1

Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* **292**: 673–679. https://doi.org/10.1126/science.292.5517.673

Dayaram A, Witkowski ETF, Raimondo DC, Bamford MK. 2020. Carbon-14 dating when there's no ring on it: Age of four Pondoland grassland geoxyles and lessons learned. *South African Journal of Botany* **132**: 415–422. https://doi.org/10.1016/j.sajb.2020.06.008

De Jong G. 2005. Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. *New Phytologist* **166**: 101–118. https://doi.org/10.1111/j.1469-8137.2005.01322.x

De Queiroz K. 2007. Species concepts and species delimitation. *Systematic biology* **56**: 879–886. https://doi.org/10.1080/10635150701701083

Demenocal PB. 1995. Plio-pleistocene African climate. *Science* **270**: 53–59. https://doi.org/10.1126/science.270.5233.53

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**: 130–144. https://doi.org/10.1043/0363-6445-28.1.130

DeWitt TJ, Sih A, Wilson DS. 1998. Costs and limits of phenotypic plasticity. *Trends in ecology & evolution* **13**: 77–81. https://doi.org/10.1016/S0169-5347(97)01274-3

Di Marco M, Chapman S, Althor G, Kearney S, Besancon C, Butt N, Maina JM, Possingham HP, Rogalla von Bieberstein K, Venter O, *et al.* **2017**. Changing trends and persisting biases in three decades of conservation science. *Global Ecology and Conservation* **10**: 32–42. https://doi.org/10.1016/j.gecco.2017.01.008

Díaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Martí G, Grime JP, Zarrinkamar F, Asri Y, *et al.* **2004**. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* **15**: 295–304. https://doi.org/10.1111/j.1654-1103.2004.tb02266.x

Dinno A. 2015. Nonparametric pairwise multiple comparisons in independent groups using Dunn's test. *The Stata Journal* **15**: 292–300. https://doi.org/10.1177/1536867X1501500117

Dixon J. 1991. Roles of clays in soils. *Applied Clay Science* **5**: 489–503. https://doi.org/10.1016/0169-1317(91)90019-6

Dixon AP, Faber-Langendoen D, Josse C, Morrison J, Loucks CJ. 2014. Distribution mapping of world grassland types. *Journal of biogeography* **41**: 2003–2019. https://doi.org/10.1111/jbi.12381

Dobrowski SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* **17**: 1022–1035. https://doi.org10.1111/j.1365-2486.2010.02263.x

Dolédec S, Chessel D, Ter Braak CJF, Champely S. 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics* **3**: 143–166. https://doi.org/10.1007/BF02427859

Donaldson J, Donaldson MJ. 2010. Package 'tsne'. *CRAN Repository*. https://github.com/jdonaldson/rtsne/

Donkpegan AS, Doucet J-L, Migliore J, Duminil J, Dainou K, Piñeiro R, Wieringa JJ, Champluvier D, Hardy OJ. 2017. Evolution in African tropical trees displaying ploidy-habitat association: the genus Afzelia (Leguminosae). *Molecular phylogenetics and evolution* **107**: 270–281. https://doi.org/10.1016/j.ympev.2016.11.004

Doxsey-Whitfield E, MacManus K, Adamo SB, Pistolesi L, Squires J, Borkovska O, Baptista SR. 2015. Taking Advantage of the Improved Availability of Census Data: A First Look at the Gridded Population of the World, Version 4. *Papers in Applied Geography* **1**: 226–234. https://doi.org/10.1080/23754931.2015.1014272

Doyle JJ, Dickson EE. 1987. Preservation of plant samples for DNA restriction endonuclease analysis. *Taxon*: 715–722. https://doi.org/10.2307/1221122

Dray S, Choler P, Doledec S, Peres-Neto PR, Thuiller W, Pavoine S, ter Braak CJ. 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* **95**: 14–21. https://doi.org/

Dray S, Dufour A-B. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of statistical software* **22**: 1–20. https://doi.org/10.1890/13-0196.1

Duker R, Cowling RM, Preez DR, Vyver ML, Weatherall-Thomas CR, Potts AJ. 2015. Community-level assessment of freezing tolerance: frost dictates the biome boundary between Albany subtropical thicket and Nama-Karoo in South Africa. *Journal of Biogeography* **42**: 167–178. https://doi.org/

Duker R, Cowling RM, Vyver ML, Potts AJ. 2020. Site selection for subtropical thicket restoration: mapping cold-air pooling in the South African sub-escarpment lowlands. *PeerJ* **8**: 8980. https://doi.org/10.7717/peerj.8980

Duminil J, Mona S, Mardulyn P, Doumenge C, Walmacq F, Doucet J, Hardy OJ. 2015. Late Pleistocene molecular dating of past population fragmentation and demographic changes in African rain forest tree species supports the forest refuge hypothesis. *Journal of biogeography* **42**: 1443–1454. https://doi.org/10.1111/jbi.12510

Dumolin S, Demesure B, Petit RJ. 1995. Inheritance of chloroplast and mitochondrial genomes in pedunculate oak investigated with an efficient PCR method. *Theoretical and Applied Genetics* **91**: 1253-1256 https://doi.org/10.1007/BF00220937

Dunn OJ. 1961. Multiple comparisons among means. *Journal of the American Statistical Association* **56**: 52–64.

Durigan G, Pilon NAL, Abreu RCR, Hoffmann WA, Martins M, Fiorillo BF, Antunes AZ, Carmignotto AP, Maravalhas JB, Vieira J, *et al.* **2020**. No Net Loss of Species Diversity After Prescribed Fires in the Brazilian Savanna. *Frontiers in Forests and Global Change* **3**: 1-13. https://doi.org/10.3389/ffgc.2020.00013

Dynesius M, Jansson R. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences* **97**: 9115–9120. https://doi.org/10.1073/pnas.97.16.9115

Earl DA, vonHoldt BM. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources* **4**: 359–361. https://doi.org/10.1007/s12686-011-9548-7

Edwards EJ, Donoghue MJ. 2013. Is it easy to move and easy to evolve? Evolutionary accessibility and adaptation. *Journal of Experimental Botany* **64**: 4047–4052. https://doi.org/10.1093/jxb/ert220

Eldredge N, Thompson JN, Brakefield PM, Gavrilets S, Jablonski D, Jackson JB, Lenski RE, Lieberman BS, McPeek MA, Miller III W. 2005. The dynamics of evolutionary stasis. *Paleobiology* **31**: 133–145. https://doi.org/10.1666/0094-8373(2005)031[0133:TDOES]2.0.CO;2

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

de la Estrella M, Forest F, Wieringa JJ, Fougère-Danezan M, Bruneau A. 2017. Insights on the evolutionary origin of Detarioideae, a clade of ecologically dominant tropical African trees. *New Phytologist* **214**: 1722–1735. https://doi.org/10.1111/nph.14523

Evanno G, Regnaut S, Goudet J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular ecology* **14**: 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Excoffier L, Smouse PE, Quattro JM. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* **131**: 479–491. https://doi.org/10.1093/genetics/131.2.479

Exell AW, Mendonça FA, Fernandes A. 1966. *Conspectus florae angolensis. Volume 4. Myrtaceae*. Ministério do ultramar. Junta de investigaçoes colonais.

Faith JT. 2014. Late Pleistocene and Holocene mammal extinctions on continental Africa. *Earth-Science Reviews* **128**: 105–121. https://doi.org/10.1016/j.earscirev.2013.10.009

Faith JT, Rowan J, Du A. 2019. Early hominins evolved within non-analog ecosystems. *Proceedings of the National Academy of Sciences* **116**: 21478. https://doi.org/10.1073/pnas.1909284116

Falster DS, Westoby M. 2005. Tradeoffs between height growth rate, stem persistence and maximum height among plant species in a post-fire succession. *Oikos* **111**: 57–66. https://doi.org/10.1111/j.0030-1299.2005.13383.x

Farrar DE, Glauber RR. 1967. Multicollinearity in regression analysis: the problem revisited. *The Review of Economic and Statistics*: 92–107.

Faucon M-P, Meersseman A, Shutcha MN, Mahy G, Luhembwe MN, Malaisse F, Meerts P. 2010. Copper endemism in the Congolese flora: a database of copper affinity and conservational value of cuprophytes. *Plant Ecology and Evolution* **143**: 5–18. https://doi.org/10.5091/plecevo.2010.411

February EC, Coetsee C, Cook GD, Ratnam J, Wigley B. 2019. Physiological Traits of Savanna Woody Species: Adaptations to Resource Availability. In: Scogings, P, & Sankaran, M, (eds.) *Savanna Woody Plants and Large Herbivores*. 309–329. https://doi.org/10.1002/9781119081111.ch11

Fedele G, Donatti CI, Bornacelly I, Hole DG. 2021. Nature-dependent people: Mapping human direct use of nature for basic needs across the tropics. *Global Environmental Change*: 102368. https://doi.org/10.1016/j.gloenvcha.2021.102368

Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas: NEW CLIMATE SURFACES FOR GLOBAL LAND AREAS. *International Journal of Climatology* **37**: 4302–4315. https://doi.org/10.1002/joc.5086

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**: 110–116. https://doi.org/10.1016/j.flora.2013.12.003

Fidelis A, Blanco C. 2014. Does fire induce flowering in Brazilian subtropical grasslands? *Applied Vegetation Science* **17**: 690–699. https://doi.org/10.1111/avsc.12098

Fife D, Fife MD. 2017. Package 'fifer': A biostatisticians toolbox for various activities, including plotting, data cleanup, and data analysis. *A biostatisticians toolbox for various activities, including plotting, data cleanup, and data analysis*. https://cran.r-project.org/package=fifer

Figueiredo E, Smith GF. 2008. *Plants of Angola / Plantas de Angola*. Pretoria, South Africa: SANBI.

Filgueiras TS. 2002. Herbaceous Plant Communities. In: Oliveira PS, Marquis RJ, (eds.) *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. Columbia University Press, 121–139. https://doi.org/10.7312/oliv12042-006

Finckh M. 1993. Die Wälder des Villarrica-Nationalparks (Südchile) - Lebensgemeinschaften als Basis für ein Schutzkonzept. *Dissertationes Botanicae* **259**.

Finckh M, Revermann R, Aidar MP. 2016. Climate refugees going underground–a response to Maurin et al.(2014). *New Phytologist* **209**: 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**: e13084. https://doi.org/10.1111/jvs.13084

Fitter AH, Hay RK. 2012. *Environmental physiology of plants*. 367 pages. Academic press.

Fjeldsaå J, Lovett JC. 1994. Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity & Conservation* **6**: 325–346. https://doi.org/10.1007/BF00055939

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**: 187–206. https://doi.org/10.1007/s10531-019-01878-6

References

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

Frost P. 1996. The ecology of miombo woodlands. In: The miombo in transition: Woodlands and welfare in Africa. Center for International Forestry Research (CIFOR), 11–57.

Furley PA, Rees RM, Ryan CM, Saiz G. 2008. Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe. *Progress in Physical Geography* **32**: 611–634. https://doi.org/10.1177/0309133308101383

Fynn RW, Morris CD, Edwards TJ. 2004. Effect of burning and mowing on grass and forb diversity in a long-term grassland experiment. *Applied Vegetation Science* **7**: 1–10. https://doi.org/10.1111/j.1654-109X.2004.tb00589.x

Fynn RWS, Murray-Hudson M, Dhliwayo M, Scholte P. 2015. African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management* **23**: 559–581. https://doi.org/10.1007/s11273-015-9430-6

García Criado M, Myers-Smith IH, Bjorkman AD, Lehmann CE, Stevens N. 2020. Woody plant encroachment intensifies under climate change across tundra and savanna biomes. *Global Ecology and Biogeography* **29**: 925–943. https://doi.org/10.1111/geb.13072

Garnier E, Navas M-L. 2012. A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. *Agronomy for Sustainable Development* **32**: 365–399. https://doi.org/10.1007/s13593-011-0036-y

Garnier E, Shipley B, Roumet C, Laurent G. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology* **15**: 688–695. https://doi.org/10.1046/j.0269-8463.2001.00563.x

Gattuso J-P, Magnan A, Billé R, Cheung WW, Howes EL, Joos F, Allemand D, Bopp L, Cooley SR, Eakin CM. 2015. Contrasting futures for ocean and society from different anthropogenic CO2 emissions scenarios. *Science* **349**: aac4722. https://doi.org/10.1126/science.aac4722

GBIF. 2021. GBIF Occurrence Download. The Global Biodiversity Information Facility. Downloaded on 02.07.2021. https://doi.org/10.15468/DL.43FWMF

Gentry AH. 1992. Bignoniaceae: Part II (Tribe Tecomeae). *Flora Neotropica* **25**: 1–370. http://www.jstor.org/stable/4393739

Giglio L, Justice C. 2015. MOD14A1 MODIS/Terra Thermal Anomalies/Fire Daily L3 Global 1km SIN Grid V006 [Data set]. *NASA EOSDIS Land Processes DAAC*. https://doi.org/10.5067/MODIS/MOD14A1.006

Giglio L, Justice C, Boschetti L, Roy D. 2015. MCD64A1 MODIS/Terra+Aqua Burned Area Monthly L3 Global 500m SIN Grid V006 [Data set]. *NASA EOSDIS Land Processes DAAC*. https://doi.org/10.5067/MODIS/MCD64A1.006

Gignoux J, Lahoreau G, Julliard R, Barot S. 2009. Establishment and early persistence of tree seedlings in an annually burned savanna. *Journal of Ecology* **97**: 484–495. https://doi.org/10.1111/j.1365-2745.2009.01493.x

Giroldo AB, Scariot A, Hoffmann WA. 2017. Trait shifts associated with the subshrub life-history strategy in a tropical savanna. *Oecologia* **185**: 281–291. https://doi.org/10.1007/s00442-017-3930-4

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

Gonçalves FMP, Revermann R, Gomes AL, Aidar MPM, Finckh M, Juergens N. 2017. Tree Species Diversity and Composition of Miombo Woodlands in South-Central Angola: A Chronosequence of Forest Recovery after Shifting Cultivation (P Corona, Ed.). *International Journal of Forestry Research* **2017**: 6202093. https://doi.org/10.1155/2017/6202093

Gossweiler J, Mendonça FA. 1939. *Carta fitogeografica de Angola*. 242 pages.Lisboã: Ministério das Colónias.

Govender N, Trollope WS, 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**: 748–758. https://doi.org/10.1111/j.1365-2664.2006.01184.x

Goyder DJ, Barker N, Bester SP, Frisby A, Janks M, Gonçalves FM. 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: Biodiversity of Angola. Springer, Cham, 79–96. https://doi.org/10.1007/978-3-030-03083-4_5

Grace J, San Jose J, Meir P, Miranda HS, Montes RA. 2006. Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography* **33**: 387–400. https://doi.org/10.1111/j.1365-2699.2005.01448.x

Gratani L. 2014. Plant Phenotypic Plasticity in Response to Environmental Factors. *Advances in Botany* **2014**: 1–17. https://doi.org/10.1155/2014/208747

Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos*: 259–281. https://doi.org/10.2307/3546011

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, Luther-Mosebach J, Landschreiber L, Eschenbach A. 2013. Cusseque - Soils. *Biodiversity and Ecology* **5**: 51-54. https://doi.org/10.7809/b-e.00245

Gupta R, Chakrabarty SK. 2013. Gibberellic acid in plant. *Plant Signaling & Behavior* **8**: e25504. https://doi.org/10.4161/psb.25504

Güsewell S. 2005. Nutrient resorption of wetland graminoids is related to the type of nutrient limitation. *Functional Ecology* **19**: 344–354. https://doi.org/10.1111/j.0269-8463.2005.00967.x

Güsewell S, Koerselman W. 2002. Variation in nitrogen and phosphorus concentrations of wetland plants. *Perspectives in Plant Ecology, Evolution and Systematics* **5**: 37–61. https://doi.org/10.1078/1433-8319-0000022

Hahn MA, van Kleunen M, Müller-Schärer H. 2012. Increased phenotypic plasticity to climate may have boosted the invasion success of polyploid Centaurea stoebe. *PloS one* **7**: e50284. https://doi.org/10.1371/journal.pone.0050284

Hall M. 1984. Man's Historical and Traditional Use of Fire in Southern Africa. In: de Booysen PV, Tainton NM, (eds.) *Ecological Effects of Fire in South African Ecosystems*. Berlin, Heidelberg: Springer Berlin Heidelberg, 39–52.

Hall JS, Harris DJ, Saltonstall K, Medjibe V de P, Ashton MS, Turner BL. 2020. Resource acquisition strategies facilitate *Gilbertiodendron dewevrei* monodominance in African lowland forests. *Journal of Ecology* **108**: 433–448. https://doi.org/10.1111/1365-2745.13278

Halverson K, Heard SB, Nason JD, Stireman III JO. 2008. Origins, distribution, and local co-occurrence of polyploid cytotypes in *Solidago altissima* (Asteraceae). *American Journal of Botany* **95**: 50–58. https://doi.org/10.3732/ajb.95.1.50

Hamilton MG, Tarifa JR. 1978. Synoptic aspects of a polar outbreak leading to frost in tropical Brazil. *Monthly Weather Review* **106**: 1545–1556. https://doi.org/10.1175/1520-0493(1978)106<1545:SAOAPO>2.0.CO;2

Hampe A. 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography* **13**: 469–471. https://doi.org/10.1111/j.1466-822X.2004.00090.x

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR. 2013. High-resolution global maps of 21st-century forest cover change. *science* **342**: 850–853. https://doi.org/10.1126/science.1244693

Harpole WS, Tilman D. 2007. Grassland species loss resulting from reduced niche dimension. *Nature* **446**: 791–793. https://doi.org/10.1038/nature05684

Harris I, Osborn TJ, Jones P, Lister D. 2020. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data* **7**: 109. https://doi.org/10.1038/s41597-020-0453-3

Hautier Y, Tilman D, Isbell F, Seabloom EW, Borer ET, Reich PB. 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science* **348**: 336–340. https://doi.org/10.1126/science.aaa1788

He T, Lamont BB, Pausas JG. 2019. Fire as a key driver of Earth's biodiversity. *Biological Reviews* **94**: 1983–2010. https://doi.org/10.1111/brv.12544

Hedin LO. 2004. Global organization of terrestrial plant–nutrient interactions. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 10849. https://doi.org/10.1073/pnas.0404222101

Hempson GP, Archibald S, Bond W. 2015. A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science* **350**: 1056–1061. https://doi.org/10.1126/science.aac7978

Hempson GP, Archibald S, Bond WJ. 2017. The consequences of replacing wildlife with livestock in Africa. *Scientific Reports* **7**: 17196. https://doi.org/10.1038/s41598-017-17348-4

Hengl T, de Jesus JM, Heuvelink GB, Gonzalez MR, Kilibarda M, Blagotić A, Shangguan W, Wright MN, Geng X, Bauer-Marschallinger B. 2017a. SoilGrids250m: Global gridded soil information based on machine learning. *PLoS one* **12**: e0169748. https://doi.org/10.1371/journal.pone.0169748

Hengl T, Leenaars JG, Shepherd KD, Walsh MG, Heuvelink GB, Mamo T, Tilahun H, Berkhout E, Cooper M, Fegraus E. 2017b. Soil nutrient maps of Sub-Saharan Africa: assessment of soil nutrient content at 250 m spatial resolution using machine learning. *Nutrient Cycling in Agroecosystems* **109**: 77–102. https://doi.org/10.1007/s10705-017-9870-x

Herben T, Klimešová J. 2020. Evolution of clonal growth forms in angiosperms. *New Phytologist* **225**: 999–1010. https://doi.org/10.1111/nph.16188

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**: 843–847. https://doi.org/10.1038/ngeo2813

Hermans C, Hammond JP, White PJ, Verbruggen N. 2006. How do plants respond to nutrient shortage by biomass allocation? *Trends in Plant Science* 11: 610–617. https://doi.org/10.1016/j.tplants.2006.10.007

Higgins SI, Bond WJ, February EC, Bronn A, Euston-Brown DI, Enslin B, Govender N, Rademan L, O'Regan S, Potgieter AL. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* 88: 1119–1125. https://doi.org/10.1890/06-1664

Hijmans RJ, Van Etten J, Cheng J, Mattiuzzi M, Sumner M, Greenberg JA, Lamigueiro OP, Bevan A, Racine EB, Shortridge A. 2015. Package 'raster': Geographic Data Analysis and Modeling. https://rspatial.org/raster/

Hillyer MJ, Boulter SL, Kitching RL, Hughes JM. 2007. Isolation and characterization of eight polymorphic microsatellite loci in the rainforest canopy tree, Syzygium sayeri (Myrtaceae). *Molecular Ecology Resources* 7: 1199–1201. https://doi.org/10.1111/j.1471-8286.2007.01828.x

Hind DJN, Goyder DJ. 2014. Stomatanthes tundavalaensis (Compositae: Eupatorieae: Eupatoriinae), a new species from Huíla Province, Angola, and a synopsis of the African species of Stomatanthes. *Kew Bulletin* 69(4): 1-9. https://doi.org/10.1007/s12225-014-9545-6

Hoffmann WA, Adasme R, Haridasan M, T. de Carvalho M, Geiger EL, Pereira MAB, Gotsch SG, Franco AC. 2009. Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. *Ecology* 90: 1326–1337. https://doi.org/10.1890/08-0741.1

Hoffmann WA, Flake SW, Abreu RC, Pilon NA, Rossatto DR, Durigan G. 2019. Rare frost events reinforce tropical savanna–forest boundaries. *Journal of Ecology* 107: 468–477. https://doi.org/10.1111/1365-2745.13047

Hoffmann WA, Franco AC, Moreira MZ, Haridasan M. 2005. Specific leaf area explains differences in leaf traits between congeneric savanna and forest trees. *Functional Ecology* 19: 932–940. https://doi.org/10.1111/j.1365-2435.2005.01045.x

Hoffmann AA, Sgrò CM. 2011. Climate change and evolutionary adaptation. *Nature* 470: 479–485. https://doi.org/10.1038/nature09670

Högberg P. 1982. Mycorrhizal associations in some woodland and forest trees and shrubs in Tanzania. *New Phytologist* 92: 407–415. https://doi.org/10.1111/j.1469-8137.1982.tb03398.x

Högberg P, Nylund J-E. 1981. Ectomycorrhizae in coastal miombo woodland of Tanzania. *Plant and Soil* 63: 283–289. https://doi.org/10.1007/BF02374606

Högberg P, Piearce GD. 1986. Mycorrhizas in Zambian Trees in Relation to Host Taxonomy, Vegetation Type and Successional Patterns. *Journal of Ecology* 74: 775–785. https://doi.org/10.2307/2260397

Holdo RM. 2006. Elephant herbivory, frost damage and topkill in Kalahari sand woodland savanna trees. *Journal of Vegetation Science* 17: 509–518. https://doi.org/10.1111/j.1654-1103.2006.tb02472.x

Holt RD. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106: 19659–19665. https://doi.org/10.1073/pnas.0905137106

Hopcraft JGC, Olff H, Sinclair ARE. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution* 25: 119–128. https://doi.org/10.1016/j.tree.2009.08.001

Houlton BZ, Wang Y-P, Vitousek PM, Field CB. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* 454: 327–330. https://doi.org/10.1038/nature07028

Hoyos N, Correa-Metrio A, Sisa A, Ramos-Fabiel MA, Espinosa JM, Restrepo JC, Escobar J. 2017. The environmental envelope of fires in the Colombian Caribbean. *Applied Geography* 84: 42–54. https://doi.org/10.1016/j.apgeog.2017.05.001

Hugouvieux V, Murata Y, Young JJ, Kwak JM, Mackesy DZ, Schroeder JI. 2002. Localization, Ion Channel Regulation, and Genetic Interactions during Abscisic Acid Signaling of the Nuclear mRNA Cap-Binding Protein, ABH1. *Plant Physiology* 130: 1276–1287. https://doi.org/10.1104/pp.009480

Hulshof CM, Spasojevic MJ. 2020. The edaphic control of plant diversity. *Global Ecology and Biogeography* 29: 1634–1650. https://doi.org/10.1111/geb.13151

Huntley BJ. 2019. Angola in outline: physiography, climate and patterns of biodiversity. In: Biodiversity of Angola. Springer, Cham, 15–42. https://doi.org/10.1007/978-3-030-03083-4_2

Huntley BJ, Beja P, Pinto PV, Russo V, Veríssimo L, Morais M. 2019. Biodiversity conservation: history, protected areas and hotspots. In: Biodiversity of Angola. Springer, Cham, 495–512. https://doi.org/10.1007/978-3-030-03083-4_18

Husson F. 2010. *Exploratory Multivariate Analysis by Example Using R*. Boca Raton: CRC Press. https://doi.org/10.1201/b10345

Huston M. 1979. A general hypothesis of species diversity. *The American Naturalist* 113: 81–101. https://doi.org/10.1086/283366

Imdad MU, Aslam M. 2018. mctest: Multicollinearity Diagnostic Measures., R package version 1.2. https://CRAN.R-project.org/package=mctest

Irl SDH, Anthelme F, Harter DEV, Jentsch AL, E. S, M.J., Beierkuhnlein C. 2016. Patterns of island treeline elevation – a global perspective. *Ecography* 39: 427–436. https://doi.org/10.1111/ecog.01266

IUSS Working Group WRB. 2006. World reference base for soil resources. *World Soil Resources Report* **103**.

James SA, Puttock CF, Cordell S, Adams RP. 2004. Morphological and genetic variation within Metrosideros polymorpha (Myrtaceae) on Hawai'i. *New Zealand Journal of Botany* **42**: 263–270. https://doi.org/10.1080/0028825X.2004.9512903

Janis C. 2008. An evolutionary history of browsing and grazing ungulates. In: Gordon I & Prins H (eds.) *The ecology of browsing and grazing*. Springer, 21–45. https://doi.org/10.1007/978-3-540-72422-3_2

Janis CM, Damuth J, Theodor JM. 2004. The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome. *Evolution of grass-dominated ecosystems during the late Cenozoic Session at the North American Paleontological Convention, 2001* **207**: 371–398. https://doi.org/10.1016/j.palaeo.2003.09.032

Jarvis A, Reuter HI, Nelson A, Guevara E. 2008. Hole-filled SRTM for the globe Version 4. *available from the CGIAR-CSI SRTM 90m Database (http://srtm. csi. cgiar. org)* **15**: 25–54. http://srtm.csi.cgiar.org

Jensen M, Michelsen A, Gashaw M. 2001. Responses in plant, soil inorganic and microbial nutrient pools to experimental fire, ash and biomass addition in a woodland savanna. *Oecologia* **128**: 85–93. https://doi.org/10.1007/s004420000627

Jew EKK, Dougill AJ, Sallu SM, O'Connell J, Benton TG. 2016. Miombo woodland under threat: Consequences for tree diversity and carbon storage. *Forest Ecology and Management* **361**: 144–153. https://doi.org/10.1016/j.foreco.2015.11.011

Jiggins CD, Mallet J. 2000. Bimodal hybrid zones and speciation. *Trends in Ecology & Evolution* **15**: 250–255. https://doi.org/10.1016/S0169-5347(00)01873-5

Jinga P, Ashley MV. 2019. Climate change threatens some miombo tree species of sub-Saharan Africa. *Flora* **257**: 151421. https://doi.org/10.1016/j.flora.2019.151421

Jinga P, Palagi J. 2020. Dry and wet miombo woodlands of south-central Africa respond differently to climate change. *Environmental monitoring and assessment* **192**: 1–16. https://doi.org/10.1007/s10661-020-08342-x.

Johansson ME, Nilsson C, Nilsson E. 1996. Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science* **7**: 593–598. https://doi.org/10.2307/3236309

Jones MW, Santín C, van der Werf GR, Doerr SH. 2019. Global fire emissions buffered by the production of pyrogenic carbon. *Nature Geoscience*. https://doi.org/10.1038/s41561-019-0403-x

Jones GM, Tingley MW. 2021. Pyrodiversity and biodiversity: a history, synthesis, and outlook. *Diversity and Distributions*. 00: 1– 18. https://doi.org/10.1111/ddi.13280

Joshi AA, Ratnam J, Sankaran M. 2020. Frost maintains forests and grasslands as alternate states in a montane tropical forest–grassland mosaic; but alien tree invasion and warming can disrupt this balance. *Journal of Ecology* **108**: 122–132. https://doi.org/10.1111/1365-2745.13239

Josse J, Husson F. 2016. missMDA: A Package for Handling Missing Values in Multivariate Data Analysis. *Journal of Statistical Software* **70**: 1–31. https://doi.org/10.18637/jss.v070.i01

Kalaba F, Quinn CH, Dougill AJ. 2012. Carbon storage, biodiversity and species composition of Miombo woodlands in recovery trajectory after charcoal production and slash and burn agriculture in Zambia's Copperbelt. Centre for Climate Change Economics and Policy. *Sustainability Research Institute. Paper* **40**.

Karp A, Faith T, Marlon J, Staver C. 2021. Global response of fire activity to late Quaternary grazer extinctions. *Science* **374**: 1145–1148. https://doi.org/10.1126/science.abj1580

Kassambara A. 2018. *ggpubr:'ggplot2'Based Publication Ready Plots. R package version 0.2.* https://cran.r-project.org/web/packages/ggpubr/index.html

Kassambara A. 2021. *Pipe-Friendly Framework for Basic Statistical Tests [R Package Rstatix Version 0.7. 0]*. https://cran.r-project.org/web/packages/rstatix/index.html

Kassambara A, Mundt F. 2017. Package 'factoextra': Extract and visualize the results of multivariate data analyses. http://www.sthda.com/english/rpkgs/factoextra

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, BÖNISCH G, GARNIER E, WESTOBY M, REICH PB, WRIGHT IJ, *et al.* 2011. TRY – a global database of plant traits. *Global Change Biology* **17**: 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Kaufman L, Rousseeuw PJ. 2009. *Finding groups in data: an introduction to cluster analysis*. John Wiley & Sons. 344 pages.

Keeley JE, Rundel PW. 2005. Fire and the Miocene expansion of C4 grasslands. *Ecology Letters* **8**: 683–690. https://doi.org/10.1111/j.1461-0248.2005.00767.x

Keppel G, Ottaviani G, Harrison S, Wardell-Johnson GW, Marcantonio M, Mucina L. 2018. Towards an eco-evolutionary understanding of endemism hotspots and refugia. *Annals of Botany* **122**: 927–934. https://doi.org/10.1093/aob/mcy173

King DA, Davies SJ, Tan S, Noor NSMD. 2006. The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology* **94**: 670–680. https://doi.org/10.1111/j.1365-2745.2006.01112.x

Körner C. 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* **115**: 445–459. https://doi.org/10.1007/s004420050540

Kral K, Limb R, Ganguli A, Hovick T, Sedivec K. 2018. Seasonal prescribed fire variation decreases inhibitory ability of Poa pratensis L. and promotes native plant diversity. *Journal of Environmental Management* **223**: 908–916. https://doi.org/10.1016/j.jenvman.2018.06.096

Kruger FJ. 1979. Fire. In: Day J, Siegfried W, Louw G, Jarman M, (eds.) *South African National Scientific Programmes Report. Fynbos ecology: a preliminary synthesis*. Pretoria, South Africa: CSIR, 43–57. http://hdl.handle.net/10204/2332

Kruger FJ, Bigalke RC. 1984. Fire in fynbos. In: de Booysen P, Tainton N (eds.) *Ecological effects of fire in South African ecosystems*. Springer, 67–114. https://doi.org/10.1007/978-3-642-69805-7_5

Küchler AW. 1949. A Physiognomic Classification of Vegetation. *Annals of the Association of American Geographers* **39**: 201–210.

Lai J, Tsai C, Yen C, Ko Y, Chen S, Weng I, Lin Y, Chiang Y. 2015. Molecular characterization of twenty polymorphic microsatellite markers in the polyploid fruit tree species Syzygium samarangense (Myrtaceae). *Genet. Mol. Res* **14**: 13013–13021. https://doi.org/10.4238/2015.October.21.22

Lamont BB, Downes KS. 2011. Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. *Plant Ecology* **212**: 2111–2125. https://doi.org/10.1007/s11258-011-9987-y

Lamont BB, He T, Downes KS. 2013. Adaptive responses to directional trait selection in the Miocene enabled Cape proteas to colonize the savanna grasslands. *Evolutionary Ecology* **27**: 1099–1115. https://doi.org/10.1007/s10682-013-9645-z

Lamont BB, He T, Pausas JG. 2017. African geoxyles evolved in response to fire; frost came later. *Evolutionary Ecology* **31**: 603–617. https://doi.org/10.1007/s10682-017-9905-4

Lamont BB, Pausas JG, He T, Witkowski ETF, Hanley ME. 2020. Fire as a Selective Agent for both Serotiny and Nonserotiny Over Space and Time. *Critical Reviews in Plant Sciences* **39**: 140–172. https://doi.org/10.1080/07352689.2020.1768465

Larcher W. 2005. Climatic constraints drive the evolution of low temperature resistance in woody plants. *Journal of Agricultural Meteorology* **61**: 189–202. https://doi.org/10.2480/agrmet.61.189

Laris P, Koné M, Dadashi S, Dembele F. 2017. The early/late fire dichotomy: Time for a reassessment of Aubréville's savanna fire experiments. *Progress in Physical Geography* **41**: 68–94. https://doi.org/10.1177/0309133316665570

Laris P, Wardell DA. 2006. Good, bad or 'necessary evil'? Reinterpreting the colonial burning experiments in the savanna landscapes of West Africa. *Geographical Journal* **172**: 271–290. https://doi.org/10.1111/j.1475-4959.2006.00215.x

Lê S, Josse J, Husson F. 2008. FactoMineR: an R package for multivariate analysis. *Journal of statistical software* **25**: 1–18. https://doi.org/10.18637/jss.v025.i01

Legendre P, Borcard D, Blanchet F, Dray S. 2012. PCNM: MEM spatial eigenfunction and principal coordinate analyses. *R package version* **2**. http://r-forge.r-project.org/R/?group_id=195

Lehmann CE, Parr CL. 2016. Tropical grassy biomes: linking ecology, human use and conservation. Philosophical Transactions of the Royal Society B: Biological Sciences **371**(1703): 20160329. https://doi.org/10.1098/rstb.2016.0329

Lehner M, Whiteman CD, Dorninger M. 2017. Inversion Build-Up and Cold-Air Outflow in a Small Alpine Sinkhole. *Boundary-Layer Meteorology* **163**: 497–522. https://doi.org/10.1007/s10546-017-0232-7

Leuning R. 1988. Leaf temperatures during radiation frost Part II. A steady state theory. *Agricultural and Forest Meteorology* **42**: 135–155. https://doi.org/10.1016/0168-1923(88)90073-1

Lewis GP, Schrire B, Mackinder B, Lock M. 2005. *Legumes of the World*. Royal Botanic Gardens Kew, London.

Liégeois J-P, Fernandez-Alonso M, Ouabadi, A, Le Gall B, Maury R, Jalludin M, Vidal M, Ouattara Gbélé C, Tchaméni R, Michard A, *et al.* 2016. Carte géologique de l'Afrique. https://doi.org/

Linder HP. 2001. Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography* **28**: 169–182. https://doi.org/10.1046/j.1365-2699.2001.00527.x

Linder HP. 2003. The radiation of the Cape flora, southern Africa. *Biological Reviews* **78**: 597–638. https://doi.org/10.1017/S1464793103006171

Linder HP. 2005. Evolution of diversity: the Cape flora. *Trends in Plant Science* **10**: 536–541. https://doi.org/10.1016/j.tplants.2005.09.006

Linder H, Lovett J, Mutke J, Barthlott W, Jürgens N, Rebelo T, Küper W. 2005. A numerical re-evaluation of the sub-Saharan Phytochoria of mainland Africa. *Biologiske Skrifter* **55**: 229–252.

Linn R, Winterkamp J, Edminster C, Colman JJ, Smith WS. 2007. Coupled influences of topography and wind on wildland fire behaviour. *International Journal of Wildland Fire* **16**: 183–195. https://doi.org/10.1071/WF06078

Lisar SYS, Motafakkerazad R, Hossain MM, Rahman IMM. 2012. *Water Stress in Plants: Causes, Effects and Responses*. In: Rahman, IMM. and Hasegawa, H. (eds.), *Water Stress*, InTech, Croatia, 1-14. https://doi.org/10.5772/39363

Lock JM. 1998. Aspects of fire in tropical African vegetation. In: Huxley CR, Lock JM & Cutler DDF (eds.) *Chorology, taxonomy and ecology of the floras of Africa and Madagascar.* Kew, UK: Royal Botanic Gardens: 181–189.

Loehle C. 1988. Tree life history strategies: the role of defenses. *Canadian Journal of Forest Research* **18**: 209–222. https://doi.org/10.1139/x88-032

Loreau M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**: 3–17. https://doi.org/10.1034/j.1600-0706.2000.910101.x

Loreau M. 2004. Does functional redundancy exist? *Oikos* **104**: 606–611. https://doi.org/10.1111/j.0030-1299.2004.12685.x

Losos JB. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* **11**: 995–1003. https://doi.org/10.1111/j.1461-0248.2008.01229.x

Lovett J, 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*. Springer, 582–601. https://doi.org/10.1007/978-94-009-0285-5_72

Lowry DB. 2012. Ecotypes and the controversy over stages in the formation of new species. *Biological Journal of the Linnean Society* **106**: 241–257. https://doi.org/10.1111/j.1095-8312.2012.01867.x

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K. 2018. cluster: Cluster Analysis Basics and Extensions. R package version 2.0.7-1. https://CRAN.R-project.org/package=cluster.

Mack RN, Thompson JN. 1982. Evolution in Steppe with Few Large, Hooved Mammals. *The American Naturalist* **119**: 757–773. https://doi.org/10.1086/283953

MacKinnon K, MacKinnon J. 1986. *Review of the protected areas system in the Afrotropical realm*. Gland (Switzerland): UNEP, IUCN Commission on National Parks and Protected Areas (CNPPA).

Malaisse F, Schaijes M, D'Outreligne C. 2016. *Copper-cobalt flora of Upper Katanga and Copperbelt. Field guide. Over 400 plants, 1,000 photographs and 500 drawings*. 422 pages. Les presses agronomiques de Gembloux. https://hdl.loc.gov/loc.gdc/gdclccn.2019666865

Mallet J. 2008. Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **363**: 2971–2986. https://doi.org/10.1098/rstb.2008.0081

Malloch DW, Pirozynski KA, Raven PH. 1980. Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (A Review). *Proceedings of the National Academy of Sciences* **77**: 2113. https://doi.org/10.1073/pnas.77.4.2113

Malunga MM, Cho MA, Chirwa PW, Yerokun OA. 2021. Land use induced land cover changes and future scenarios in extent of Miombo woodland and Dambo ecosystems in the Copperbelt province of Zambia. *African Journal of Ecology* 00, 1– 15. https://doi.org/10.1111/aje.12921

Manel S, Schwartz MK, Luikart G, Taberlet P. 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in ecology & evolution* **18**: 189–197. https://doi.org/10.1016/S0169-5347(03)00008-9

Manry D, Knight R. 1986. Lightning density and burning frequency in South African vegetation. *Vegetatio* **66**: 67–76. http://www.jstor.org/stable/20037306

Mapaure IN, Campbell BM. 2002. Changes in miombo woodland cover in and around Sengwa Wildlife Research Area, Zimbabwe, in relation to elephants and fire. *African Journal of Ecology* **40**: 212–219. https://doi.org/10.1046/j.1365-2028.2002.00355.x

Matayaya G, Wuta M, Nyamadzawo G. 2017. Effects of different disturbance regimes on grass and herbaceous plant diversity and biomass in Zimbabwean dambo systems. *International Journal of Biodiversity Science, Ecosystem Services & Management* **13**: 181–190. https://doi.org/10.1080/21513732.2017.1299222

Maurin O, Davies TJ, Burrows JE, Daru BH, Yessoufou K, Muasya AM, Van der Bank M, Bond WJ. 2014. Savanna fire and the origins of the 'underground forests' of Africa. *New Phytologist* **204**: 201–214. https://doi.org/10.1111/nph.12936

Mayaux P, Bartholomé E, Fritz S, Belward A. 2004. A new land-cover map of Africa for the year 2000. *Journal of Biogeography* **31**: 861–877. https://doi.org/10.1111/j.1365-2699.2004.01073.x

McConnell RB. 1972. Geological Development of the Rift System of Eastern Africa. *GSA Bulletin* **83**: 2549–2572. https://doi.org/10.1130/0016-7606(1972)83[2549:GDOTRS]2.0.CO;2

McGroddy ME, Daufresne T, Hedin LO. 2004. Scaling of C:N:P Stochiometry in forests worldwide: implications of terrestrial redfield-type ratios. *Ecology* **85**: 2390–2401. https://doi.org/10.1890/03-0351

McKey D. 1994. Legumes and nitrogen: the evolutionary ecology of a nitrogen-demanding lifestyle. In: McKey D & Sprent J (eds.). *Advances in legume systematics 5: the nitrogen factor*: 221–228. Royal Botanic Gardens, Kew, London.

McLeman R, Smit B. 2006. Migration as an adaptation to climate change. *Climatic change* **76**: 31–53. https://doi.org/10.1007/s10584-005-9000-7

Meadows M, Linder H. 1993. Special paper: a palaeoecological perspective on the origin of afromontane grasslands. *Journal of Biogeography* **20**: 345–355. https://doi.org/10.2307/2845584

Means RE. 2011. Synthesis of lower treeline limber pine (Pinus flexilis) woodland knowledge, research needs, and management considerations. In: Keane R, Tomback DF, Murray MP, Smith CM, (eds.) *The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.* Missoula: U.S. Department of Agriculture,Forest Service, Rocky Mountain Research Station, 29–36.

Meave J, Kellman M. 1994. Maintenance of rain forest diversity in riparian forests of tropical savannas: implications for species conservation during Pleistocene drought. *Journal of Biogeography* **21**: 121–135. https://www.jstor.org/stable/2845467

Meave J, Kellman M, MacDougall A, Rosales J. 1991. Riparian habitats as tropical forest refugia. *Global ecology and biogeography letters* **1**: 69–76. https://www.jstor.org/stable/2997492

Medina E. 1983. Adaptations of tropical trees to moisture stress. *Ecosystems of the world A* **14**: 225–237.

Meerts P. 2017. Geoxylic suffrutices of African savannas: short but remarkably similar to trees. *Journal of tropical ecology* **33**: 295–298. https://doi.org/10.1017/S0266467417000165

Meerts P, Hasson M. 2016. *Arbres et Arbustes du Haut-Katanga*. 385 pages. Bruxelles: National Botanic Garden of Belgium.

Meller, P., Frazão, R., Lages, F., Jürgens, N. & Finckh, M. 2021a. Tipping the scales: How fire controls the balance among functional groups in Angolan grasslands. Journal of Range and Forage Science, 00, 1-14. https://doi.org/10.2989/10220119.2021.2012822

Meller, P., Stellmes, M., Fidelis, A. & Finckh, M. 2021b. Correlates of geoxyles diversity in Afrotropical grasslands. Journal of Biogeography, 00, 1– 14. https://doi.org/10.1111/jbi.14305

Metcalfe DJ, Ford AJ. 2008. Floristics and plant biodiversity of the rainforests of the wet tropics. In: Stork NE, Turton S, (eds.) *Living in a Dynamic Tropical Forest Landscape*. Blackwell Publishing Ltd, 123–132.

Meyer VW. 2003. Intracolonial demography, biomass and food consumption of Macrotermes natalensis (Haviland)(Isoptera: Termitidae) colonies in the northern Kruger National Park, South Africa. Dissertation, University of Pretoria, South Africa. https://repository.up.ac.za/handle/2263/27703

Midgley JJ, Lawes MJ, Chamaillé-Jammes S. 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany* **58**: 1–11. https://doi.org/10.1071/BT09034

Miehe G, Miehe S. 1994. Zur oberen Waldgrenze in tropischen Gebirge. *Phytocoenologia* **24**: 53–110. https://doi.org/10.1127/phyto/24/1994/53

Miller C. 2000. Understanding the carbon-nitrogen ratio. *Acres USA* **30**: 20–21.

Mills AJ, Fey MV. 2005. Interactive response of herbivores, soils and vegetation to annual burning in a South African savanna. *Austral Ecology* **30**: 435–444. https://doi.org/10.1111/j.1442-9993.2005.01487.x

Minden V, Kleyer M. 2014. Internal and external regulation of plant organ stoichiometry. *Plant Biology* **16**: 897–907. https://doi.org/10.1111/plb.12155

Miyanishi K, Kellman M. 1986. The role of root nutrient reserves in regrowth of two savanna shrubs. *Canadian Journal of Botany* **64**: 1244–1248. https://doi.org/10.1139/b86-171

Moore AE, Larkin PA. 2001. Drainage evolution in south-central Africa since the breakup of Gondwana. *South African Journal of Geology* **104**: 47–68. https://doi.org/10.2113/104.1.47

Moura I, Maquia I, Rija AA, Ribeiro N, Ribeiro-Barros AI. 2017. Biodiversity Studies in Key Species from the African Mopane and Miombo Woodlands. In: Bitz L (eds.) *Genetic Diversity*. InTech. https://doi.org/10.5772/66845

Muche G, Kruger S, Hillmann T, Josenhans K, Ribeiro C, Bazibi M, Jürgens N. 2018. SASSCAL WeatherNet: present state, challenges, and achievements of the regional climatic observation network and database. *Biodiversity and Ecology* **6**: 34–43. https://doi.org/10.7809/b-e.00302

Mucina L, Scott-Shaw C, Rutherford M, Camp K, Matthews W, Powrie L, Hoare D. 2006. Indian ocean coastal belt. In: Mucina L & Rutherford M (eds.) *The Vegetation of South Africa, Lesotho and Swaziland*. Pretoria, South Africa: SANBI, 568–583.

Mueller-Dombois D, Perera M. 1971. Ecological differentiation and soil fungal distribution in the montane grasslands of Ceylon. *Ceylon Journal of Science (Biological Sciences)* **9**(1): 1–39.

Müller J. 2017. Dumas or Kjeldahl for reference analysis. Comparison and considerations for nitrogen/protein analysis of food and feed Denmark: *Foss Report*. 1-5

Muller K, O'Connor TG, Henschel JR. 2016. Impact of a severe frost event in 2014 on woody vegetation within the Nama-Karoo and semi-arid savanna biomes of South Africa. *Journal of Arid Environments* **133**: 112–121. https://doi.org/10.1016/j.jaridenv.2016.06.010

References

Muñoz-Marí J, Bovolo F, Gómez-Chova L, Bruzzone L, Camp-Valls G. 2010. Semisupervised one-class support vector machines for classification of remote sensing data. *IEEE transactions on geoscience and remote sensing* **48**: 3188–3197. https://doi.org/10.1109/TGRS.2010.2045764

Murphy BP, Andersen AN, Parr CL. 2016. The underestimated biodiversity of tropical grassy biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**: 20150319. https://doi.org/

Murphy BP, Bowman DM. 2012. What controls the distribution of tropical forest and savanna? *Ecology letters* **15**: 748–758. https://doi.org/10.1098/rstb.2015.0319

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858. https://doi.org/10.1038/35002501

N'dri AB, Soro TD, Gignoux J, Dosso K, Koné M, N'dri JK, Koné NA, Barot S. 2018. Season affects fire behavior in annually burned humid savanna of West Africa. *Fire Ecology* **14**: 1–11. https://doi.org/10.1186/s42408-018-0005-9

Nduwamungu J, Bloesch U, Munishi P, Hagedorn F, Lulu K. 2008. Recent land cover and use changes in Miombo woodlands of eastern Tanzania. *Tanzan. J. For. Nat. Conserv* **78**.

Nei M. 1973. Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences* **70**: 3321–3323. https://doi.org/10.1073/pnas.70.12.3321

Nerlekar AN, Chorghe AR, Dalavi JV, Kusom RK, Karuppusamy S, Kamath V, Pokar R, Rengaian G, Sardesai MM, Kambale SS. 2022. Exponential rise in the discovery of endemic plants underscores the need to conserve the Indian savannas. *Biotropica* 00, 1– 13. https://doi.org/10.1111/btp.13062

Nerlekar AN, Veldman JW. 2020. High plant diversity and slow assembly of old-growth grasslands. *Proceedings of the National Academy of Sciences* **117**: 18550–18556. https://doi.org/10.1073/pnas.1922266117

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F. 2010. Plant phenotypic plasticity in a changing climate. *Trends in plant science* **15**: 684–692. https://doi.org/10.1016/j.tplants.2010.09.008

Ogrin M. 2007. The minimum temperatures in the winter 2006/07 in Slovenian frost hollows and cold basins. *Dela* **28**: 221–237. https://doi.org/10.4312/dela.28.16.221-237

Ohiagu CE. 1979. A quantitative study of seasonal foraging by the grass harvesting termite, *Trinervitermes geminatus* (Wasmann),(Isoptera, Nasutitermitinae) in Southern Guinea Savanna, Mokwa, Nigeria. *Oecologia* **40**: 179–188. https://doi.org/10.1007/BF00347935

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2013. Package 'vegan'. *Community ecology package, version* **2**. https://cran.r-project.org/package=vegan

Oksanen J, Kindt R, Legendre P, O'Hara B, Stevens MHH, Oksanen MJ, Suggests M. 2007. The vegan package. *Community ecology package* **10**: 631–637. https://cran.r-project.org/package=vegan

Okullo P, Moe SR. 2012. Termite activity, not grazing, is the main determinant of spatial variation in savanna herbaceous vegetation. *Journal of Ecology* **100**: 232–241. https://doi.org/10.1111/j.1365-2745.2011.01889.x

Oliveras I, Malhi Y. 2016. Many shades of green: the dynamic tropical forest–savannah transition zones. *Philosophical Transactions of the Royal Society B* **371**: 20150308. https://doi.org/10.1098/rstb.2015.0308

Olson DM, Dinerstein E. 2002. The Global 200: Priority Ecoregions for Global Conservation. *Annals of the Missouri Botanical Garden* **89**: 199. https://doi.org/10.2307/3298564

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GV, Underwood EC, D'amico JA, Itoua I, Strand HE, Morrison JC. 2001. Terrestrial Ecoregions of the World: A New Map of Life on EarthA new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* **51**: 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Osazuwa-Peters O, Zanne AE. 2011. PrometheusWiki, Wood density protocol. Available at: http://prometheuswiki.publish.csiro.au/tiki-index.php?page=Wood+density+protocol.

Osborne CP. 2008. Atmosphere, ecology and evolution: what drove the Miocene expansion of C4 grasslands? *Journal of Ecology* **96**: 35–45. https://doi.org/10.1111/j.1365-2745.2007.01323.x

Ott JP, Klimešová J, Hartnett DC. 2019. The ecology and significance of below-ground bud banks in plants. *Annals of botany* **123**: 1099–1118. https://doi.org/10.1093/aob/mcz051

Ottaviani G, Molina-Venegas R, Charles-Dominique T, Chelli S, Campetella G, Canullo R, Klimešová J. 2020. The Neglected Belowground Dimension of Plant Dominance. *Trends in Ecology & Evolution* **35**: 763–766. https://doi.org/10.1016/j.tree.2020.06.006

Otto SP, Whitton J. 2000. Polyploid incidence and evolution. *Annual review of genetics* **34**: 401–437. https://doi.org/10.1146/annurev.genet.34.1.401

Overbeck GE, Müller SC, Pillar VD, Pfadenhauer J. 2005. Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *Journal of vegetation Science* **16**: 655–664. https://doi.org/10.1111/j.1654-1103.2005.tb02408.x

Oyedeji S, Onuche FJ, Animasaun DA, Ogunkunle CO, Agboola OO, Isichei AO. 2016. Short-term effects of early-season fire on herbaceous composition, dry matter production and soil fertility in Guinea savanna, Nigeria. *Archives of Biological Sciences* **68**: 7–16. https://doi.org/10.2298/ABS1505260020

Pagani M, Freeman KH, Arthur MA. 1999. Late Miocene Atmospheric CO2 Concentrations and the Expansion of C4 Grasses. *Science* **285**: 876–879. https://doi.org/10.1126/science.285.5429.876

Parisod C, Holderegger R, Brochmann C. 2010. Evolutionary consequences of autopolyploidy. *New phytologist* **186**: 5–17. https://doi.org/10.1111/j.1469-8137.2009.03142.x

Parolin P. 2008. Submerged in darkness: adaptations to prolonged submergence by woody species of the Amazonian floodplains. *Annals of Botany* **103**: 359–376. https://doi.org/10.1093/aob/mcn216

Parr CL, Andersen AN. 2006. Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation biology* **20**: 1610–1619. https://doi.org/10.1111/j.1523-1739.2006.00492.x

Parr CL, Brockett BH. 1999. Patch-mosaic burning: a new paradigm for savanna fire management in protected areas? *Koedoe* **42**: 117–130. https://doi.org/10.4102/koedoe.v42i2.237

Parr CL, Lehmann CER, Bond WJ, Hoffmann WA, Andersen AN. 2014. Tropical grassy biomes: misunderstood, neglected, and under threat. *Trends in Ecology & Evolution* **29**: 205–213. https://doi.org/10.1016/j.tree.2014.02.004

Partridge TC, Maud R. 1987. Geomorphic evolution of Southern Africa since the Mesozoic. *South African Journal of Geology* **90**: 179–208. https://hdl.handle.net/10520/AJA10120750_958

Paula S, Naulin P, Arce C, Galaz C, Pausas J. 2016. Lignotubers in Mediterranean basin plants. *Plant Ecology* **217:** 661-676. https://doi.org/10.1007/s11258-015-0538-9

Pausas JG, Lamont BB, Paula S, Appezzato-da-Glória B, Fidelis A. 2018. Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist* **217**: 1435–1448. https://doi.org/10.1111/nph.14982

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen I-C, Clark TD, Colwell RK, Danielsen F, Evengård B. 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* **355**: eaai9214. https://doi.org/10.1126/science.aai9214

Pennington RT. 2003. Monograph of Andira (Leguminosae-Papilionoideae). *Systematic Botany Monographs* **64**: 1–143. http://www.jstor.org/stable/25027903

Pennington RT, Hughes CE. 2014. The remarkable congruence of New and Old World savanna origins. *New Phytologist* **204**: 4–6. https://doi.org/10.1111/nph.12996

Pennington RT, Lehmann CER, Rowland LM. 2018. Tropical savannas and dry forests. *Current Biology* **28**: R541–R545. https://doi.org/10.1016/j.cub.2018.03.014

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, *et al.* 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**: 1-167. https://doi.org/10.1071/BT12225

Peterson DW, Reich PB. 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. *Plant Ecology* **194**: 5–16. https://doi.org/10.1007/s11258-007-9270-4

Petit C, Bretagnolle F, Felber F. 1999. Evolutionary consequences of diploid–polyploid hybrid zones in wild species. *Trends in Ecology & Evolution* **14**: 306–311. https://doi.org/10.1016/S0169-5347(99)01608-0

Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker CJ, Stenseth NC. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in ecology & evolution* **20**: 503–510. https://doi.org/10.1016/j.tree.2005.05.011

Pfennig DW, Wund MA, Snell-Rood EC, Cruickshank T, Schlichting CD, Moczek AP. 2010. Phenotypic plasticity's impacts on diversification and speciation. *Trends in Ecology & Evolution* **25**: 459–467. https://doi.org/10.1016/j.tree.2010.05.006

Pilon NA, Cava MG, Hoffmann WA, Abreu RC, Fidelis A, Durigan G. 2021. The diversity of post-fire regeneration strategies in the cerrado ground layer. *Journal of Ecology* **109**: 154–166. https://doi.org/10.1111/1365-2745.13456

Pivello VR, Oliveras I, Miranda HS, Haridasan M, Sato MN, Meirelles ST. 2010. Effect of fires on soil nutrient availability in an open savanna in Central Brazil. *Plant and Soil* **337**: 111–123. https://doi.org/10.1007/s11104-010-0508-x

Poorter L, Bongers F. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **87**: 1733–1743. https://doi.org/10.1890/0012-9658(2006)87[1733:LTAGPO]2.0.CO;2

Powers LA, Johnson TC, Werne JP, Castaneda IS, Hopmans EC, Sinninghe Damsté JS, Schouten S. 2005. Large temperature variability in the southern African tropics since the Last Glacial Maximum. *Geophysical Research Letters* **32**. https://doi.org/10.1029/2004GL022014

Prance GT. 2021. Sixty Years with the Chrysobalanaceae. *The Botanical Review* **87**: 197–232. https://doi.org/10.1007/s12229-020-09234-y

Prentice I, Harrison S, Bartlein P. 2011. Global vegetation and terrestrial carbon cycle changes after the last ice age. *New Phytologist* **189**: 988–998. https://doi.org/10.1111/j.1469-8137.2010.03620.x

Pritchard JK, Stephens M, Donnelly P. 2000. Inference of population structure using multilocus genotype data. *Genetics* **155**: 945–959. https://doi.org/10.1093/genetics/155.2.945

Pröpper M, Gröngröft A, Finckh M, Stirn S, De Cauwer V. 2015. *The Future Okavango: Findings, Scenarios and Recommendations for Action: Research Project Final Synthesis Report 2010-2015*. University of Hamburg-Biocentre Klein Flottbek. https://www.future-okavango.org/downloads/TFO_Report_engl_compiled_small_version.pdf

QGIS Development Team. 2019. *QGIS Geographic Information System*. Open Source Geospatial Foundation.

Questad EJ, Foster BL. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology letters* 11: 717–726. https://doi.org/10.1111/j.1461-0248.2008.01186.x

R Core Team. 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Ratter JA, Ribiero JF, Bridgewater S. 1997. The Brazilian Cerrado Vegetation and Threats to its Biodiversity. *Annals of Botany* 80: 223–230. https://doi.org/10.1006/anbo.1997.0469

Rehm EM, Feeley KJ. 2015. Freezing temperatures as a limit to forest recruitment above tropical Andean treelines. *Ecology* 96: 1856–1865. https://doi.org/10.1890/14-1992.1

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB. 2003. The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies. *International Journal of Plant Sciences* 164: S143–S164. https://doi.org/10.1086/374368

Revermann R, Finckh M. 2013. Cusseque - Microclimatic Conditions. *Biodiversity and Ecology* 5: 47-50. https://doi.org/10.7809/b-e.00244

Revermann R, Gomes AL, Gon\ccalves FM, Wallenfang J, Hoche T, Jürgens N, Finckh M. 2016. Vegetation Database of the Okavango Basin. *Phytocoenologia* 46: 103–104. https://doi.org/10.1127/phyto/2016/0103

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: 2030. https://doi.org/10.15560/13.1.2030

Revermann R, Maiato F, Gomes A, Lages F, Finckh M. 2013. Cusseque—vegetation. *Biodiversity & Ecology* 5: 59–63. https://doi.org/10.7809/b-e.00247

Revermann R, Oldeland J, Gonçalves FM, Luther-Mosebach J, Gomes AL, Jürgens N, Finckh M. 2018. Dry tropical forests and woodlands of the Cubango Basin in southern Africa–First classification and assessment of their woody species diversity. *Phytocoenologia*: 23–50. https://doi.org/10.1127/phyto/2017/0154.

Rissi MN, Baeza MJ, Gorgone-Barbosa E, Zupo T, Fidelis A. 2017. Does season affect fire behaviour in the Cerrado? *International Journal of Wildland Fire* 26: 427–433. https://doi.org/10.1071/WF14210

Robbrecht E. 1988. *Tropical woody Rubiaceae*. 272 pages. Bruxelles, Belgium: Nationale Plantentuin van Belgie, Meise.

Robbrecht E, Huysmans S, Figueiredo E. 1996. The generic status of Oxyanthus gossweileri (Rubiaceae) from Angola. *South African Journal of Botany* 62: 17–22. https://doi.org/10.1016/S0254-6299(15)30572-X

Rodriguez-Zaccaro FD, Groover A. 2019. Wood and water: How trees modify wood development to cope with drought. *PLANTS, PEOPLE, PLANET* 1: 346–355. https://doi.org/10.1002/ppp3.29

Rorato DG, Araujo MM, Tabaldi LA, Turchetto F, Griebeler AM, Berghetti ALP, Barbosa FM. 2018. Tolerance and resilience of forest species to frost in restoration planting in southern Brazil. *Restoration Ecology* 26: 537–542. https://doi.org/10.1111/rec.12596

Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, Menzel A, Root TL, Estrella N, Seguin B. 2008. Attributing physical and biological impacts to anthropogenic climate change. *Nature* 453: 353–357. https://doi.org/10.1038/nature06937

Roy S, Balling RC. 2014. Spatial patterns of diurnal lightning activity in southern Africa during austral summer. *Atmospheric Research* 145–146: 182–188. https://doi.org/10.1016/j.atmosres.2014.03.026

Rundell RJ, Price TD. 2009. Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology & Evolution* 24: 394–399. https://doi.org/10.1016/j.tree.2009.02.007

Ruvuga PR, Selemani IS, Sangeda AZ. 2019. Ecological Sustainability: Miombo Woodland Conservation with Livestock Production in Sub-Saharan Africa. In: Bamutaze Y, Kyamanywa S, Singh BR, Nabanoga G, Lal R (eds.) *Agriculture and Ecosystem Resilience in Sub Saharan Africa*. Springer, 237–256. https://doi.org/10.1007/978-3-030-12974-3_11

Ryan CM, Williams M. 2011. How does fire intensity and frequency affect miombo woodland tree populations and biomass? *Ecological Applications* 21: 48–60. https://doi.org/10.1890/09-1489.1

Saarinen J, Mantzouka D, Sakala J. 2020. Aridity, Cooling, Open Vegetation, and the Evolution of Plants and Animals During the Cenozoic. In: Martinetto E, Tschopp E, Gastaldo RA (eds.) *Nature Through Time*. United States: Springer, 83–108. https://doi.org/10.1007/978-3-030-35058-1_3

Saarnak CF. 2001. A shift from natural to human-driven fire regime: implications for trace-gas emissions. *The Holocene* 11: 373–375. https://doi.org/10.1191/095968301669139230

Sakai A, Larcher W. 1987. Frost survival of plants. Responses and adaptation to freezing stress. *Ecological Studies* 62.

Sakai A, Larcher W. 2012. *Frost survival of plants: responses and adaptation to freezing stress*. Springer Science & Business Media.

Sanfilippo M. 2014. *Trinta árvores e arbustos do Miombo Angolano*. Firenzi, Italy: Cooperazione per lo Sviluppo dei Paesi Emergenti (COSPE).

Sanguino G. 2015. Wood anatomy and adaptation strategies of suffrutescent shrubs in south-central Angola. Master thesis, University Hamburg, Germany.

Sankaran M. 2009. Diversity patterns in savanna grassland communities: implications for conservation strategies in a biodiversity hotspot. *Biodiversity and Conservation* **18**: 1099–1115. https://doi.org/10.1007/s10531-008-9519-9

Sankaran M, Hanan NP, Scholes RJ, Ratnam J. 2005. Determinants of woody cover in African savannas. *Nature* **438**: 846-849. https://doi.org/10.1038/nature04070

Sankaran M, Ratnam J, Hanan NP. 2004. Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* **7**: 480–490. https://doi.org/10.1111/j.1461-0248.2004.00596.x

Sankaran M, Ratnam J, Hanan N. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* **17**: 236–245. https://doi.org/10.1111/j.1466-8238.2007.00360.x

Savadogo P, Tiveau D, Sawadogo L, Tigabu M. 2008. Herbaceous species responses to long-term effects of prescribed fire, grazing and selective tree cutting in the savanna-woodlands of West Africa. *Perspectives in Plant Ecology, Evolution and Systematics* **10**: 179–195. https://doi.org/10.1016/j.ppees.2008.03.002

Sawadogo L, Tiveau D, Nygård R. 2005. Influence of selective tree cutting, livestock and prescribed fire on herbaceous biomass in the savannah woodlands of Burkina Faso, West Africa. *Agriculture, ecosystems & environment* **105**: 335–345. https://doi.org/10.1016/j.agee.2004.02.004

Sayre R, Comer P, Hak J. 2013. *A New Map of Standardized Terrestrial Ecosystems of Africa*. African Geographical Review. 24 pages Association of American Geographers, Washington D.C., US

Schefuß E, Schouten S, Jansen JF, Damsté JSS. 2003. African vegetation controlled by tropical sea surface temperatures in the mid-Pleistocene period. *Nature* **422**: 418-421. https://doi.org/10.1038/nature01500

Scheiter S, Higgins SI. 2009. Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. *Global Change Biology* **15**: 2224–2246. https://doi.org/10.1111/j.1365-2486.2008.01838.x

Schmidt H-P, Anca-Couce A, Hagemann N, Werner C, Gerten D, Lucht W, Kammann C. 2019. Pyrogenic carbon capture and storage. *GCB Bioenergy* **11**: 573–591. https://doi.org/10.1111/gcbb.12553

Schneibel A, Stellmes M, Frantz D, Finckh M, Revermann R. 2013. Cusseque—earth Observation. *Biodiversity and Ecology* **5**: 55–57. https://doi.org/10.7809/b-e.00246

Schneibel A, Stellmes M, Röder A, Frantz D, Kowalski B, Haß E, Hill J. 2017. Assessment of spatio-temporal changes of smallholder cultivation patterns in the Angolan Miombo belt using segmentation of Landsat time series. *Remote Sensing of Environment* **195**: 118–129. https://doi.org/10.1016/j.rse.2017.04.012

Scholander P. F., Bradstreet Edda D., Hemmingsen E. A., Hammel H. T. 1965. Sap Pressure in Vascular Plants. *Science* **148**: 339–346. https://doi.org/10.1126/science.148.3668.339

Scholes RJ, Archer SR. 1997. Tree-Grass Interactions in Savannas. *Annual Review of Ecology and Systematics* **28**: 517–544. https://doi.org/10.1146/annurev.ecolsys.28.1.517

Schrire BD. 2005. Biogeography of the Leguminosae. In: Lewis G, Schrire B, MacKinder B, Lock M (eds.). *Legumes of the World;* Royal Botanic Gardens, Kew, London. 21–54.

Schumacher V, Setzer A, Saba MMF, Naccarato KP, Mattos E, Justino F. 2022. Characteristics of lightning-caused wildfires in central Brazil in relation to cloud-ground and dry lightning. *Agricultural and Forest Meteorology* **312**: 108723. https://doi.org/10.1016/j.agrformet.2021.108723

Schutz AE, Bond WJ, Cramer MD. 2011. Defoliation depletes the carbohydrate reserves of resprouting Acacia saplings in an African savanna. *Plant Ecology* **212**: 2047–2055. https://doi.org/10.1007/s11258-010-9883-x

Scott JD. 1966. Veld burning in South Africa. *African Wild Life* **20**: 93–102.

Scowcroft PG, Jeffrey J. 1999. Potential significance of frost, topographic relief, and Acacia koa stands to restoration of mesic Hawaiian forests on abandoned rangeland. *Forest Ecology and Management* **114**: 447–458. https://doi.org/10.1016/S0378-1127(98)00374-0

Seehausen O. 2004. Hybridization and adaptive radiation. *Trends in ecology & evolution* **19**: 198–207. https://doi.org/10.1016/j.tree.2004.01.003

Shirima DD, Munishi PKT, Lewis SL, Burgess ND, Marshall AR, Balmford A, Swetnam RD, Zahabu EM. 2011. Carbon storage, structure and composition of miombo woodlands in Tanzania's Eastern Arc Mountains. *African Journal of Ecology* **49**: 332–342. https://doi.org/10.1111/j.1365-2028.2011.01269.x

Siebert F, Dreber N. 2019. Forb ecology research in dry African savannas: Knowledge, gaps, and future perspectives. *Ecology and Evolution* **9**: 7875–7891. https://doi.org/10.1002/ece3.5307

Silberbauer-Gottsberger I, Morawetz W, Gottsberger G. 1977. Frost Damage of Cerrado Plants in Botucatu, Brazil, as Related to the Geographical Distribution of the Species. *Biotropica* **9**: 253–261. https://doi.org/10.2307/2388143

References

Silleos NG, Alexandridis TK, Gitas IZ, Perakis K. 2006. Vegetation indices: advances made in biomass estimation and vegetation monitoring in the last 30 years. *Geocarto International* 21: 21–28. https://doi.org/10.1080/10106040608542399

da Silva EMS, Hayashi AH, Appezzato-da-Gloria B. 2014. Anatomy of vegetative organs in Aldama tenuifolia and A. kunthiana (Asteraceae: Heliantheae). *Brazilian Journal of Botany* 37: 505–517. https://doi.org/10.1007/s40415-014-0101-2

Simon MF, Grether R, de Queiroz LP, Skema C, Pennington RT, Hughes CE. 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences* 106: 20359–20364. https://doi.org/10.1073/pnas.0903410106

Simon M, Pennington T. 2012. Evidence for Adaptation to Fire Regimes in the Tropical Savannas of the Brazilian Cerrado. *International Journal of Plant Sciences* 173: 711–723. https://doi.org/10.1086/665973

Singh S, Verma AK. 2020. Plant Functional Traits in Tropical Dry Forests: A Review. In: Bhadouria R, Tripathi S, Srivastava P, Singh P, (eds.) *Handbook of Research on the Conservation and Restoration of Tropical Dry Forests*. Hershey, PA, USA: IGI Global, 66–88. https://doi.org/10.4018/978-1-7998-0014-9.ch004

Smart SM, Glanville HC, Blanes M del C, Mercado LM, Emmett BA, Jones DL, Cosby BJ, Marrs RH, Butler A, Marshall MR, *et al.* 2017. Leaf dry matter content is better at predicting above-ground net primary production than specific leaf area. *Functional Ecology* 31: 1336–1344. https://doi.org/10.1111/1365-2435.12832

Smith P, Cotrufo MF, Rumpel C, Paustian K, Kuikman PJ, Elliott JA, McDowell R, Griffiths RI, Asakawa S, Bustamante M, *et al.* 2015. Biogeochemical cycles and biodiversity as key drivers of ecosystem services provided by soils. *SOIL* 1: 665–685. https://doi.org/10.5194/soil-1-665-2015

Smith MD, van Wilgen BW, Burns CE, Govender N, Potgieter AL, Andelman S, Biggs HC, Botha J, Trollope WS. 2013. Long-term effects of fire frequency and season on herbaceous vegetation in savannas of the Kruger National Park, South Africa. *Journal of Plant Ecology* 6: 71–83. https://doi.org/10.1093/jpe/rts014

Soberón J, Nakamura M. 2009. Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences* 106: 19644–19650. https://doi.org/10.1073/pnas.0901637106

Sosef MS, Dauby G, Blach-Overgaard A, van der Burgt X, Catarino L, Damen T, Deblauwe V, Dessein S, Dransfield J, Droissart V. 2017. Exploring the floristic diversity of tropical Africa. *BMC biology* 15: 1–23. https://doi.org/10.1186/s12915-017-0356-8

Staver AC, Abraham JO, Hempson GP, Karp AT, Faith JT. 2021. The past, present, and future of herbivore impacts on savanna vegetation. *Journal of Ecology* 109: 2804–2822. https://doi.org/10.1111/1365-2745.13685

Staver AC, Archibald S, Levin SA. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334: 230–232. https://doi.org/10.1126/science.1210465

Staver AC, Bond WJ. 2014. Is there a 'browse trap'? Dynamics of herbivore impacts on trees and grasses in an African savanna. *Journal of Ecology* 102: 595–602. https://doi.org/10.1111/1365-2745.12230

Staver AC, Hempson GP. 2020. Seasonal dietary changes increase the abundances of savanna herbivore species. *Science advances* 6: eabd2848. https://doi.org/10.1126/sciadv.abd2848

Steinacker R, Whiteman CD, Dorninger M, Pospichal B, Eisenbach S, Holzer AM, Weihs P, Mursch-Radlgruber E, Baumann K. 2007. A sinkhole field experiment in the eastern Alps. *Bulletin of the American Meteorological Society* 88: 701–716. https://doi.org/10.1175/BAMS-88-5-701

Stellmes M, Frantz D, Finckh M, Revermann R. 2013a. Fire frequency, fire seasonality and fire intensity within the Okavango region derived from MODIS fire products. *Biodiversity and Ecology* 5: 351–362. https://doi.org/10.7809/b-e.00288

Stellmes M, Frantz D, Finckh M, Revermann R. 2013b. Okavango Basin - Earth Observation. *Biodiversity and Ecology* 5: 23. https://doi.org/10.7809/b-e.00239

Sultan S, Bazzaz F. 1993. Phenotypic plasticity in Polygonum persicaria. I. Diversity and uniformity in genotypic norms of reaction to light. *Evolution* 47: 1009–1031. https://doi.org/10.1111/j.1558-5646.1993.tb02132.x

Sussman R. 2014. *The oldest living things in the world*. University of Chicago Press.

Syampungani S, Chirwa PW, Akinnifesi FK, Sileshi G, Ajayi OC. 2009. The miombo woodlands at the cross roads: Potential threats, sustainable livelihoods, policy gaps and challenges. *Natural Resources Forum* 33: 150–159. https://doi.org/10.1111/j.1477-8947.2009.01218.x

Tedersoo L, Bahram M, Zobel M. 2020. How mycorrhizal associations drive plant population and community biology. *Science* 367: eaba1223. https://doi.org/10.1126/science.aba1223

The GIMP Development Team. 2020. *GIMP*.

Thomas DSG, Shaw PA. 1993. The evolution and characteristics of the Kalahari, southern Africa. *Journal of Arid Environments* 25: 97–108. https://doi.org/10.1006/jare.1993.1045

Thornhill AH, Ho SY, Külheim C, Crisp MD. 2015. Interpreting the modern distribution of Myrtaceae using a dated molecular phylogeny. *Molecular Phylogenetics and Evolution* 93: 29–43. https://doi.org/10.1016/j.ympev.2015.07.007

References

Thurlby KA, Connelly C, Wilson PG, Rossetto M. 2011. Development of microsatellite loci for Syzygium paniculatum (Myrtaceae), a rare polyembryonic rainforest tree. *Conservation Genetics Resources* 3: 205–208. https://doi.org/10.1007/s12686-010-9323-1

Tiessen H. 2008. Phosphorus in the global environment. In: White PJ, Hammond JP, (eds.) *Plant Ecophysiology. The Ecophysiology of Plant-Phosphorus Interactions*. Dordrecht: Springer Netherlands, 1–7. https://doi.org/10.1007/978-1-4020-8435-5_1

Tilman D, Downing JA. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363–365. https://doi.org/10.1038/367363a0

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Timberlake J, Chidumayo E. 2011. *Miombo Ecoregion Vision Report*. Biodiversity Foundation for Africa. http://www.biodiversityfoundation.org/documents/BFA%20No.20_Miombo%20Ecoregion%20Vision%20report.pdf

Tinley KL. 1982. The influence of soil moisture balance on ecosystem patterns in southern Africa. In: Ecology of tropical savannas. Springer, 175–192. https://doi.org/10.1007/978-3-642-68786-0_9

Tosso F, Doucet J-L, Kaymak E, Daïnou K, Duminil J, Hardy OJ. 2016. Microsatellite development for the genus Guibourtia (Fabaceae, Caesalpinioideae) reveals diploid and polyploid species. *Applications in plant sciences* 4: 1600029. https://doi.org/10.3732/apps.1600029

Trapnell CG. 1959. Ecological results of woodland and burning experiments in Northern Rhodesia. *The Journal of Ecology*: 129–168. https://dx.doi.org/10.2307/2257252

Trauernicht C, Brook BW, Murphy BP, Williamson GJ, Bowman DM. 2015. Local and global pyrogeographic evidence that indigenous fire management creates pyrodiversity. *Ecology and Evolution* 5: 1908–1918. https://doi.org/10.1002/ece3.1494

Trauth MH, Larrasoana JC, Mudelsee M. 2009. Trends, rhythms and events in Plio-Pleistocene African climate. *Quaternary Science Reviews* 28: 399–411. https://doi.org/10.1016/j.quascirev.2008.11.003

Treier UA, Broennimann O, Normand S, Guisan A, Schaffner U, Steinger T, Müller-Schärer H. 2009. Shift in cytotype frequency and niche space in the invasive plant Centaurea maculosa. *Ecology* 90: 1366–1377. https://doi.org/10.1890/08-0420.1

Troll C. 1973. The upper timberlines in different climatic zones. *Arctic and Alpine Research* 5: 3–18.

Trollope WSW. 1982. Ecological effects of fire in South African savannas. In: Huntley BJ, Walker BH (eds.) *Ecology of tropical savannas*. Springer, 292–306.

Trollope W, van Wilgen B, Trollope LA, Govender N, Potgieter AL. 2014. The long-term effect of fire and grazing by wildlife on range condition in moist and arid savannas in the Kruger National Park. *African Journal of Range & Forage Science* 31: 199–208. https://doi.org/10.2989/10220119.2014.884511

Tucker CJ. 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment* 8: 127–150. https://doi.org/10.1016/0034-4257(79)90013-0

Tůma J, Skalicky M, Tůmova L, Bláhová P, Rosůlková M. 2004. Potassium, magnesium and calcium content in individual parts of Phaseolus vulgaris L. plant as related to potassium and magnesium nutrition. *Plant, Soil and Environment* 50: 18–26. https://doi.org/10.17221/3637-PSE

Tuohy JM, Prior JAB, Stewart GR. 1991. Photosynthesis in relation to leaf nitrogen and phosphorus content in Zimbabwean trees. *Oecologia* 88: 378–382. https://doi.org/10.1007/BF00317582

Tydecks L, Jeschke JM, Wolf M, Singer G, Tockner K. 2018. Spatial and topical imbalances in biodiversity research. *PloS one* 13: e0199327. https://doi.org/10.1371/journal.pone.0199327

Tyson PD, Preston-Whyte RA. 2000. *Weather and Climate of Southern Africa*. Oxford University Press.

Uys RG, Bond WJ, Everson TM. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biological conservation* 118: 489–499. https://doi.org/10.1016/j.biocon.2003.09.024

Valente LM, Reeves G, Schnitzler J, Mason IP, Fay MF, Rebelo TG, Chase MW, Barraclough TG. 2010. Diversification of the African genus Protea (Proteaceae) in the Cape biodiversity hotspot and beyond: equal rates in different biomes. *Evolution* 64: 745–760. https://doi.org/10.1111/j.1558-5646.2009.00856.x

Van Wilgen BW, Govender N, Biggs HC. 2007. The contribution of fire research to fire management: a critical review of a long-term experiment in the Kruger National Park, South Africa. *International Journal of Wildland Fire* 16: 519–530. https://doi.org/10.1071/WF06115

Van Wilgen BW, Govender N, MacFadyen S. 2008. An assessment of the implementation and outcomes of recent changes to fire management in the Kruger National Park : original research. *Koedoe : African Protected Area Conservation and Science* 50: 22–31. https://doi.org/10.10520/EJC139701

Van Wyk B-E, Venter M, Boatwright JS. 2010. A revision of the genus Bolusia (Fabaceae, Crotalarieae). *South African Journal of Botany* 76: 86–94. https://doi.org/10.1016/j.sajb.2009.08.010

References

Veldman JW. 2016. Clarifying the confusion: old-growth savannahs and tropical ecosystem degradation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**(1703): 20150306. https://doi.org/10.1098/rstb.2015.0306

Veldman JW, Buisson E, Durigan G, Fernandes GW, Le Stradic S, Mahy G, Negreiros D, Overbeck GE, Veldman RG, Zaloumis NP, *et al.* **2015a.** Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment* **13**: 154–162. https://doi.org/10.1890/140270

Veldman JW, Overbeck GE, Negreiros D, Mahy G, Le Stradic S, Fernandes GW, Durigan G, Buisson E, Putz FE, Bond WJ. 2015b. Tyranny of trees in grassy biomes. *Science* **347**: 484–485. https://doi.org/10.1126/science.347.6221.484-c

Vendramini F, Díaz S, Gurvich DE, Wilson PJ, Thompson K, Hodgson JG. 2002. Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytologist* **154**: 147–157. https://doi.org/10.1046/j.1469-8137.2002.00357.x

Vesk PA, Westoby M. 2004. Funding the bud bank: a review of the costs of buds. *Oikos* **106**: 200–208. https://doi.org/10.1111/j.0030-1299.2004.13204.x

Vinya R, Malhi Y, Brown N, Fisher JB. 2012. Functional coordination between branch hydraulic properties and leaf functional traits in miombo woodlands: implications for water stress management and species habitat preference. *Acta Physiologiae Plantarum* **34**: 1701–1710. https://doi.org/10.1007/s11738-012-0965-3

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* **116**: 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Volaire F. 2018. A unified framework of plant adaptive strategies to drought: Crossing scales and disciplines. *Global Change Biology* **24**: 2929–2938. https://doi.org/10.1111/gcb.14062

Vollesen K. 1981. Catunaregam pygmaea (Rubiaceae) – a new geoxylic suffrutex from the woodlands of SE Tanzania. *Nordic Journal of Botany* **1**: 735–740. https://doi.org/10.1111/j.1756-1051.1981.tb01160.x

Vollesen K, Merrett L. 2020. *Field Guide to the (Wetter) Zambian Miombo Woodland: Part 1 (Ferns & Monocots) & Part 2 (Dicots)*. GVPedia Communications, Pretoria, South Africa.

Waite M, Sack L. 2010. How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. *New Phytologist* **185**: 156–172. https://doi.org/10.1111/j.1469-8137.2009.03061.x

Wakeling JL, Cramer MD, Bond WJ. 2012. The savanna-grassland 'treeline': why don't savanna trees occur in upland grasslands? *Journal of Ecology* **100**: 381–391. https://doi.org/10.1111/j.1365-2745.2011.01921.x

Wakeling JL, Staver AC, Bond WJ. 2011. Simply the best: the transition of savanna saplings to trees. *Oikos* **120**: 1448–1451. https://doi.org/10.1111/j.1600-0706.2011.19957.x

Walker J, Peet RK. 1984. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* **55**: 163–179. https://doi.org/10.1007/BF00045019

Wallenfang J, Finckh M, Oldeland J, Revermann R. 2015. Impact of shifting cultivation on dense tropical woodlands in southeast Angola. *Tropical Conservation Science* **8**: 863–892. https://doi.org/10.1177/194008291500800402

Wang S -W., Boru BH, Njogu AW, Ochola AC, Hu G-W, Zhou Y-D, Wang Q-F. 2020. Floristic composition and endemism pattern of vascular plants in Ethiopia and Eritrea. *J. Syst. Evol* **58**: 33–42. https://doi.org/10.1111/jse.12527

Wardle P. 1971. An explanation for alpine timberline. *New Zealand Journal of Botany* **9**: 371–402. https://doi.org/10.1080/0028825X.1971.10430192

Weber T. 2013. Cusseque—Climate. *Biodiversity and Ecology* **5**: 45–46. https://doi.org/10.7809/b-e.00243

Wei N, Cronn R, Liston A, Ashman T-L. 2018. Both functional trait divergence and trait plasticity confer polyploid advantage in changing environments. *bioRxiv*: 274399. https://doi.org/10.1101/274399

Wei T, Simko V, Levy M, Xie Y, Jin Y, Zemla J. 2017. R package 'corrplot': Visualization of a Correlation Matrix. *Statistician* **56**: 316–324. https://github.com/taiyun/corrplot

West O. 1965. *Fire in vegetation and its use in pasture management with special reference to tropical and subtropical Africa.* Commonwealth Bureau of Pastures and Field Crops. 53 pages. United Kingdom, Farnham Royal, Commonwealth Agricultural Bureaux

White F. 1976. The underground forests of Africa : a preliminary review. *Gard Bull Singapore* **29**: 55–71. https://ci.nii.ac.jp/naid/10017457486/en/

White F. 1983. *The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa (3 Plates, Northwestern Africa, Northeastern Africa, and Southern Africa, 1: 5,000,000).* Unesco, Paris.

White F. 1993. The AETFAT chorological classification of Africa: history, methods and applications. *Bulletin du jardin botanique national de Belgique/Bulletin van de Nationale Plantentuin van België*: 225–281.

White PJ, Hammond JP. 2008. *The ecophysiology of plant-phosphorus interactions*. Springer.

Whitecross MA, Archibald S, Witkowski ETF. 2012. Do freeze events create a demographic bottleneck for *Colophospermum mopane*? *South African Journal of Botany* **83**: 9–18. https://doi.org/10.1016/j.sajb.2012.07.008

Whittaker RH. 1960. Vegetation of the Siskiyou mountains, Oregon and California. *Ecological monographs* **30**: 279–338. https://doi.org/10.2307/1943563

Wickham H. 2016. *ggplot2: elegant graphics for data analysis*. Springer. https://ggplot2.tidyverse.org

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Jonathan Davies T, Grytnes J-A, Harrison SP. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology letters* **13**: 1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

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

van Wilgen BW. 1981. Some Effects of Fire Frequency on Fynbos Plant Community Composition and Structure at Jonkershoek, Stellenbosch. *South African Forestry Journal* **118**: 42–55. https://doi.org/10.1080/00382167.1981.9630524

Willan RG. 1957. SOME NOTES ON THE COLD SPELL IN AUGUST 1955. *The Nyasaland Journal* **10**: 7–10.

Williams M, Ryan CM, Rees RM, Sambane E, Fernando J, Grace J. 2008. Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique. *Forest Ecology and Management* **254**: 145–155. https://doi.org/10.1016/j.foreco.2007.07.033

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**: 993–1008. https://doi.org/10.2307/3668733

Wilson SA, Scholes RJ. 2020. The climate impact of land use change in the miombo region of south central Africa. *Journal of Integrative Environmental Sciences* **17**: 187–203. https://doi.org/10.1080/1943815X.2020.1825228

Wilson PJ, Thompson K, Hodgson JG. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* **143**: 155–162. https://doi.org/10.1046/j.1469-8137.1999.00427.x

Wright S. 1943. Isolation by distance. *Genetics* **28**: 114–138. https://doi.org/10.1093/genetics/28.2.114

Young KR. 1993. Tropical Timberlines: Changes in Forest Structure and Regeneration between Two Peruvian Timberline Margins. *Arctic and Alpine Research* **25**: 167–174. https://www.jstor.org/stable/1551809

Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present. *Science* **292**: 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**: 20150310. https://doi.org/10.1098/rstb.2015.0310

Zhao Y, Liu Z, Wu J. 2020. Grassland ecosystem services: a systematic review of research advances and future directions. *Landscape Ecology* **35**: 793–814. https://doi.org/10.1007/s10980-020-00980-3

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: Science & Conservation: A Modern Synthesis. Cham: Springer International Publishing, 109–121. https://doi.org/10.1007/978-3-030-03083-4_7

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

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 and Ecology* **6**: 438–447. https://doi.org/10.7809/b-e.00356

Zirondi HL, Ooi MKJ, Fidelis A. 2021. Fire-triggered flowering is the dominant post-fire strategy in a tropical savanna. *Journal of Vegetation Science* **32**: e12995. https://doi.org/10.1111/jvs.12995

Zupo T, Daibes LF, Pausas JG, Fidelis A. 2021. Post-fire regeneration strategies in a frequently burned Cerrado community. *Journal of Vegetation Science* **32**: e12968. https://doi.org/10.1111/jvs.12968

Co-author affiliations

Marcos P.M. Aidar:
Plant Physiology and Biochemistry, Institute of Botany, São Paulo CP 3005, CEP 01061-970, Brazil. <maidar@uol.com.br>

Alessandra Fidelis:
Departamento de Biodiversidade; UNESP/Rio Claro; Av. 24A, 1515; Bela Vista, CEP 13506-900; Rio Claro, São Paulo, Brazil. <alessandra.fidelis@unesp.br>

Manfred Finckh:
Biodiversity, Evolution and Ecology of Plants, Institute of Plant Science and Microbiology, University of Hamburg, Ohnhorststr. 18, Hamburg 22609, Germany. <manfred.finckh@uni-hamburg.de>

Raquel Frazao:
Herbário do Lubango, Instituto Superior de Ciências de Educação da Huíla, Lubango, Angola; Biodiversity, Evolution and Ecology of Plants, Institute of Plant Science and Microbiology, University of Hamburg, Ohnhorststr. 18, Hamburg 22609, Germany. <rvsfrazao@gmail.com>

Amândio L. Gomes:
Faculty of Sciences, Agostinho Neto University, Av. 4 de Fevereiro 71, Luanda CP 815, Angola. <algomes.jg.elb@gmail.com>

Francisco M. P. Gonçalves:
Department of Natural Sciences, Herbarium of Lubango, ISCED Huíla, Sarmento Rodrigues str., Lubango CP 230, Angola. <francisco.goncalves@isced-huila.ed.ao>

David Goyder:
Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK. <d.goyder@kew.org>

Norbert Jürgens:
Biodiversity, Evolution and Ecology of Plants, Institute of Plant Science and Microbiology, University of Hamburg, Ohnhorststr. 18, Hamburg 22609, Germany. <norbert.juergens@uni-hamburg.de>

Fernanda Lages:
Herbário do Lubango, Instituto Superior de Ciências de Educação da Huíla, Lubango, Angola. <f_lages@yahoo.com.br>

Jens Oldeland:
Biodiversity, Evolution and Ecology of Plants, Institute of Plant Science and Microbiology, University of Hamburg, Ohnhorststr. 18, Hamburg 22609, Germany. <oldeland@eco-syst.de>

Barbara Rudolph:
Biodiversity, Evolution and Ecology of Plants, Institute of Plant Science and Microbiology, University of Hamburg, Ohnhorststr. 18, Hamburg 22609, Germany. <barbara.rudolph@uni-hamburg.de>

Rasmus Revermann:
Biodiversity, Evolution and Ecology of Plants, Institute of Plant Science and Microbiology, University of Hamburg, Ohnhorststr. 18, Hamburg 22609, Germany; Faculty of Natural Resources and Spatial Sciences, Namibia University of Science and Technology, Windhoek 10005, Namibia. <rasmus.revermann@posteo.de>

Marion Stellmes:
Freie Universität Berlin; Institute of Geographical Sciences; Remote Sensing and Geoinformatics; Malteserstraße 74 – 100, 12249 Berlin, Germany. <marion.stellmes@fu-berlin.de>

Janika Wendefeuer:
Biodiversity, Evolution and Ecology of Plants, Institute of Plant Science and Microbiology, University of Hamburg, Ohnhorststr. 18, Hamburg 22609, Germany. <janika.wendefeuer@gmail.com>

Author contributions

Article 1 (-III-): All authors did a thorough literature research and contributed their knowledge to this review. **PM** and MF conceptualized the review afterwards and led the writing process.

Article 2 (-IV-): **PM**, MF and AG did the literature research for this review. FL and DG contributed to this with their expertise on the Angolan Flora. **PM** compiled, analysed and visualized the data. All authors commented on and contributed to the article.

Article 3 (-V-): **PM** and MF designed the research and conducted fieldwork. MS contributed and processed environmental data and helped to deal with it in this study. AF contributed a holistic understanding of tropical grasslands globally and enriched the discussion. **PM** analyzed the data and led the writing of the manuscript, to which all authors contributed and commented.

Article 4 (-VI-): MF and **PM** designed the research. **PM**, RF and MF conducted fieldwork and collected the data, and FL and NJ greatly supported fieldwork, logistics and organisation. **PM** analysed the data, and led the writing of the manuscript, to which all authors contributed and commented.

Article 5 (-VII-): MF and JW designed the study; MF collected the field data. JW did the remote sensing study; **PM** analysed the climate data; MF, JW and **PM** jointly drafted the manuscript and gave approval for publication.

Article 6 (-VIII-): **PZ**, MF and BR designed the research, **PZ** and MF conducted fieldwork, FL and NJ supported fieldwork and contributed material from herbaria LUB and HBG, **PZ** conducted molecular analyses, BR supervised and supported molecular analyses, **PZ** and JO did statistical analyses, **PZ** led the writing of the manuscript, all authors commented on and contributed to the paper.

Article 7 (-IX-): The research was first conceived by ALG and MPMA and subsequently performed by all co-authors. Fieldwork was carried out by ALG together with FMPG, MPMA, RR and MF. Laboratory analysis was carried out by **PM**. FL ensured logistical and bureaucratic support for the research. Data analysis and interpretation of the results were performed by ALG, RR, MF, MPMAA and **PM**. Writing of the manuscript was done by ALG, **PM** and MF with contribution from all co-authors.

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Supplementary Material

A list of all supplemental material:

- Chapter IV: High diversity and endemism of geoxylic plants in the Angolan highlands:
  - o Table S4.1: List of endemic geoxyles occurring in highlands.

- Chapter V: Correlates of geoxyle diversity in Afrotropical grasslands:
  - o Figure S5.1: Sankey network of minor families
  - o Figure S5.2: PCA of single BBB types, dimensions 1-2.
  - o Figure S5.3: PCA of single BBB types, dimensions 1-3.
  - o Figure S5.4: PCA of single biomes, dimensions 1-2.
  - o Figure S5.5: PCA of single biomes, dimensions 1-3.
  - o Figure S5.6: Violinplots grouped by biomes of origin.
  - o Table S5.1: List of geoxyles included in the study.
  - o Table S5.2: Correlation matrix.
  - o Table S5.3: References for biogeographic origins.
  - o Table S5.4: Geoxyle counts across family, site, and BBB type.
  - o Table S5.5: Welch's ANOVA testing.

- Chapter VI: Tipping the scales:
  - o Table S6.1: Mean and standard deviation of geoxyle traits.
  - o Table S6.2: Mean and standard deviation of species richness, diversity, evenness.

- Chapter VII: Frost-driven lower treelines in Angola:
  - o Figure S7.1: Satellite image of the Cusseque area.
  - o Figure S7.2: Parameters for the valley depth analysis.
  - o Figure S7.3: Daily minimum temperatures for different habitats.
  - o Figure S7.4: Dry season temperature pattern in southern Africa.
  - o Table S7.1: Positions of loggers and weather stations.
  - o Table S7.2: Recorded fire events in the Cusseque area.

- Chapter VIII: The Tough, the Wet, and the Hidden:
  - o Figure S8.1: Photos of phenotypes.
  - o Figure S8.2: Evanno.
  - o Figure S8.3: Distribution of ecotypes.
  - o Table S8.1: Complete data set.
  - o Table S8.2: Documented outcome of the STRUCTURE analysis.

- Chapter IX: Plant functional traits and symbiotic associations:
  - o Table S9.1: Overview of families and species sampled for this study.
  - o Table S9.2: Mean values of plant functional traits for geoxyles.
  - o Table S9.3: Mean values of plant functional traits for trees.
  - o Table S9.4: ANOVA of traits between Fabaceae and non-Fabaceae species.
  - o Table S9.5: ANOVA of traits between ectomycorrhizal and nonectomycorrhizal species

Chapter IV Supplement

Table S4.1: Full list of geoxyles endemic to Angola that occur in highland areas (> 1500 m). All species here have a woody base (broad geoxyle definition), it is indicated which of them are also geoxyles in a stricter sense (with a woody underground storage organ (USO)), which are geoxyle in the strictest sense (With a woody USO and a close tree relative), and which of them are not only endemic to Angola, but to Angolan highlands, occurring nowhere else.

Taxon	Family	Distribution	With congeneric tree relative	With a woody USO	Highland endemic
Acalypha dumetorum Müll.Arg.	Euphorbiaceae	Benguela		x	
Acalypha eriophylla Hutch.	Euphorbiaceae	Bié plateau		x	x
Acalypha eriophylloides S.Moore	Euphorbiaceae	Bié plateau		x	x
Acalypha gossweileri S.Moore	Euphorbiaceae	Cuanza Norte, Cazengo		x	
Acalypha huillensis Pax & K.Hoffm.	Euphorbiaceae	Huíla escarpment		x	x
Adenodolichos mendesii Torre	Fabaceae	Bié plateau		x	x
Aeschynomene benguellensis Torre	Fabaceae	Bié, Benguela, Huambo, Huíla			x
Aeschynomene debilis Baker	Fabaceae	Huíla escarpment, Humpata			x
Aeschynomene dimidiata subsp. *dimidiata* Baker	Fabaceae	Cuando-Cubango, Huambo, Huíla, Lunda Sul, Malange		x	
Ampelocissus dekindtiana Gilg	Vitaceae	Huíla escarpment, Tchivinguiro		x	x
Antizoma angolensis Exell & Mendonça	Menispermaceae	Huambo plateau		x	x
Baphia sp. nov.	Fabaceae	Cuando-Cubango, Bié, Moxíco	x	x	
Barleria antunesii Lindau	Acanthaceae	Huíla plateau		x	x
Barleria buddleoides S.Moore	Acanthaceae	Cuando-Cubango, Huíla		x	
Barleria crabbeoides I.Darbysh.	Acanthaceae	Huíla escarpment, Lubango			x
Barleria eburnea I.Darbysh.	Acanthaceae	Bié and Huíla plateaus		x	
Barleria imatensis I.Darbysh.	Acanthaceae	Huíla escarpment, Tchivinguiro		x	
Barleria kacondensis subsp. *glabrescens* I.Darbysh.	Acanthaceae	Huambo plateau		x	x
Barleria kacondensis subsp. *kacondensis* S.Moore	Acanthaceae	Bié and Huíla plateaus		x	x
Barleria polyneura S.Moore	Acanthaceae	Huíla plateau		x	
Barleria violascens var. *humpatana* I.Darbysh.	Acanthaceae	Huíla escarpment, Monino			x
Basananthe nummularia Welw.	Passifloraceae	Huíla escarpment, Lopollo		x	x
Bolusia ervoides (Baker) Torre	Fabaceae	Huíla escarpment, Lopollo			x
Ceratoteca reniformis Abels	Pedaliaceae	Benguela, Cuanza, Huambo, Huíla, Malange			

Species	Family	Location			
Chamaecrista huillensis (Mendonca & Torre) Lock	Fabaceae	Cuando-Cubango, Huíla, Namibe		x	
Chamaecrista newtonii (Mendonca & Torre) Lock	Fabaceae	Benguela, Huíla			x
Clutia benguelensis Müll.Arg.	Euphorbiaceae	Benguela, Bié, Huambo, Huíla	x	x	x
Combretum argyrotrichum Welw. ex M.A.Lawson	Combretaceae	Huambo plateau, Huíla escarpment	x	x	x
Combretum viscosum Exell	Combretaceae	Benguela, Bié, Huambo, Huíla	x	x	x
Crossandra angolensis S.Moore	Acanthaceae	Benguela			x
Crotalaria bondii Torre	Fabaceae	Huíla plateau		x	x
Crotalaria griseofusca Baker f.	Fabaceae	Bié plateau		x	x
Crotalaria ivantalensis Baker	Fabaceae	Huíla, Namibe			x
Crotalaria mendesii Torre	Fabaceae	Cunene, Huíla			
Crotalaria pittardiana Torre	Fabaceae	Benguela, Cunene, Huambo, Huíla			
Crotalaria pseudovirgultatis Torre	Fabaceae	Huíla escarpment, Lubango			x
Crotalaria subsessilis Harms	Fabaceae	Cuando-Cubango			
Cryptosepalum sp. nov. aff. *maraviense*	Fabaceae	Bié plateau	x	x	x
Dissotis benguellensis A.Fern. & R.Fern.	Melastomataceae	Huambo, Serra de Moco	x		x
Dissotis carrissoi A.Fern. & R.Fern.	Melastomataceae	Cuanza Sul, Huambo	x		
Dolichos dongaluta Baker	Fabaceae	Bié plateau		x	x
Dolichos elatus Baker	Fabaceae	Benguela, Malange		x	
Droogmansia dorae var. *dorae* Torre	Fabaceae	Bié plateau		x	x
Droogmansia gossweileri Torre	Fabaceae	Huambo plateau			x
Droogmansia vanderystii De Wild.	Fabaceae	Cuanza Sul, Huambo		x	
Eminia benguellensis Torre	Fabaceae	Benguela, Huambo, Huíla, Lunda Sul, Malange		x	
Eriosema albo-griseum Baker f.	Fabaceae	Huíla Escarpment, Tundavala		x	x
Eriosema cyclophyllum Baker f.	Fabaceae	Bié and Huíla plateaus		x	x
Eriosema gossweileri Baker f.	Fabaceae	Huíla escarpment, Tundavala		x	x
Eriosema pygmaeum Baker	Fabaceae	Huíla plateau		x	
Eriosema speciosum Baker	Fabaceae	Cuanza Norte, Benguela, Huambo, Huíla		x	
Erythrina pygmaea Torre	Fabaceae	Huíla plateau	x	x	x
Euclea angolensis Gürke	Ebenaceae	Huíla plateau	x	x	x

Euphorbia asclepiadea Milne-Redh.	Euphorbiaceae	Bié plateau	x		
Euphorbia parifolia N.E.Br.	Euphorbiaceae	Huíla escarpment, Tundavala	x	x	x
Fadogia caespitosa Robyns	Rubiaceae	Huíla plateau	x	x	
Fadogia chrysantha K.Schum.	Rubiaceae	Huambo plateau	x	x	x
Fadogia graminea Wernham	Rubiaceae	Bié plateau	x	x	
Fadogia punctulata Robyns	Rubiaceae	Huambo plateau	x	x	x
Fadogia stenophylla Welw. ex Hiern	Rubiaceae	Huíla escarpment, Lubango	x	x	
Fuerstia adpressa A.J.Paton	Lamiaceae	Huíla, Benguela			x
Fuerstia rigida (Benth.) A.J.Paton	Lamiaceae	Huíla Escarpment, Lopollo			x
Ganguelia gossweileri (S.Moore) Robbr.	Rubiaceae	Bié plateau		x	x
Gnidia fruticulosa Gilg	Thymelaeaceae	Huíla plateau	x		x
Gnidia newtonii Gilg	Thymelaeaceae	Huíla escarpment, Humpata	x		x
Gnidia rendlei Hiern	Thymelaeaceae	Huíla escarpment, Mumpulla	x		x
Gnidia welwitschii Hiern	Thymelaeaceae	Huíla escarpment, Humpata	x		x
Grewia suffruticosa K.Schum.	Malvaceae	Huíla plateau	x	x	x
Hypericum abilianum N.Robson	Hypericaceae	Huíla escarpment, Humpata	x		x
Indigofera corallinosperma Torre	Fabaceae	Huíla escarpment, Humpata			x
Indigofera huillensis Baker f.	Fabaceae	Benguela, Huíla			x
Indigofera mendesii Torre	Fabaceae	Huíla escarpment, Humpata			x
Indigofera nummularia Baker	Fabaceae	Benguela, Huambo			x
Indigofera paraoxalidea Torre	Fabaceae	Huíla escarpment, Humpata			x
Jamesbrittenia angolensis Hilliard	Scrophulariaceae	Huíla escarpment, Tundavala			x
Julbernardia gossweileri (Baker f.) Torre & Hillc.	Fabaceae	Cuando-Cubando, Huambo, Huíla, Malange	x	x	
Lannea gossweileri Exell & Mendonça	Anacardiaceae	Bié plateau	x	x	x
Lannea rubra Hiern (Engl.)	Anacardiaceae	Huíla escarpment, Tundavala	x	x	x
Lepidagathis gossweileri S.Moore	Acanthaceae	Benguela, Huíla			x
Leptactina prostrata K.Schum.	Rubiaceae	Bié plateau, Moxico	x	x	
Linariopsis prostrata Welw.	Pedaliaceae	Huíla			x
Macrotyloma bieense (Torre) Verdc.	Fabaceae	Huíla escarpment, Tchivinguiro		x	x

Species	Family	Distribution			
Meineckia phyllanthoides subsp. *trichopoda* (Müll.Arg.) G.L.Webster	Euphorbiaceae	NW Angola	x		
Oldenlandia sipaneoides K.Schum.	Rubiaceae	Huíla Escarpment, Lopollo			x
Orthosiphon violaceus Briq.	Lamiaceae	Huíla Escarpment, Lopollo			x
Ozoroa xylophylla (Engl. & Gilg) R.Fern. & A.Fern.	Anacardiaceae	Bié and Huíla plateaus	x	x	x
Pavetta nana K.Schum.	Rubiaceae	Huíla escarpment, Tchivinguiro	x	x	x
Pentanisia rubricaulis (K.Schum.) Kårehed & B.Bremer	Rubiaceae	Bié, Huambo, Huíla			x
Phaulopsis lankesterioides (Lindau) Lindau	Acanthaceae	Benguela, Huambo, Huíla			x
Phyllanthus microdendron Müll.Arg.	Phyllanthaceae	Bié plateau	x	x	x
Polygala huillensis Welw. ex Oliv.	Polygalaceae	Huíla Escarpment, Lopollo			x
Protea dekindtiana Engl.	Proteaceae	Huíla escarpment, Tchivinguiro	x	x	x
Protea ongotium Beard	Proteaceae	Bié and Huíla plateaus	x	x	x
Protea paludosa subsp. *paludosa* Hiern (Engl.)	Proteaceae	Bié and Huíla plateaus	x	x	x
Protea poggei subsp. *haemantha* (Engl. & Gilg) Chisumpa & Brummitt	Proteaceae	Bié plateau, Moxico	x	x	
Protea poggei subsp. *heliophila* Chisumpa & Brummitt	Proteaceae	Huambo plateau	x	x	x
Pseudeminia benguellensis (Torre) Verdc.	Fabaceae	Cuando-Cubando, Benguela, Huambo, Huíla		x	
Psychotria moninensis (Hiern) E.M.A.Petit	Rubiaceae	Cuando-Cubango, Benguela, Bié, Huambo, Huíla, Malange	x	x	
Psychotria welwitschii (Hiern) Bremek.	Rubiaceae	Huambo, Huíla and Namibe escarpment	x	x	x
Spermacoce aprica (Hiern) Govaerts	Rubiaceae	Huíla plateau, Ivantala			x
Spermacoce terminaliflora R.D.Good	Rubiaceae	Huíla plateau			
Spermacoce thymoidea (Hiern) Verdc.	Rubiaceae	Huíla escarpment, Humpata			x
Sphedamnocarpus barbosae Launert	Malpighiaceae	Huambo plateau			x
Stachys huillensis Hiern	Lamiaceae	Huíla plateau			x
Stomatanthes tundavalaensis D.J.N.Hind	Asteraceae	Huíla Escarpment		x	x
Tephrosia gossweileri Baker f.	Fabaceae	Bié, Benguela, Huambo, Huíla			x
Tephrosia huillensis Baker	Fabaceae	Huíla, Huambo Plateau			x
Tephrosia melanocalyx Baker	Fabaceae	Huíla Escarpment, Lopollo		x	x
Tephrosia newtoniana Torre	Fabaceae	Huíla escarpment, Tundavala			x
Tephrosia rigidula Baker	Fabaceae	Benguela, Cunene, Huambo, Huíla			

Species	Family	Distribution			
Tephrosia tundavalensis Bamps	Fabaceae	Huíla escarpment, Tundavala		x	x
Thesium lycopodioides Gilg	Santalaceae	Bié plateau		x	x
Thesium triste A.W.Hill	Santalaceae	Cuando-Cubango, Huíla, Malange		x	
Thunbergia cycnium S.Moore	Acanthaceae	Bié plateau			x
Thunbergia huillensis S.Moore	Acanthaceae	Bié and Huíla plateaus			x
Thunbergia retefolia S.Moore	Acanthaceae	Bié plateau			x
Tinnea benguellensis Gürke	Lamiaceae	Bié plateau, Moxico		x	
Tinnea gossweileri Robyns & Lebrun	Lamiaceae	Huambo plateau		x	x
Tricalysia angolensis A.Rich. ex DC.	Rubiaceae	Cuando-Cubango, Cunene, Bié and Huila plateaus	x	x	
Triumfetta gossweileri Exell & Mendonça	Malvaceae	Bié and Huíla plateaus		x	x
Triumfetta hundtii Exell & Mendonça	Malvaceae	Benguela, Caconda		x	x
Triumfetta macrocoma K.Schum.	Malvaceae	Huíla escarpment, Tchivinguiro		x	x
Triumfetta rhodoneura K.Schum.	Malvaceae	Huíla plateau		x	x
Vangueria cistifolia var. *cistifolia* (Welw. ex Hiern) Lantz	Rubiaceae	Bié, Huíla, Malange	x	x	
Vangueria fulva (Robyns) Lantz	Rubiaceae	Bié and Huíla plateaus	x	x	x
Vitex caespitosa Exell	Lamiaceae	Bié, Benguela, Huambo	x	x	x

Chapter V Supplement

Figure S5.1: Proportions of minor plant families, with three geoxyle taxa or less, across BBB types and biomes of origin. The biogeographic origins refer to occurrence and diversity centres of the respective genera of the geoxyle taxa, so that a single taxon can have multiple biogeographic origins, if the genus is widely spread. The absolute number of geoxyle taxa per family is provided in parentheses. The family Convolvulaceae was excluded on the biome side to improve readability, because the genus Ipomoea (Convolvulaceae) is cosmopolitan and has links to all biomes.

Li: lignotuber; RC: root crown; Ro: bud-bearing root; WR: woody rhizome; Xy: xylopodium; AM: Afromontane archipelago; AR: Arid regions; CP: Cape region; DW: Dry woodlands; EC: Eastern coast; TF: Central African tropical forests; MD: Madagascar.

Figure S5.2: Principal Component Analysis (PCA) showing the environmental preferences of geoxyle species to selected parameters in the **first two** dimensions. Preferences of BBB types are shown separately, ellipses define 95% confidence intervals. The diamond shapes represent the ordination of the three study sites Bicuar (B), Cusseque (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).

Figure S5.3: Principal Component Analysis (PCA) showing the environmental preferences of geoxyle species to selected parameters in the **first and third** dimensions. Preferences of BBB types are shown separately, ellipses define 95% confidence intervals. The diamond shapes represent the ordination of the three study sites Bicuar (B), Cusseque (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).

Figure S5.4: Principal Component Analysis (PCA) showing the environmental preferences of geoxyle species to selected parameters in the **first two** dimensions. Preferences of geoxyles grouped by biomes (i.e. biogeographic origin) (see table 3) are shown separately, ellipses define 95% confidence intervals. The diamond shapes represent the ordination of the three study sites Bicuar (B), Cusseque (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. The biomes are Afromontane archipelago (AM), Arid regions (AR), Cape region (CP), Dry woodlands (DW), Tropical forests (TF), Eastern coast (EC) and Madagascar (MD).

Figure S5.5: Principal Component Analysis (PCA) showing the environmental preferences of geoxyle species to selected parameters in the **first and third** dimensions. Preferences of geoxyles grouped by biomes (i.e. biogeographic origin) (see table 3) are shown separately, ellipses define 95% confidence intervals. The diamond shapes represent the ordination of the three study sites Bicuar (B), Cusseque (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. The biomes are Afromontane archipelago (AM), Arid regions (AR), Cape region (CP), Dry woodlands (DW), Tropical forests (TF), Eastern coast (EC) and Madagascar (MD).

Figure S5.6: Selected environmental spaces occupied by geoxyles, grouped by biomes of origin (biogeographical background). The violinplot 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 significance of differences, tested with Welch's ANOVA and posthoc Games-Powell 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 environmental conditions at our study sites (T: Tundavala, B: Bicuar, C: Cusseque) have been added to visualise whether preferences and prevalent conditions at the study sites coincide. Separate violins represent each biome of origin: Afromontane archipelago (AM), Arid regions (AR), Cape region (CP), Dry woodlands (DW), Tropical forests (TF), Eastern coast (EC) and Madagascar (MD).

Table S5.1: Geoxyle species list. Plant family, site occurrence and functional belowground bud bank type are given, as well as information about whether the species is endemic to Angola, and whether it has close congeneric tree relatives.

Li: lignotuber; RC: root crown; Ro: bud-bearing root, WR: woody rhizome, Xy: xylopodium. BIC: Bicuar, CUS: Cusseque, TUN: Tundavala.

SITE	SPECIES	FAMILY	BBB TYPE	SECONDARY BBB TYPE	ANGOLA ENDEMIC	TREE RELATIVE
BIC	*Acalypha ambigua*	Euphorbiaceae	Li		no	(x)
TUN	*Acalypha dumetorum*	Euphorbiaceae	Li		yes	(x)
CUS	*Acalypha polymorpha*	Euphorbiaceae	Li		no	(x)
TUN	*Acalypha polymorpha*	Euphorbiaceae	Li		no	(x)
CUS	*Adenodolichos mendesii*	Fabaceae	WR		yes	
CUS	*Aeschynomene bracteosa*	Fabaceae	Xy		no	
TUN	*Aeschynomene tenuirama*	Fabaceae	WR		no	
TUN	*aff Thesium, light green, glandular*		Xy			
CUS	*Alectra* sp.	Orobanchaceae	Xy			
CUS	*Anisophyllea quangensis*	Anisophyllaceae	WR		no	x
BIC	*Annona stenophylla* subsp. *nana*	Annonaceae	WR		no	x
CUS	*Annona stenophylla* subsp. *nana*	Annonaceae	WR		no	x
CUS	*Aspilia natalensis*	Asteraceae	RC		no	
CUS	*Baphia* sp. nov.	Fabaceae	WR			x
BIC	*Basananthe baumii var caerulescens*	Passifloraceae	RC		no	
CUS	*Brachystegia russelliae*	Fabaceae	WR		no	
BIC	*Brackenridgea arenaria*	Ochnaceae	WR		no	x
CUS	*Brackenridgea arenaria*	Ochnaceae	WR		no	x
TUN	*Brackenridgea arenaria*	Ochnaceae	WR		no	x
CUS	*Caloncoba suffruticosa*	Flacourtiaceae	Li		no	x
BIC	*Chamaeclitandra henriquesiana*	Apocynaceae	WR		no	
CUS	*Chamaeclitandra henriquesiana*	Apocynaceae	WR		no	
BIC	*Chamaecrista mimosoides*	Fabaceae	RC		no	
CUS	*Chamaecrista mimosoides*	Fabaceae	RC		no	
TUN	*Chamaecrista newtonii*	Fabaceae	RC		yes	
BIC	*Clematis chrysocarpa*	Ranunculaceae	WR		no	
CUS	*Clematis villosa*	Ranunculaceae	WR		no	
BIC	*Clerodendrum pusillum*	Verbenaceae	WR		no	
BIC	*Combretum platypetalum*	Combretaceae	WR		no	x
CUS	*Combretum platypetalum*	Combretaceae	WR		no	x
TUN	*Combretum platypetalum*	Combretaceae	WR		no	x
BIC	*Crotalaria bequaertii*	Fabaceae	RC		no	
CUS	*Crotalaria griseofusca*	Fabaceae	Li		yes	

CUS	*Cryptosepalum* sp. nov.	Fabaceae	WR		no	x
CUS	*Dianthus angolensis*	Caryophyllaceae	RC		yes	
BIC	*Dicoma anomala*	Asteraceae	RC		no	
CUS	*Dicoma anomala*	Asteraceae	RC		no	
TUN	*Dicoma anomala*	Asteraceae	RC		no	
BIC	*Diospyros chamaethamnus*	Ebenaceae	WR		no	x
BIC	*Diospyros virgata*	Ebenaceae	Li		no	x
CUS	*Dissotis* sp.	Melastomataceae	RC	Xy		(x)
BIC	*Dolichos cardiophylla* var. *subsessilis*	Fabaceae	RC		yes	
CUS	*Dolichos dongaluta*	Fabaceae	Xy		yes	
CUS	*Droogmansia huillensis*	Fabaceae	WR		no	
CUS	*Droogmansia megalantha*	Fabaceae	WR	Li/Tuber	no	
TUN	*Droogmansia megalantha*	Fabaceae	WR	Li/Tuber	no	
CUS	*Eriosema affine*	Fabaceae	Li		no	
CUS	*Eriosema cyclophyllum*	Fabaceae	WR		yes	
TUN	*Eriosema gossweileri*	Fabaceae	Xy		yes	
BIC	*Eriosema pauciflorum*	Fabaceae	WR	taproot	no	
BIC	*Eriosema shirense*	Fabaceae	Xy		no	
CUS	*Eriosema shirense*	Fabaceae	Xy		no	
BIC	*Euclea crispa*	Ebenaceae	WR		no	x
CUS	*Euclea crispa*	Ebenaceae	WR		no	x
TUN	*Euclea crispa*	Ebenaceae	WR		no	x
BIC	*Fadogia chlorantha* var. *thamnus*	Rubiaceae	WR		no	x
CUS	*Fadogia chlorantha* var. *thamnus*	Rubiaceae	WR		no	x
CUS	*Fadogia chrysantha*	Rubiaceae	WR		yes	
CUS	*Fadogia fuchsioides*	Rubiaceae	Li		no	
CUS	*Fadogia graminea*	Rubiaceae	WR		yes	
TUN	*Fadogia homblei*	Rubiaceae	WR		no	
CUS	*Fadogia* sp.	Rubiaceae	WR			
CUS	*Fadogia stenophylla*	Rubiaceae	WR		no/yes	
CUS	*Fadogia triphylla*	Rubiaceae	WR		no	
CUS	*Fadogia variifolia*	Rubiaceae	WR		no	
CUS	*Garcinia buchneri*	Clusiaceae	WR		no	x
TUN	*Garcinia buchneri*	Clusiaceae	WR		no	x
BIC	*Gardenia brachythamnus*	Rubiaceae	WR		no	x
TUN	*Gnidia kraussiana*	Thymeleaceaea	RC		no	x
BIC	*Grewia avellana*	Tiliaceae	WR		no	x
BIC	*Helichrysum candolleanum*	Asteraceae	RC		no	
TUN	*Helichrysum candolleanum*	Asteraceae	RC		no	
CUS	*Helichrysum mechowianum*	Asteraceae	WR		no	
TUN	*Helichrysum mechowianum*	Asteraceae	WR		no	
CUS	*Hibiscus rhodanthus*	Malvaceae	WR		no	x
TUN	*Hibiscus rhodanthus*	Malvaceae	WR		no	x
CUS	*Indigofera astragalina*	Fabaceae	Ro		no	
BIC	*Indigofera* sp. 1	Fabaceae	Li			
TUN	*Indigofera* sp. 2	Fabaceae	RC			
TUN	*Indigofera sutherlandoides*	Fabaceae	Ro		no	

BIC	*Ipomoea welwitschii*	Convolvulaceae	Ro		no	
TUN	*Kalanchoe lindmanii*	Crassulaceae	RC	ST	yes	
CUS	*Kotschya strobilantha*	Fabaceae	RC		no	
BIC	*Landolphia gossweileri*	Apocynaceae	WR		yes	x
CUS	*Landolphia gossweileri*	Apocynaceae	WR		yes	x
BIC	*Lannea edulis*	Anacardiaceae	Li		no	x
CUS	*Lannea edulis*	Anacardiaceae	Li		no	x
CUS	*Lannea gossweileri*	Anacardiaceae	WR		yes	x
TUN	*Lannea rubra*	Anacardiaceae	WR		yes	x
CUS	*Lannea rubra*	Anacardiaceae	WR		yes	x
CUS	*Leptactina benguelensis*	Rubiaceae	WR		no	x
CUS	*Leptactina prostrata*	Rubiaceae	WR		yes	x
TUN	*Lopholaena decurrens*	Asteraceae	RC		no	
BIC	*Macrotyloma rupestre*	Fabaceae	WR	Ro/RC	no	
TUN	*Myrsine africana*	Myrsinaceae	WR		no	x
CUS	*Ochna katangensis*	Ochnaceae	WR		no	x
CUS	*Ochna manikensis*	Ochnaceae	WR		no	x
CUS	*Ochna pygmaea*	Ochnaceae	WR		no	x
TUN	*Ochna pygmaea*	Ochnaceae	WR		no	x
BIC	*Ocimum obovatum* subsp. *obovatum*	Lamiaceae	RC		no	
CUS	*Ocimum obovatum* var. *galpinii*	Lamiaceae	Xy		no	
CUS	*Oxygonum fruticosum*	Polygonaceae	Li		no	
CUS	*Oxygonum pachybasis*	Polygonaceae	WR		no	
BIC	*Ozoroa xylophylla*	Anacardiaceae	Li		yes	x
CUS	*Ozoroa xylophylla*	Anacardiaceae	Li		yes	x
BIC	*Parinari capensis*	Chrysobalanaceae	WR		no	x
CUS	*Parinari capensis*	Chrysobalanaceae	WR		no	x
BIC	*Pentanisia schweinfurthii*	Rubiaceae	RC		no	
CUS	*Phyllanthus virgulatus*	Phyllanthaceae	RC		no	x
CUS	*Phyllanthus welwitschianus*	Phyllanthaceae	WR		no	x
CUS	*Protea angolensis* var. *divaricata*	Proteaceae	Li		no	x
TUN	*Protea angolensis* var. *divaricata*	Proteaceae	Li		no	x
CUS	*Protea micans* subsp. *trichophylla*	Proteaceae	Li		no	x
CUS	*Protea ongotium*	Proteaceae	Li		yes	x
CUS	*Protea paludosa*	Proteaceae	Li		no	x
TUN	*Protea paludosa*	Proteaceae	Li		no	x
CUS	*Protea poggei* subsp. *haemantha*	Proteaceae	WR		yes	x
CUS	*Psorospermum mechowii*	Hypericaceae	Li		no	x
CUS	*Psychotria kirkii*	Rubiaceae	WR		no	x
BIC	*Pygmaeothamnus zeyheri*	Rubiaceae	WR		no	
CUS	*Pygmaeothamnus zeyheri*	Rubiaceae	WR		no	
CUS	*Rhus arenaria*	Anacardiaceae	WR		no	x
TUN	*Rhus arenaria*	Anacardiaceae	WR		no	x
TUN	*Rhus humpatensis*	Anacardiaceae	WR		no	x
BIC	*Rhynchosia castroi*	Fabaceae	WR		no	
CUS	*Rhynchotropis poggei*	Fabaceae	RC		no	
CUS	*Rytigynia orbicularis*	Rubiaceae	Xy		no	x

CUS	*Sclerocroton oblongifolius*	Euphorbiaceae	WR		no	x
CUS	*Searsia kirkii*	Anacardiaceae	WR		no	x
TUN	*Stomatanthes tundavalaensis*	Asteraceae	Xy		yes	
BIC	*Strychnos gossweileri*	Loganiaceae	WR		no	x
BIC	*Syncolostemon bracteosus*	Lamiaceae	WR		no	
BIC	*Syzygium guineense* subsp. *huillense*	Myrtaceae	Li		no	x
CUS	*Syzygium guineense* subsp. *huillense*	Myrtaceae	Li		no	x
CUS	*Syzygium guineense* subsp. *macrocarpum*	Myrtaceae	Li		no	x
TUN	*Syzygium guineense* subsp. *macrocarpum*	Myrtaceae	Li		no	x
TUN	*Tephrosia acaciifolia*	Fabaceae	Li		no	
CUS	*Thesium atrum*	Santalaceae	Li		no	
CUS	*Thesium lycopodioides*	Santalaceae	Xy		yes	
BIC	*Thesium* sp.	Santalaceae	Li			
TUN	*Thesium triste*	Santalaceae	Li		no	
BIC	*Triumfetta geoides*	Tiliaceae	WR	Xy	no	
BIC	*Triumfetta gossweileri*	Tiliaceae	Xy	WR	yes	
CUS	*Triumfetta gossweileri*	Tiliaceae	Xy	WR	yes	
TUN	*Triumfetta gossweileri*	Tiliaceae	Xy	WR	yes	
CUS	*Uapaca nitida* var. *suffrutescens*	Phyllanthaceae	Li		no	x
BIC	*Vangueria pygmaea*	Rubiaceae	WR		no	x
TUN	*Vangueria pygmaea*	Rubiaceae	WR		no	x
CUS	*Vernonia teucrioides*	Asteraceae	WR	Li	no	
CUS	*Vigna antunesii*	Fabaceae	WR		no	
BIC	*Vitex angolensis*	Lamiaceae	Ro		no	x
CUS	*Xylopia tomentosa*	Annonaceae	WR		no	x

Table S5.2: Pearson-correlation matrix of all original environmental variables. The eight variables that were used in the analyses are located in the upper left corner, they are a compromise between representing all important environmental facets, and reasonably low correlation ($r^2 < 0.65$).

	Precipitation seasonality	Mean annual temperature	Mean annual precipitation	Frost days	$NDVI_{median}$	Isothermality	Clay content	Fire pause	Fire DOY	Mean fire intensity	Max. fire intensity	Bulk density	Soil organic carbon	Silt content	Sand content	Phosphorous content	Nitrogen content	Mean temperature range	$NDVI_{std}$	Exchangeable bases	Altitude	Temperature of coldest month	Cation exchange capacity
Fire frequency	0.23	0.10	0.17	-0.12	0.16	0.12	-0.23	-0.79	0.58	0.25	0.20	0.05	-0.08	-0.27	0.27	-0.18	-0.22	0.05	0.26	-0.21	0.14	0.01	-0.23
Precipitation seasonality		0.26	-0.04	-0.31	-0.18	0.16	-0.28	-0.21	0.22	0.02	0.03	0.29	-0.28	-0.40	0.37	-0.50	-0.57	0.15	0.46	-0.23	0.29	0.01	-0.38
Mean annual temperature			0.18	-0.62	0.13	0.42	-0.28	-0.05	0	-0.12	-0.11	0.35	-0.28	-0.37	0.38	-0.38	-0.49	-0.21	0.07	-0.18	-0.67	0.76	-0.29
Mean annual precipitation				-0.36	0.64	0.54	0.29	-0.12	0.06	0	0.03	-0.41	0.44	0.05	-0.24	-0.09	0.13	-0.65	-0.01	-0.50	0.05	0.53	-0.07
Frost days					-0.39	-0.55	0.10	0.06	-0.02	0.03	0	0	-0.08	0.24	-0.17	0.34	0.31	0.50	0.04	0.29	0.30	-0.70	0.21
$NDVI_{med}$						0.33	0.23	-0.16	0.12	0.11	0.11	-0.45	0.47	0.07	-0.19	-0.07	0.18	-0.57	-0.12	-0.44	-0.13	0.45	-0.03
Isothermality							0.12	-0.05	-0.02	-0.07	-0.04	-0.13	0.26	-0.05	-0.07	-0.24	-0.01	-0.67	0.10	-0.31	0.07	0.69	-0.08
Clay content								0.21	-0.17	-0.05	0.01	-0.61	0.55	0.76	-0.87	0.36	0.54	-0.39	-0.05	0.12	0.12	0.09	0.50
Fire pause									-0.86	-0.26	-0.21	-0.04	0.07	0.23	-0.22	0.17	0.19	-0.08	-0.28	0.20	-0.13	0.05	0.19
Fire DOY										0.25	0.21	0.02	-0.07	-0.20	0.18	-0.17	-0.17	0.11	0.27	-0.17	0.15	-0.09	-0.16
Mean fire intensity											0.80	-0.07	0.03	-0.07	0.04	-0.01	0.04	0.05	0.05	-0.04	0.08	-0.11	-0.02
Max. fire intensity												-0.10	0.06	-0.05	0	0	0.05	0.01	0.03	-0.06	0.08	-0.08	-0.03
Bulk density													-0.57	-0.53	0.53	-0.30	-0.51	0.48	0.17	0.11	-0.18	-0.10	-0.26
Soil organic carbon														0.42	-0.66	0.37	0.70	-0.55	-0.18	0.05	0.18	0.19	0.58
Silt content															-0.74	0.48	0.58	-0.24	-0.15	0.26	0.06	-0.05	0.51
Sand content																-0.44	-0.62	0.38	0.07	-0.29	-0.14	-0.03	-0.68
Phosphorous content																	0.65	-0.01	-0.32	0.41	0.01	-0.21	0.53
Nitrogen content																		-0.31	-0.32	0.27	0.12	-0.09	0.60
Mean temperature range																			0.14	0.23	0.10	-0.79	-0.16
$NDVI_{std}$																				-0.14	0.22	-0.07	-0.17
Exchangeable bases																					-0.11	-0.24	0.65
Altitude																						-0.52	0.02
Temperature of coldest month																							-0.05

Table S5.3: Biogeographic origins of geoxyle genera. For some genera, timely information about origins was unavailable; these genera were left out of the analyses. Abbreviations are as follows for biomes: AM: Afromontane belt; AR: Southern African arid regions; CP: Cape region; DW: Dry woodland/savannah; EC: Eastern coast; TF: Central African tropical forests; MD: Madagascar. The reference Flora Zambesiaca relates to the online version of the ongoing project by the Royal Botanic Garden KEW (http://apps.kew.org/efloras/search.do).

GENUS	FAMILY	BIOGEOGRAPHY	REFERENCE
ACALYPHA	Euphorbiaceae	AM, EC	Sagun *et al.*, 2010
ADENODOLICHOS	Fab. Papilionoidae	DW	Flora Zambesiaca; GBIF
AESCHYNOMENE	Fab. Papilionoidae	DW	Flora Zambesiaca; GBIF
ALECTRA	Orobanchaceae	AM, CP, DW, EC	Morawetz & Wolfe, 2009; GBIF
ANISOPHYLLEA	Anisophyllaceae	TF	Zhang *et al.*, 2007
ANNONA	Annonaceae	TF	Richardson *et al.*, 2004; GBIF
ASPILIA	Asteraceae	EC, TF	Beentje *et al.*, 2005
BAPHIA	Fab. Papilionoidae	TF	Flora Zambesiaca; GBIF
BASANANTHE	Passifloraceae	DW, EC	Flora Zambesiaca; GBIF
BRACHYSTEGIA	Fab. Detarioidae	DW	Flora Zambesiaca; GBIF
BRACKENRIDGEA	Ochnaceae	EC	Bissiengou & Sosef, 2014; Flora Zambesiaca; GBIF
CALONCOBA	Achariaceae	TF	Flora Zambesiaca; GBIF
CHAMAECLITANDRA	Apocynaceae	TF	Endress *et al.*, 2018; Flora Zambesiaca; GBIF
CHAMAECRISTA	Fab. Caesalpinioidae	DW, EC, TF, MD	Flora Zambesiaca; GBIF
CLEMATIS	Ranunculaceae	AM, DW, EC, TF, MD	Flora Zambesiaca; GBIF
CLERODENDRUM	Lamiaceae	EC, TF, MD	Yuan *et al.*, 2010; GBIF
COMBRETUM	Combretaceae	AR, DW	Maurin, 2009
CROTALARIA	Fab. Papilionoidae	AM, DW	Rockinger *et al.*, 2017; Flora Zambesiaca
CRYPTOSEPALUM	Fab. Detarioidae	TF	Tedersoo, 2017; Flora Zambesiaca; GBIF
DIANTHUS	Caryophyllaceae	AM, AR	Flora Zambesiaca; GBIF
DICOMA	Asteraceae	AR, DW	Ortiz *et al.*, 2013; Flora Zambesiaca; GBIF
DIOSPYROS	Ebenaceae	EC, TF	Duangjai *et al.*, 2009; Flora Zambesiaca; GBIF
DISSOTIS	Melastomataceae	DW, EC, TF	Flora Zambesiaca; GBIF
DOLICHOS	Fab. Papilionoidae	AM, AR, DW	Flora Zambesiaca; GBIF
DROOGMANSIA	Fab. Papilionoidae	TF	Jabbour *et al.*, 2018; Flora Zambesiaca; GBIF
ERIOSEMA	Fab. Papilionoidae	DW, EC, TF	Manyelo, 2015; GBIF
EUCLEA	Ebenaceae	AR, CP	Duangjai *et al.*, 2009; Flora Zambesiaca; GBIF
FADOGIA	Rubiaceae	DW	Lantz & Bremer, 2005; Flora Zambesiaca; GBIF
GARCINIA	Clusiaceae	DW, EC	Sosef & Dauby, 2012; Flora Zambesiaca; GBIF
GARDENIA	Rubiaceae	DW, EC, TF	Flora Zambesiaca; GBIF
GNIDIA	Thymeleaceae	AR, MD	Beaumont *et al.*, 2009; Flora Zambesiaca; GBIF
GREWIA	Malvaceae	AR, CP, DW, EC, TF	Flora Zambesiaca; GBIF
HELICHRYSUM	Asteraceae	AM, CP	Galbany-Casals *et al.*, 2014
HIBISCUS	Malvaceae		**NO MODERN STUDIES AVAILABLE**
INDIGOFERA	Fab. Papilionoidae	AR, DW	Schrire *et al.*, 2009
IPOMOEA	Convolvulaceae		**NO REFERENCE AVAILABLE**
KALANCHOE	Crassulaceae	EC, MD	Gehrig *et al.*, 2001
KOTSCHYA	Fab. Papilionoidae	DW	Flora Zambesiaca, GBIF

LANDOLPHIA	Apocynaceae	AM, TF	Endress *et al.*, 2018; GBIF
LANNEA	Anacardiaceae	DW, EC, TF	Flora Zambesiaca, GBIF
LEPTACTINA	Rubiaceae	TF	Neuba *et al.*, 2014; Flora Zambesiaca, GBIF
LOPHOLAENA	Asteraceae	AM, AR	GBIF
MACROTYLOMA	Fab. Papilionoidae	DW, EC	Flora Zambesiaca, GBIF
MYRSINE	Primulaceae		Flora Zambesiaca
OCHNA	Ochnaceae	DW, EC, TF	Bissiengou & Sosef, 2014; Flora Zambesiaca, GBIF
OCIMUM	Lamiaceae	AM	Paton *et al.*, 1999; GBIF
OXYGONUM	Polygonaceae	AR, DW, EC	Schuster *et al.*, 2015; Flora Zambesiaca, GBIF
OZOROA	Anacardiaceae	AR, DW, EC	Flora Zambesiaca, GBIF
PARINARI	Chrysobalanaceae	TF	Jud *et al.*, 2016; Flora Zambesiaca, GBIF
PENTANISIA	Rubiaceae	DW, EC	Flora Zambesiaca, GBIF
PHYLLANTHUS	Phyllanthaceae		**NO REFERENCE AVAILABLE**
PROTEA	Proteaceae	CP	Valente *et al.*, 2010
PSOROSPERMUM	Hypericaceae	EC, TF, MD	Ranarivelo, 2017; Flora Zambesiaca, GBIF
PYGMAEOTHAMNUS	Rubiaceae	DW, EC	Verstraete *et al.*, 2017; Flora Zambesiaca, GBIF
RHUS	Anacardiaceae	AM, AR, CP	Flora Zambesiaca, GBIF
RHYNCHOSIA	Fab. Papilionoidae	DW, EC	Manyelo, 2015; GBIF
RHYNCHOTROPIS	Fab. Papilionoidae	DW	GBIF
RYTIGYNIA	Rubiaceae	EC, TF	Lantz & Bremer, 2005; Flora Zambesiaca, GBIF
SCLEROCROTON	Euphorbiaceae	EC, TF	Flora Zambesiaca, GBIF
SEARSIA	Anacardiaceae	AM, AR, CP	Flora Zambesiaca, GBIF
STOMATANTHES	Asteraceae	AM	Grossi & Katinas, 2013; Hind & Goyder, 2014; GBIF
STRYCHNOS	Loganiaceae	DW, EC, TF, MD	Flora Zambesiaca, GBIF
SYNCOLOSTEMON	Lamiaceae	AM	Otieno *et al.*, 2006; Flora Zambesiaca, GBIF
SYZYGIUM	Myrtaceae	DW, EC, TF	Biffin *et al.*, 2006; Flora Zambesiaca, GBIF
TEPHROSIA	Fab. Papilionoidae		Flora Zambesiaca
THESIUM	Santalaceae	CP	Moore *et al.*, 2010
TRIUMFETTA	Malvaceae	DW, EC, TF	Flora Zambesiaca, GBIF
UAPACA	Phyllanthaceae	TF, MD	Breteler, 2013; Flora Zambesiaca, GBIF
VANGUERIA	Rubiaceae	DW, EC	Lantz & Bremer, 2005; Flora Zambesiaca, GBIF
VERNONIA	Asteraceae	AM, DW, EC, TF, MD	Keeley *et al.*, 2007; Flora Zambesiaca, GBIF
VIGNA	Fab. Papilionoidae		**NO REFERENCE AVAILABLE**
VITEX	Lamiaceae	DW, EC, TF, MD	Callmander *et al.*, 2014; Flora Zambesiaca, GBIF
XYLOPIA	Annonaceae	TF	Stull *et al.*, 2017; GBIF

References

Beaumont AJ, EdwardsTJ, Manning J, Maurin O, Rautenbach M, Motsi MC, Fay MF, Chase MW, Van der Bank M. 2009. Gnidia (Thymelaeaceae) is not monophyletic: taxonomic implications for Thymelaeoideae and a partial new generic taxonomy for Gnidia. *Botanical Journal of the Linnean Society* **160**: 402–417.

Beentje HJ, Jeffrey C, Hind DJN. 2005. Compositae (part 3), Flora of tropical East Africa. 547, *Kew, Royal Botanic Gardens*.

Biffin E, Craven LA, Crisp MD, Gadek PA. 2006. Molecular systematics of Syzygium and allied genera (Myrtaceae): evidence from the chloroplast genome. *TAXON* **55**: 79–94.

Bissiengou P. 2014. Systematics, evolution and historical biogeography of the family Ochnaceae with emphasis on the genus Campylospermum. Wageningen University (Netherlands), dissertation.

Breteler FJ. 2013. Uapaca (Phyllanthaceae) in the Guineo-Congolian forest region: a synoptic revision. *Plant Ecology and Evolution* **146**: 75–94.

Callmander MW, Phillipson PB, Schatz GE. 2014. Towards a Revision of the Genus Vitex L. (Lamiaceae) in Madagascar I : a Distinctive New Species from Northeastern Madagascar. *Candollea* **69**: 141–147.

Duangjai S, Samuel R, Munzinger J, Forest F, Wallnöfer B, Barfuss MHJ, Fischer G, Chase MW. 2009. A multi-locus plastid phylogenetic analysis of the pantropical genus Diospyros (Ebenaceae), with an emphasis on the radiation and biogeographic origins of the New Caledonian endemic species. *Molecular Phylogenetics and Evolution* **52**: 602–620.

Endress ME, Meve U, Middleton DJ, Liede-Schuhmann S. 2018. Apocynaceae. In: Kadereit J., Bittrich V. (eds.) Flowering Plants. Eudicots. Springer International Publishing, 264.

Galbany-Casals M, Unwin M, Garcia-Jacas N, Smissen RD, Susanna A, Bayer RJ. 2014. Phylogenetic relationships in Helichrysum (Compositae: Gnaphalieae) and related genera: Incongruence between nuclear and plastid phylogenies, biogeographic and morphological patterns, and implications for generic delimitation. *Taxon* **63**: 608–624.

Gehrig H, Gaußmann O, Marx H, Schwarzott D, Kluge M. 2001. Molecular phylogeny of the genus Kalanchoe (Crassulaceae) inferred from nucleotide sequences of the ITS-1 and ITS-2 regions. *Plant Science* **160**: 827–835.

Grossi MA, Katinas L. 2013. A New Circumscription of the Genus Stomatanthes (Asteraceae, Eupatorieae). *Systematic Botany* **38**: 830–849.

Hind DJN, Goyder DJ. 2014. Stomatanthes tundavalaensis (Compositae: Eupatorieae: Eupatoriinae), a new species from Huíla Province, Angola, and a synopsis of the African species of Stomatanthes. *Kew Bulletin* **69(4),** 9545.

Jabbour F, Gaudeul M, Lambourdière J, Ramstein G, Hassanin A, Labat J-N, Sarthou C. 2018. Phylogeny, biogeography and character evolution in the tribe Desmodieae (Fabaceae: Papilionoideae), with special emphasis on the New Caledonian endemic genera. *Molecular Phylogenetics and Evolution* **118**: 108–121.

Jud NA, Nelson CW, Herrera F. 2016. Fruits and wood of Parinari from the early Miocene of Panama and the fossil record of Chrysobalanaceae. *American Journal of Botany* **103**: 277–289.

Keeley SC, Forsman ZH, Chan R. 2007. A phylogeny of the "evil tribe" (Vernonieae: Compositae) reveals Old/New World long distance dispersal: Support from separate and combined congruent datasets (trnL-F, ndhF, ITS). *Molecular Phylogenetics and Evolution* **44**: 89–103.

Lantz H, Bremer B. 2005. Phylogeny of the complex Vanguerieae (Rubiaceae) genera Fadogia, Rytigynia, and Vangueria with close relatives and a new circumscription of Vangueria. *Plant Systematics and Evolution* **253**: 159–183.

Manyelo TS. 2015. A phylogenetic study of South African species of Rhynchosia (Phaseoleae, Fabaceae). University of Johannesburg (South Africa), dissertation.

Maurin O. 2009. A phylogenetic study of the family Combretaceae with emphasis on the genus Combretum in Africa. University of Johannesburg (South Africa), dissertation.

Moore TE, VERBOOM GA, FOREST F. 2010. Phylogenetics and biogeography of the parasitic genus Thesium L. (Santalaceae), with an emphasis on the Cape of South Africa. *Botanical Journal of the Linnean Society* **162**: 435–452.

Morawetz J, Wolfe A. 2009. Assessing the Monophyly of Alectra and Its Relationship to Melasma (Orobanchaceae). *Systematic Botany* **34**: 561–569.

Neuba DFR, Malan DF, Kouadio YL. 2014. Notes sur le genre Africain Leptactina Hook.f. (Rubiaceae, Pavetteae). *Adansonia* **36**: 121–153.

Ortiz S, Carbajal R, Serrano M, Rodríguez-Oubiña J, Iglesias I. 2013. Phylogeny of the African Mutisieae s.l. (Asteraceae) based on ndhF and trnL-F sequences (cpDNA). *TAXON* **62**: 525–536.

Paton A, Harley R, Harley M. 1999. Ocimum: an overview of classification and relationships. In: Holm, Y. and Hiltunen, R. (eds.), *Medicinal and Aromatic Plants—Industrial Profiles*, Harwood Academic, Amsterdam, 1-38.

Ranarivelo HS. 2017. Systematics, Biogeography, and Species Delimitation of the Malagasy Psorospermum (Hypericaceae). University of Missouri – Saint Louis (USA), dissertation.

Richardson JE, Chatrou LW, Mols JB, Erkens RHJ, Pirie MD. 2004. Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae (PT Pennington, QCB Cronk, and JA Richardson, Eds.). *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **359**: 1495–1508.

Rockinger A, Flores AS, Renner SS. 2017. Clock-dated phylogeny for 48% of the 700 species of Crotalaria (Fabaceae–Papilionoideae) resolves sections worldwide and implies conserved flower and leaf traits throughout its pantropical range. *BMC Evolutionary Biology* **17**: 61.

Sagun VG, Levin GA, van Welzen PC. 2010. Revision and phylogeny of Acalypha (Euphorbiaceae) in malesia. *Blumea - Biodiversity, Evolution and Biogeography of Plants* **55**: 21–60.

Schrire B, Lavin M, Barker N, Forest F. 2009. Phylogeny of the tribe Indigofereae (Leguminosae-Papilionoideae): Geographically structured more in succulent-rich and temperate settings than in grass-rich environments. *American journal of botany* **96**: 816–52.

Schuster TM, Reveal JL, Bayly MJ, Kron KA. 2015. An updated molecular phylogeny of Polygonoideae (Polygonaceae): Relationships of Oxygonum, Pteroxygonum, and Rumex, and a new circumscription of Koenigia. *Taxon* **64**: 1188–1208.

Sosef M, Dauby G. 2012. Contribution to the taxonomy of Garcinia (Clusiaceae) in Africa, including two new species from Gabon and a key to the Lower Guinean species. *PhytoKeys* **17**: 41–62.

Stull GW, Johnson DM, Murray NA, Couvreur TLP, Reeger JE, Roy CM. 2017. Plastid and Seed Morphology Data Support a Revised Infrageneric Classification and an African Origin of the Pantropical Genus Xylopia (Annonaceae). *Systematic Botany* **42**: 211–225.

Tedersoo L. 2017. Global Biogeography and Invasions of Ectomycorrhizal Plants: Past, Present and Future. In Tedersoo L. (eds.): *Biogeography of Mycorrhizal Symbiosis*. Springer, 469–531.

Valente LM, Reeves G, Schnitzler J, Mason IP, Fay MF, Rebelo TG, Chase MW, Barraclough TG. 2010. Diversification of the African genus Protea (Proteaceae) in the Cape biodiversity hotspot and beyond: equal rates in different biomes. *Evolution* **64**: 745–760.

Verstraete B, Steyn HM, Van Wyk AE. 2017. Taxonomic status of some geofrutex members of Vanguerieae (Rubiaceae): notes on Eriosemopsis and Pygmaeothamnus and the description of a new genus Bridsonia. *Botanical Journal of the Linnean Society* **186**: 47–65.

Yuan Y-W, Mabberley DJ, Steane DA, Olmstead RG. 2010. Further disintegration and redefinition of Clerodendrum (Lamiaceae): Implications for the understanding of the evolution of an intriguing breeding strategy. *TAXON* **59**: 125–133.

Zhang L-B, Simmons MP, Renner SS. 2007. A phylogeny of Anisophylleaceae based on six nuclear and plastid loci: Ancient disjunctions and recent dispersal between South America, Africa, and Asia. *Molecular Phylogenetics and Evolution* **44**: 1057–1067.

GBIF and Flora Zambesiaca online sources:

Adenodolichos Harms in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2970548 accessed via GBIF.org on 2020-06-09.

Mackinder B, Pasquet R, Polhill RM and Verdcourt B (2001). Adenodolichos Harms in Flora Zambesiaca volume:3, part:5: Leguminosae. Royal Botanic Gardens Kew, Richmond.

Aeschynomene L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2949034 accessed via GBIF.org on 2020-06-09.

Verdcourt B (2000). Aeschynomene L. in Flora Zambesiaca volume:3, part:6: Leguminosae. Royal Botanic Gardens Kew, Richmond.

Alectra Thunb. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3172194 accessed via GBIF.org on 2020-06-09.

Annona L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3155252 accessed via GBIF.org on 2020-06-09.

Baphia Afrel. ex Lodd. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2954106 accessed via GBIF.org on 2020-06-09.

Brummitt RK, Harder DK, Lewis GP, Lock JM, Polhill RM & Verdcourt B (2007). Baphia Afrel. ex Lodd. in Flora Zambesiaca volume:3, part:3: Leguminosae. Royal Botanic Gardens Kew, Richmond.

Basananthe Peyr. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/7313460 accessed via GBIF.org on 2020-06-09.

Fernandes R & Fernandes A (1978). Basananthe Peyr. in Flora Zambesiaca volume:4, part:0: Passifloraceae. Royal Botanic Gardens Kew, Richmond.

Brachystegia Benth. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2952646 accessed via GBIF.org on 2020-06-09.

Brummitt RK, Chikuni AC, Lock JM and Polhill RM (2007). Brachystegia Benth. in Flora Zambesiaca volume:3 part:2: Leguminosae.

Brackenridgea A.Gray in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/7326797 accessed via GBIF.org on 2020-06-09.

Robson NKB (1963). Brackenridgea A.Gray in Flora Zambesiaca volume:2 part:1: Ochnaceae.

Caloncoba Gilg in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2874146 accessed via GBIF.org on 2020-06-09.

Wild H (1960). Caloncoba Gilg in Flora Zambesiaca volume:1 part:1: Flacourtiaceae.

Chamaeclitandra (Stapf) Pichon in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/7316926 accessed via GBIF.org on 2020-06-09.

Leeuwenberg AJM and Kupicha FK (1985). Chamaeclitandra (Stapf) Pichon in FZ volume:7 part:2: Apocynaceae.

Chamaecrista (L.) Moench in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2949492 accessed via GBIF.org on 2020-06-09.

Brummitt RK, Chikuni AC, Lock JM and Polhill RM (2007). Chamaecrista (L.) Moench in Flora Zambesiaca volume:3 part:2: Leguminosae.

Clematis L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3033512 accessed via GBIF.org on 2020-06-09.

Exell AW and Milne-Redhead E (1960). Clematis L. in Flora Zambesiaca volume:1 part:1: Ranunculaceae.

Clerodendrum L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2925347 accessed via GBIF.org on 2020-06-09.

Fernandes R (2005). Clerodendrum L. in Flora Zambesiaca volume:8 part:7: Lamiaceae.

Various authors (2003). *Crotalaria* L. in Flora Zambesiaca volume:3 part:7: Leguminosae.

Cryptosepalum Benth. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2956479 accessed via GBIF.org on 2020-06-09.

Brummitt RK, Chikuni AC, Lock JM and Polhill RM (2007). Cryptosepalum Benth. in Flora Zambesiaca volume:3 part:2: Leguminosae.

Dianthus L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3085411 accessed via GBIF.org on 2020-06-09.

Wild H (1961). Dianthus L. in Flora Zambesiaca volume:1 part:2: Caryophyllaceae.

Diospyros L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3030169 accessed via GBIF.org on 2020-06-09.

White F (1983). Diospyros L. in Flora Zambesiaca volume:7 part:1: Ebenaceae.

Dissotis Benth. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3188495 accessed via GBIF.org on 2020-06-09.

Fernandes R and Fernandes A (1978). Dissotis Benth. in Flora Zambesiaca volume:4 part:0: Melastomataceae.

Dolichos L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2975549 accessed via GBIF.org on 2020-06-09.

Mackinder B, Pasquet R, Polhill RM and Verdcourt B (2001). Dolichos L.. In Flora Zambesiaca volume:3, part:5: Leguminosae. Royal Botanic Gardens Kew, Richmond.

Droogmansia De Wild. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2945535 accessed via GBIF.org on 2020-06-09.

Verdcourt B (2000). Aeschynomene. In Flora Zambesiaca volume:3, part:6: Leguminosae. Royal Botanic Gardens Kew, Richmond.

Eriosema (DC.) Desv. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/5348905 accessed via GBIF.org on 2020-06-09.

Euclea L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3234203 accessed via GBIF.org on 2020-06-09.

White F (1983). Euclea L. in Flora Zambesiaca volume:7 part:1: Ebenaceae. Royal Botanic Gardens Kew, Richmond.

Fadogia Schweinf. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2892835 accessed via GBIF.org on 2020-06-09.

Bridson D (1998). Fadogia Schweinf. in Flora Zambesiaca volume:5 part:2: Rubiaceae. Royal Botanic Gardens Kew, Richmond.

Garcinia L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3189556 accessed via GBIF.org on 2020-06-09.

Robson NKB (1961) Garcinia L. in Flora Zambesiaca volume:1 part:2: Guttiferae. Royal Botanic Gardens Kew, Richmond.

Gardenia Ellis. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2894320 accessed via GBIF.org on 2020-06-09.

Bridson DM and Verdcourt B (2003). Gardenia Ellis. in Flora Zambesiaca volume:5 part:3: Rubiaceae. Royal Botanic Gardens Kew, Richmond.

Gnidia L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3233897 accessed via GBIF.org on 2020-06-09.

Peterson B (2006). Gnidia L. in Flora Zambesiaca volume:9 part:3: Thymelaeaceae. Royal Botanic Gardens Kew, Richmond.

Grewia L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3152078 accessed via GBIF.org on 2020-06-09.

Wild H (1963). Grewia L. in Flora Zambesiaca volume:2 part:1: Tiliaceae. Royal Botanic Gardens Kew, Richmond.

Kotschya Endl. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2948957 accessed via GBIF.org on 2020-06-09.

Verdcourt B (2000). Kotschya Endl. in Flora Zambesiaca volume:3 part:6: Leguminosae. Royal Botanic Gardens Kew, Richmond.

Landolphia P.Beauv. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3169739 accessed via GBIF.org on 2020-06-09.

Lannea A.Rich. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/7321650 accessed via GBIF.org on 2020-06-09.

Fernandes R and Fernandes A (1966). Lannea A.Rich. in Flora Zambesiaca volume:2 part:2: Anacardiaceae. Royal Botanic Gardens Kew, Richmond.

Leptactina Hook.f. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/4938017 accessed via GBIF.org on 2020-06-09.

Bridson DM and Verdcourt B (2003). Leptactina Hook.f. in Flora Zambesiaca volume:5 part:3: Rubiaceae. Royal Botanic Gardens Kew, Richmond.

Lopholaena DC. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3122390 accessed via GBIF.org on 2020-06-09.

Macrotyloma (Wight & Arn.) Verdc. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2976914 accessed via GBIF.org on 2020-06-09.

Mackinder B, Pasquet R, Polhill RM and Verdcourt B (2001). Macrotyloma (Wight & Arn.) Verdc. in Flora Zambesiaca volume:3, part:5: Leguminosae. Royal Botanic Gardens Kew, Richmond.

Ochna L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3189675 accessed via GBIF.org on 2020-06-09.

Robson NKB (1963). Ochna L. in Flora Zambesiaca volume:2 part:1: Ochnaceae. Royal Botanic Gardens Kew, Richmond.

Ocimum L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2874693 accessed via GBIF.org on 2020-12-10.

Oxygonum Burch. ex Campd. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/7441486 accessed via GBIF.org on 2020-06-09.

Nogueira I, Ortiz S and Paiva JAR (2006). Oxygonum Burch. ex Campd. in Flora Zambesiaca volume:9 part:3: Polygonaceae. Royal Botanic Gardens Kew, Richmond.

Ozoroa Delile in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/7321498 accessed via GBIF.org on 2020-06-09.

Fernandes R and Fernandes A (1966). Ozoroa Delile in Flora Zambesiaca volume:2 part:2: Anacardiaceae. Royal Botanic Gardens Kew, Richmond.

Parinari Aubl. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2984937 accessed via GBIF.org on 2020-06-09.

White F (1978). Parinari Aubl. in Flora Zambesiaca volume:4 part:0: Chrysobalanaceae. Royal Botanic Gardens Kew, Richmond.

Pentanisia Harv. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2898425 accessed via GBIF.org on 2020-06-09.

Verdcourt B (1989). Pentanisia Harv. in Flora Zambesiaca volume:5 part:1: Rubiaceae. Royal Botanic Gardens Kew, Richmond.

Psorospermum Spach in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/7330280 accessed via GBIF.org on 2020-06-09.

Robson NKB (1961 Psorospermum Spach in Flora Zambesiaca volume:1 part:2: Guttiferae. Royal Botanic Gardens Kew, Richmond.

Pygmaeothamnus Robyns in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2898287 accessed via GBIF.org on 2020-06-09.

Bridson D (1998). Pygmaeothamnus Robyns in Flora Zambesiaca volume:5 part:2: Rubiaceae. Royal Botanic Gardens Kew, Richmond.

Rhus L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3190534 accessed via GBIF.org on 2020-06-09.

Fernandes R and Fernandes A (1966). Rhus L. in Flora Zambesiaca volume:2 part:2: Anacardiaceae. Royal Botanic Gardens Kew, Richmond.

Rhynchosia Lour. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2947992 accessed via GBIF.org on 2020-06-09.

Rhynchotropis Harms in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2962718 accessed via GBIF.org on 2020-12-10.

Rytigynia Blume in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2904236 accessed via GBIF.org on 2020-06-09.

Bridson D (1998). Rytigynia Blume in Flora Zambesiaca volume:5 part:2: Rubiaceae. Royal Botanic Gardens Kew, Richmond.

Sclerocroton Hochst. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/8265323 accessed via GBIF.org on 2020-06-09.

Radcliffe-Smith A (1996). Excoecaria L. in Flora Zambesiaca volume:9 part:4: Euphorbiaceae. Royal Botanic Gardens Kew, Richmond.

Searsia F.A.Barkley in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3190590 accessed via GBIF.org on 2020-06-09.

Fernandes R and Fernandes A (1966). Rhus L. in Flora Zambesiaca volume:2 part:2: Anacardiaceae. Royal Botanic Gardens Kew, Richmond.

Stomatanthes R.M.King & H.Rob. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3141813 accessed via GBIF.org on 2020-06-09.

Strychnos L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3169589 accessed via GBIF.org on 2020-06-09.

Leeuwenberg AJM (1983). Strychnos L. in Flora Zambesiaca volume:7 part:1: Loganiaceae. Royal Botanic Gardens Kew, Richmond.

Syncolostemon E.Mey. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/7308909 accessed via GBIF.org on 2020-06-09.

Syzygium R.Br. ex Gaertn. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3029010 accessed via GBIF.org on 2020-06-09.

White F (1978). Syzygium R.Br. ex Gaertn. in Flora Zambesiaca volume:4 part:0: Myrtaceae. Royal Botanic Gardens Kew, Richmond.

Triumfetta L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3152064 accessed via GBIF.org on 2020-06-09.

Wild H (1963). Triumfetta L. in Flora Zambesiaca volume:2 part:1: Tiliaceae. Royal Botanic Gardens Kew, Richmond.

Uapaca Baill. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3076064 accessed via GBIF.org on 2020-06-09.

Radcliffe-Smith A (1996). Uapaca Baill. in Flora Zambesiaca volume:9 part:4: Euphorbiaceae. Royal Botanic Gardens Kew, Richmond.

Vangueria Juss. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2917735 accessed via GBIF.org on 2020-06-09.

Bridson D (1998). Vangueria Juss. in Flora Zambesiaca volume:5 part:2: Rubiaceae. Royal Botanic Gardens Kew, Richmond.

Vernonia Schreb. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3123781 accessed via GBIF.org on 2020-06-09.

Pope GV (1992). Vernonia Schreb. in Flora Zambesiaca volume:6 part:1: Compositae. Royal Botanic Gardens Kew, Richmond.

Vitex L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/2925556 accessed via GBIF.org on 2020-06-09.

Fernandes R (2005). Vitex L. in Flora Zambesiaca volume:8 part:7: Lamiaceae. Royal Botanic Gardens Kew, Richmond.

Xylopia L. in GBIF Secretariat (2019). GBIF Backbone Taxonomy. https://www.gbif.org/species/3157015 accessed via GBIF.org on 2020-06-09.

Robson NKB (1960). Xylopia L. in Flora Zambesiaca volume:1 part:1: Annonaceae. Royal Botanic Gardens Kew, Richmond.

Table S5.4: Family distributions across sites and BBB types. Major families with at least four geoxyle species are highlighted. The counts for the sites can add up to more than those for the BBB types, as some species occurred at multiple sites. Li: lignotuber; RC: root crown; Ro: bud-bearing root, WR: woody rhizome, Xy: xylopodium.

Order	Family	Li	RC	Ro	WR	Xy	Bicuar	Cusseque	Tundavala
Asterales	Asteraceae	1	4	0	2	0	2	4	5
Caryophyllales	Caryophyllaceae	0	1	0	0	0	0	1	0
	Polygonaceae	1	0	0	1	0	0	2	0
Cucurbitales	Anisophyllaceae	0	0	0	1	0	0	1	0
Ericales	Ebenaceae	1	0	0	2	0	3	1	0
	Primulaceae	0	0	0	1	0	0	0	1
Fabales	Fabaceae	4	7	2	12	4	8	17	7
Gentianales	Apocynaceae	0	0	0	2	0	1	2	0
	Loganiaceae	0	0	0	1	0	1	0	0
	Rubiaceae	1	1	0	14	1	5	13	2
Lamiales	Lamiaceae	0	1	1	2	1	4	1	1
	Orobanchaceae	0	0	0	0	1	0	1	0
Magnoliales	Annonaceae	0	0	0	2	0	1	2	0
Malpighiales	Achariaceae	1	0	0	0	0	0	1	0
	Chrysobalanaceae	0	0	0	1	0	1	1	0
	Clusiaceae	0	0	0	1	0	0	1	1
	Euphorbiaceae	3	0	0	1	0	1	2	2
	Hypericaceae	1	0	0	0	0	0	1	0
	Ochnaceae	0	0	0	4	0	1	4	2
	Passifloraceae	0	1	0	0	0	1	0	0
	Phyllanthaceae	1	1	0	1	0	0	3	0
Malvales	Malvaceae	0	0	0	3	1	3	2	2
	Thymelaeaceae	0	1	0	0	0	0	0	1
Myrtales	Combretaceae	0	0	0	1	0	1	1	1
	Melastomataceae	0	1	0	0	0	0	1	0
	Myrtaceae	2	0	0	0	0	1	2	1
Proteales	Proteaceae	4	0	0	1	0	0	5	2
Ranunculales	Ranunculaceae	0	0	0	2	0	1	1	0
Santalales	Santalaceae	3	0	0	0	1	1	2	1
Sapindales	Anacardiaceae	2	0	0	5	0	2	6	3
Saxifragales	Crassulaceae	0	1	0	0	0	0	0	1
Solanales	Convolvulaceae	0	0	1	0	0	1	0	0

Table S5.5: Welch's ANOVA with pairwise posthoc Games-Powell tests to determine differences among of BBB types with regard to environmental parameters. The comparisons were done on the five replicates of thinned data sets, outcomes are subsequently averaged and standard deviation is provided. Variables are ordered according to their power of separating BBB types (F value). Li: lignotuber; RC: root crown; Ro: bud-bearing root, WR: woody rhizome, Xy: xylopodium.

Parameter	Welch's ANOVA, F	Pairwise comparison	t test	p value	
Precipitation seasonality	97.51 ± 0.40	RC-Li	14.95 ± 0.06	0.000 ± 0.000	***
		Ro-Li	5.75 ± 0.03	0.000 ± 0.000	***
		WR-Li	8.03 ± 0.07	0.000 ± 0.000	***
		Xy-Li	3.46 ± 0.02	0.006 ± 0.001	**
		Ro-RC	15.89 ± 0.01	0.000 ± 0.000	***
		WR-RC	8.72 ± 0.09	0.000 ± 0.000	***
		Xy-RC	4.03 ± 0.07	0.000 ± 0.000	***
		WR-Ro	11.37 ± 0.03	0.000 ± 0.000	***
		Xy-Ro	7.01 ± 0.01	0.000 ± 0.000	***
		Xy-WR	0.45 ± 0.03	0.991 ± 0.002	
Clay content	77.83 ± 0.72	RC-Li	7.70 ± 0.07	0.000 ± 0.000	***
		Ro-Li	5.27 ± 0.04	0.000 ± 0.000	***
		WR-Li	3.05 ± 0.15	0.021 ± 0.008	*
		Xy-Li	1.90 ± 0.10	0.321 ± 0.053	
		Ro-RC	9.92 ± 0.04	0.000 ± 0.000	
		WR-RC	16.16 ± 0.13	0.000 ± 0.000	
		Xy-RC	2.53 ± 0.12	0.092 ± 0.027	.
		WR-Ro	4.05 ± 0.09	0.000 ± 0.000	***
		Xy-Ro	5.80 ± 0.08	0.000 ± 0.000	***
		Xy-WR	3.88 ± 0.10	0.001 ± 0.001	**
Mean annual precipitation	64.70 ± 1.37	RC-Li	10.26 ± 0.13	0.000 ± 0.000	***
		Ro-Li	10.90 ± 0.06	0.000 ± 0.000	***
		WR-Li	12.90 ± 0.17	0.000 ± 0.000	***
		Xy-Li	0.04 ± 0.03	1.000 ± 0.000	
		Ro-RC	5.92 ± 0.01	0.000 ± 0.000	***
		WR-RC	2.81 ± 0.08	0.040 ± 0.009	*
		Xy-RC	6.83 ± 0.08	0.000 ± 0.000	***
		WR-Ro	4.83 ± 0.04	0.000 ± 0.000	***
		Xy-Ro	9.44 ± 0.05	0.000 ± 0.000	***
		Xy-WR	8.37 ± 0.11	0.000 ± 0.000	***
Annual mean temperature	54.75 ± 0.51	RC-Li	9.40 ± 0.04	0.000 ± 0.000	***
		Ro-Li	5.45 ± 0.09	0.000 ± 0.000	***
		WR-Li	9.43 ± 0.08	0.000 ± 0.000	***
		Xy-Li	2.82 ± 0.05	0.041 ± 0.005	*
		Ro-RC	11.34 ± 0.03	0.000 ± 0.000	***
		WR-RC	0.91 ± 0.09	0.890 ± 0.034	
		Xy-RC	3.29 ± 0.03	0.010 ± 0.001	*
		WR-Ro	11.22 ± 0.04	0.000 ± 0.000	***
		Xy-Ro	6.69 ± 0.03	0.000 ± 0.000	***
		Xy-WR	2.89 ± 0.05	0.034 ± 0.005	*

		RC-Li	12.73 ± 0.07	0.000 ± 0.000	***
		Ro-Li	3.68 ± 0.02	0.003 ± 0.001	**
		WR-Li	13.98 ± 0.08	0.000 ± 0.000	***
		Xy-Li	0.31 ± 0.04	0.998 ± 0.001	
Isothermality	48.76 ± 0.41	Ro-RC	4.93 ± 0.01	0.000 ± 0.000	***
		WR-RC	0.30 ± 0.09	0.797 ± 0.446	
		Xy-RC	6.91 ± 0.03	0.000 ± 0.000	***
		WR-Ro	5.27 ± 0.04	0.000 ± 0.000	***
		Xy-Ro	2.40 ± 0.01	0.116 ± 0.001	
		Xy-WR	7.20 ± 0.04	0.000 ± 0.000	***
		RC-Li	8.56 ± 0.20	0.000 ± 0.000	***
		Ro-Li	6.85 ± 0.08	0.000 ± 0.000	***
		WR-Li	10.33 ± 0.22	0.000 ± 0.000	***
		Xy-Li	0.70 ± 0.06	0.955 ± 0.013	
$NDVI_{med}$	41.37 ± 1.50	Ro-RC	2.91 ± 0.02	0.033 ± 0.002	*
		WR-RC	1.43 ± 0.12	0.606 ± 0.075	
		Xy-RC	6.69 ± 0.13	0.000 ± 0.000	***
		WR-Ro	2.39 ± 0.05	0.122 ± 0.012	
		Xy-Ro	6.61 ± 0.06	0.000 ± 0.000	***
		Xy-WR	7.69 ± 0.14	0.000 ± 0.000	***
		RC-Li	2.70 ± 0.10	0.056 ± 0.015	.
		Ro-Li	5.24 ± 0.05	0.000 ± 0.000	***
		WR-Li	9.29 ± 0.09	0.000 ± 0.000	***
		Xy-Li	3.11 ± 0.04	0.017 ± 0.002	*
Inverse annual frost nights	37.46 ± 0.61	Ro-RC	4.02 ± 0.01	0.000 ± 0.000	***
		WR-RC	9.71 ± 0.09	0.000 ± 0.000	***
		Xy-RC	1.69 ± 0.09	0.445 ± 0.058	
		WR-Ro	0.08 ± 0.03	1.000 ± 0.000	
		Xy-Ro	1.72 ± 0.05	0.428 ± 0.031	
		Xy-WR	2.24 ± 0.07	0.166 ± 0.025	
		RC-Li	7.47 ± 0.10	0.000 ± 0.000	***
		Ro-Li	0.07 ± 0.08	1.000 ± 0.000	
		WR-Li	2.21 ± 0.17	0.182 ± 0.059	
		Xy-Li	2.34 ± 0.21	0.142 ± 0.063	
Fire frequency	28.50 ± 0.98	Ro-RC	4.28 ± 0.08	0.000 ± 0.000	***
		WR-RC	8.88 ± 0.24	0.000 ± 0.000	***
		Xy-RC	2.18 ± 0.21	0.199 ± 0.084	
		WR-Ro	1.23 ± 0.08	0.732 ± 0.048	
		Xy-Ro	1.78 ± 0.15	0.392 ± 0.085	
		Xy-WR	1.19 ± 0.24	0.744 ± 0.138	

Chapter VI Supplement

Table S6.1: Mean value and standard deviation of selected performance traits, compared between fire treatments, between years, and between the two dominant geoxyle species *Brachystegia russelliae* and *Cryptosepalum* aff. *maraviense.*

Taxon	Treatment	Year	Shoot length [cm]	Leaf length [cm]	Leaf number
Brachystegia russelliae	Early burning	2018	7.06 ± 3.35	13.14 ± 2.27	3.91 ± 1.57
	Early burning	2019	7.65 ± 2.95	14.66 ± 2.73	4.08 ± 1.14
	Early burning	2020	10.22 ± 3.79	14.98 ± 2.26	4.73 ± 1.24
	Late burning	2018	7.64 ± 3.22	13.71 ± 3.51	4.85 ± 2.83
	Late burning	2019	6.44 ± 2.93	12.09 ± 2.58	4.05 ± 1.20
	Late burning	2020	6.49 ± 3.26	12.39 ± 2.78	4.45 ± 1.84
	No burning	2018	8.25 ± 3.40	12.31 ± 2.18	6.68 ± 4.15
	No burning	2019	9.21 ± 3.51	12.91 ± 2.20	5.50 ± 3.42
	No burning	2020	10.50 ± 3.47	13.13 ± 2.92	5.87 ± 2.49
Cryptosepalum aff. maraviense	Early burning	2018	2.78 ± 1.14	3.93 ± 0.74	4.22 ± 1.07
	Early burning	2019	3.01 ± 1.25	4.09 ± 0.93	4.27 ± 1.47
	Early burning	2020	2.53 ± 0.88	3.96 ± 0.84	4.14 ± 1.11
	Late burning	2018	2.68 ± 0.97	3.68 ± 0.92	4.68 ± 1.38
	Late burning	2019	2.12 ± 0.84	3.79 ± 0.87	3.98 ± 1.14
	Late burning	2020	2.30 ± 0.66	3.41 ± 0.82	4.10 ± 0.93
	No burning	2018	3.49 ± 1.30	4.35 ± 1.13	5.40 ± 3.34
	No burning	2019	3.11 ± 1.92	4.70 ± 0.96	4.02 ± 1.35
	No burning	2020	3.33 ± 1.20	4.58 ± 1.08	4.50 ± 1.15

Table S6.2: Comparison of mean values and standard deviations of species richness, diversity (Shannon index), and evenness between fire treatments and years, across the three life forms grasses, geoxyles, and herbs.

Lifeform	Treatment	Year	Species richness (S)	Species diversity (H' - Shannon index)	Species evenness (J')
geoxyles	Early burning	2018	14.75 ± 2.56	1.43 ± 0.19	0.54 ± 0.06
	Early burning	2019	15.00 ± 3.05	1.21 ± 0.20	0.45 ± 0.06
	Early burning	2020	15.08 ± 2.19	1.29 ± 0.24	0.48 ± 0.08
	Late burning	2018	15.50 ± 4.25	1.38 ± 0.26	0.51 ± 0.11
	Late burning	2019	15.92 ± 4.60	1.38 ± 0.25	0.51 ± 0.09
	Late burning	2020	16.50 ± 4.19	1.52 ± 0.24	0.55 ± 0.08
	No burning	2018	14.33 ± 2.15	1.26 ± 0.29	0.47 ± 0.11
	No burning	2019	13.55 ± 1.63	1.12 ± 0.19	0.43 ± 0.07
	No burning	2020	13.58 ± 2.19	1.28 ± 0.33	0.49 ± 0.13
grasses	Early burning	2018	15.42 ± 2.57	2.07 ± 0.23	0.76 ± 0.06
	Early burning	2019	15.17 ± 2.33	2.03 ± 0.19	0.75 ± 0.05
	Early burning	2020	17.17 ± 3.10	2.30 ± 0.18	0.81 ± 0.04
	Late burning	2018	15.50 ± 2.97	2.13 ± 0.22	0.78 ± 0.06
	Late burning	2019	13.58 ± 2.02	1.93 ± 0.19	0.74 ± 0.06
	Late burning	2020	17.17 ± 3.21	2.10 ± 0.26	0.75 ± 0.09
	No burning	2018	14.58 ± 2.81	1.90 ± 0.23	0.72 ± 0.08
	No burning	2019	13.36 ± 2.42	1.76 ± 0.26	0.68 ± 0.09
	No burning	2020	15.58 ± 3.48	1.74 ± 0.36	0.64 ± 0.12
herbs	Early burning	2018	15.67 ± 2.71	2.35 ± 0.18	0.86 ± 0.05
	Early burning	2019	19.33 ± 2.57	2.78 ± 0.19	0.94 ± 0.04
	Early burning	2020	18.50 ± 2.65	2.77 ± 0.16	0.95 ± 0.03
	Late burning	2018	16.67 ± 3.98	2.39 ± 0.24	0.86 ± 0.05
	Late burning	2019	18.58 ± 2.15	2.76 ± 0.15	0.95 ± 0.03
	Late burning	2020	19.33 ± 3.96	2.81 ± 0.19	0.95 ± 0.02
	No burning	2018	16.42 ± 3.78	2.40 ± 0.30	0.86 ± 0.04
	No burning	2019	16.36 ± 3.61	2.64 ± 0.30	0.95 ± 0.03
	No burning	2020	16.83 ± 3.07	2.66 ± 0.20	0.95 ± 0.02

Chapter VII Supplement

Figure S7.1: Satellite image showing the surrounding of the Cusseque study area. The original landscape configuration of woody hills and grasslands in the valleys is still clearly visible. Smallholder agriculture is rapidly replacing the closed miombo woodlands. The black frame indicates the position of **Fig. 7.2.** (Google Earth, earth.google.com/web/; Image © 2020 Maxar Technologies; Image © 2020 CNES/Airbus).

Figure S7.2: Parameters for the Valley Depth analysis in SAGA GIS.

Figure S7.3: Daily minimum temperatures for grasslands, ecotone grasslands and miombo forests during the frost season (1 May – 1 October) in the Sovi/Cusseque valley in Bié Province, Angola, from 2012 - 2016. The median minimum temperatures lay at 3.1°C, 4.1°C and 7.3°C for grasslands, ecotone grasslands and miombo forests, respectively. The significance at $p < 0.05$ for the different habitats was assessed with Kruskal-Wallis and post-hoc Dunn tests, and is indicated by letters.

Figure S7.4: Subregional dry season temperature pattern of southern Africa the 13th of June 2020 at 4 a.m. (left) and at 10 a.m. (right). Blue conditions indicate temperatures below 0°C. The patterns clearly vizualise the nocturnal heat loss through outgoing net longwave radiation, culminating at dawn, and the rapid subsequent temperature increase (https://earth.nullschool.net).

Table S7.1: Positions of Tinytag data-loggers (TT) and automated weather stations (AWS) and their respective time of recording within our study area.

ID	Site	Lat	Lon	Altitude	Habitat	Data available
TT02	Cusseque	-13.704	17.06939	1526	Grassland	Oct2011-May2012 / Mar2013-Jun2015 / Jul2015-Jan2016
TT05	Cusseque	-13.7011	17.06832	1555	Ecotone grassland	Oct2011-Sep2013 / Feb2014-Jun2015 / Jul2015-Jan2016
TT07	Cusseque	-13.6897	17.06605	1601	Miombo woodland	Oct2011-Jun2015 / Jul2015-Jan2016
TT16	Cusseque	-13.7065	17.09696	1545	Grassland	May2012-Sep2012 / Nov2012-Jul2014
TT08	Cusseque	-13.7079	17.10376	1547	Grassland	Oct2011-Apr2013 / Jun2013-Jun2015 / Aug2015-Nov2015
TT14	Cusseque	-13.7103	17.10729	1545	Miombo woodland	May2012-Jun2015 / Aug2015-Apr2016
TT13	Cusseque	-13.705	17.04578	1550	Grassland	Oct2011-May2012 / Nov2012-Jun2015 / Aug2015-Oct2016 / Nov2016-Dec2016
TT12	Cusseque	-13.6989	17.04451	1553	Ecotone grassland	Oct2011-May2012 / Apr2013-Sep2013
TT09	Cusseque	-13.6878	17.04486	1605	Miombo woodland	Oct2011-Apr2016
TT22	Cusseque	-13.7062	17.0458	1529	Grassland	May2013-Sep2013 / Feb2014-Jun2015 / Nov2015-Oct2016 / Nov2016-Dec2016 / Jan2017-Aug2017
TT21	Cusseque	-13.71	17.05228	1544	Ecotone grassland	Apr2013-Jun2015 / Aug2015-Oct2016 / Nov2016-Dec2016
TT20	Cusseque	-13.7114	17.05192	1554	Miombo woodland	Mar2013-Jun2015
AWSCus	Cusseque	-13.7101	17.0806	1529	Ecotone grassland	Mar2015-Jan2017 / May2017-Jun2017
TTBic	Bicuar	-15.1003	14.8361	1237	Grassland	Jun2017-today
AWSBic	Bicuar	-15.1	14.8333	1235	Ecotone grassland	Mar2015-June2018

Table S7.2: Fire events at the positions of Tinytag data-loggers (TT) and automated weather stations (AWS) at Cusseque during their respective time of recording.

Logger ID	Vegetation	Date
TT02	Grassland	12.10.2011
TT08	Grassland	07.07.2012
TT08	Grassland	17.08.2014
TT13	Grassland	17.08.2013
TT13	Grassland	02.09.2015
TT16	Grassland	11.07.2012
TT16	Grassland	29.05.2013

TT21	Ecotone grassland	17.08.2013
AWSCus	Ecotone grassland	06.06.2015
AWSCus	Ecotone grassland	29.06.2016
TT05	Ecotone grassland	25.08.2013
TT05	Ecotone grassland	18.09.2015
TT14	Miombo forest	25.08.2013
TT14	Miombo forest	02.09.2015
TT20	Miombo forest	17.08.2013

Chapter VIII Supplement

Figure S8.1: a) Phenotype SB, population Sb28569 (not included in this study) at a tributary to the Cubango in Cuando-Cubango, Angola. b) same individual, close up. Both photos: P. Zigelski, July 2017. c) Phenotype SC, population Sc28565 (not included in this study) in seasonally flooded wetlands in Moxíco, Angola. d) same individual, close up. Both photos: P. Zigelski, June 2017. e) Phenotype SGB, population Sgb28555 (not included in this study) in the Kafue National Park in Zambia. f) population Sgb28316 along the Cunene River near Xangongo, Angola, close up. Photos: P. Zigelski, June 2017 (e); May 2016 (f). g) Phenotype SGG, population Sgg05 in the Liuwa Plains National Park in Zambia. h) population Sgg01 in the Liuwa Plains National Park in Zambia, close up. Both photos: P. Zigelski, November 2014. i) Phenotype SGGx, population Sggx28552 in a meadow in Cuando-Cubango, Angola. j) same population, close up. Both photos: P. Zigelski, December 2016. k) Phenotype SGH, population Sgh10 in a forest grassland ecotone in Cuando-Cubango, Angola. l) population Sgh07 from the Bíe Plateau, Angola, close up at excavated geoxylic structures. Both photos: P. Zigelski, December 2014. m) Phenotype SGM, population Sgm28343 in frequently disturbed open woodlands on the Bíe Plateau, Angola. n) population Sgm28337 in the Cameia National Park, Angola, close up. Both photos: P. Zigelski, November 2016. o) Phenotype SGMx, population Sgm13 in a forest grassland ecotone on the Bíe Plateau, Angola. p) population Sgm08 in a forest grassland ecotone on the Bíe Plateau, Angola, close up at excavated geoxylic structures. Both photos: P. Zigelski, December 2014. q) Phenotype ST, population St01 on the Angolan Escarpment at Tundavala, Lubango, Angola a forest grassland ecotone on the Bíe Plateau, Angola. r) same individual, close up. Both photos: P. Zigelski, December 2014.

Figure S8.2: Plotting of mean likelihood and delta K for 2 < K < 9 from the analysis of the STRUCTURE results following Evanno et al. (2005). The plots are derived from STRUCTURE Harvester (Earl and von Holdt, 2012).

Figure S8.3: Geographic distribution of the five ecotypes. Points represent populations; they are shaped according to their ecotype and colored according to their genetic ancestry. a) All populations belonging to ET 1; b) all populations belonging to ET 2; c) all populations belonging to ET 3; d) all populations belonging to ET 4; e) all populations belonging to ET 5.

Table S8.1: Complete data set. Every individual that was used in the analysis is listed here. Indicated are: the population and phenotype to which it belongs, the position where it was collected, its affiliation to each of the three genetic clusters identified in the STRUCTURE analysis, its mean leaf area [cm²], mean leaf stiffness and growing height [m], whether it has a geoxylic growth, in which soil type it was encountered (derived from Hengl et al., 2017a), how much annual precipitation it recieves (derived from WorldClim2, Fick & Hijmans, 2017), the hydrological conditions on its site, and to which ecotype it belongs (derived from PAM analysis). NA = no data available.

ID	Phenotype	Population	Longitude	Latitude	STRUCTURE cluster I	STRUCTURE cluster II	STRUCTURE cluster III	Leaf area [cm²]	Leaf stiffness	Height [m]	Geoxyle?	Soil type (WRB)	Mean annual precipitation	observed or estimated hydrology	Eco-types
Ba01	SGB	Sgb09	21.67357	-18.11995	0.0437	0.1339	0.8222	50.1305	soft	5	no_geox	Haplic Calcisols	531	slow_river	ET 1
Ba02	SGB	Sgb09	21.66927	-18.11515	0.0425	0.1206	0.837	50.1305	soft	5	no_geox	Haplic Calcisols	531	slow_river	ET 1
Ba03	SGB	Sgb_H	25.8651	-17.9258	0.0817	0.1557	0.7623	NA	NA	NA	NA	Haplic Lixisols	NA	NA	ET 1
Ba04	SGB	Sgb09	21.6816	-18.13985	0.0616	0.1259	0.8126	50.1305	soft	5	no_geox	Haplic Calcisols	531	slow_river	ET 1
Ba05	SGB	Sgb06	22.85377	-15.1794	0.5819	0.1803	0.2379	46.388	soft	7	no_geox	Haplic Arenosols	925	s_flooded	ET 1
Ba06	SGB	Sgb07	23.55755	-16.63358	0.37	0.1113	0.5188	31.8635	soft	6	no_geox	Gleyic Luvisols	697	slow_river	ET 1
Ba07	SGB	Sgb678	14.7725	-14.90133	0.124	0.1498	0.7264	22.622	soft	8	no_geox	Haplic Arenosols	899	slow_river	ET 1
Ba08	SGB	Sgb28315	14.73597	-17.06845	0.0359	0.1224	0.8417	30.53	soft	7	no_geox	Ferralic Arenosols	493	slow_river	ET 1
Ba09	SGB	Sgb28315	14.73598	-17.06844	0.0356	0.1231	0.8414	30.53	soft	7	no_geox	Ferralic Arenosols	493	slow_river	ET 1
Ba10	SGB	Sgb28315	14.73599	-17.06846	0.0359	0.1226	0.8414	30.53	soft	7	no_geox	Ferralic Arenosols	493	slow_river	ET 1
Ba11	SGB	Sgb28315	14.73596	-17.06842	0.0357	0.1228	0.8413	30.53	soft	7	no_geox	Ferralic Arenosols	493	slow_river	ET 1
Ba12	SGB	Sgb28316	14.95853	-16.73381	0.0761	0.2463	0.6777	74.01	soft	6	no_geox	Haplic Luvisols	593	s_flooded	ET 1
Ba13	SGB	Sgb28316	14.95852	-16.73383	0.0748	0.2456	0.6797	74.01	soft	6	no_geox	Haplic Luvisols	593	s_flooded	ET 1
Ba14	SGB	Sgb28316	14.95854	-16.73385	0.0753	0.2453	0.6796	74.01	soft	6	no_geox	Haplic Luvisols	593	s_flooded	ET 1
Ba15	SGB	Sgb28317	15.03926	-14.82904	0.0372	0.1278	0.835	31.62	soft	8	no_geox	Haplic Lixisols	894	slow_river	ET 1
Ba16	SGB	Sgb28318	17.8136	-16.47611	0.5719	0.0732	0.3549	20.145	soft	5	no_geox	Ferralic Arenosols	703	slow_river	ET 1
Ba17	SGB	Sgb28318	17.81361	-16.4761	0.1135	0.1403	0.7462	20.145	soft	5	no_geox	Ferralic Arenosols	703	slow_river	ET 1
Ba18	SGB	Sgb28318	17.81362	-16.47612	0.5888	0.1173	0.2941	20.145	soft	5	no_geox	Ferralic Arenosols	703	slow_river	ET 1
Ba19	SGB	Sgb28318	17.81363	-16.47614	0.2437	0.183	0.5734	20.145	soft	5	no_geox	Ferralic Arenosols	703	slow_river	ET 1

Ba20	SGB	Sgb28319	18.15963	-17.05285	0.1408	0.1545	0.7048	41.625	soft	8	no_geox	Haplic Calcisols	651	slow_river	ET 1
Be01	SB	Sb01	15.31283	-14.72857	0.3066	0.5334	0.1602	32.9225	soft	8	no_geox	Haplic Luvisols	939	slow_river	ET 4
Be02	SB	Sb28573	13.17952	-14.84662	0.7215	0.0702	0.2083	35.705	soft	6	no_geox	Calcic Luvisols	490	s_flooded	ET 2
Be03	SB	Sb28573	13.17951	-14.84663	0.4014	0.322	0.2766	35.705	soft	6	no_geox	Calcic Luvisols	490	s_flooded	ET 2
C01	SC	Sc23751	18.64008	-15.72272	0.1621	0.6806	0.1571	14.9105	soft	8	no_geox	Haplic Arenosols	799	fast_river	ET 2
C02	SC	Sc23751	18.64009	-15.72275	0.1567	0.7346	0.1086	14.9105	soft	8	no_geox	Haplic Arenosols	799	fast_river	ET 2
C03	SC	Sc23751	18.6401	-15.72271	0.1537	0.7193	0.1269	14.9105	soft	8	no_geox	Haplic Arenosols	799	fast_river	ET 2
C04	SC	Sc01	22.43997	-18.83187	0.8113	0.0348	0.1538	33.7105	soft	11	no_geox	Haplic Arenosols	466	s_flooded	ET 1
C05	SC	Sc03	22.40385	-18.80765	0.8401	0.0272	0.1325	58.258	soft	10	no_geox	Haplic Arenosols	462	s_flooded	ET 1
C06	SC	Sc03	22.40405	-18.80792	0.8352	0.0231	0.1419	58.258	soft	10	no_geox	Haplic Arenosols	462	s_flooded	ET 1
C07	SC	Sc01	22.43198	-18.82767	0.7735	0.0549	0.1714	33.7105	soft	11	no_geox	Ferralic Arenosols	466	s_flooded	ET 1
C08	SC	Sc01	22.42467	-18.82958	0.7359	0.0377	0.2267	33.7105	soft	11	no_geox	Haplic Arenosols	466	s_flooded	ET 1
C09	SC	Sc04	23.345	-17.79052	0.2551	0.4768	0.268	35.5565	soft	2	no_geox	Haplic Arenosols	577	slow_river	ET 1
C10	SC	Sc02	13.20072	-15.04012	0.6427	0.1066	0.2506	46.714	soft	3	no_geox	Haplic Luvisols	499	fast_river	ET 1
C11	SC	Sc02	13.20178	-15.0392	0.679	0.0638	0.2569	46.714	soft	3	no_geox	Haplic Luvisols	499	fast_river	ET 1
C12	SC	Sc02	13.20325	-15.03843	0.3855	0.1171	0.4973	46.714	soft	3	no_geox	Haplic Luvisols	499	fast_river	ET 1
C13	SC	Sc02	13.20188	-15.03922	0.7691	0.0634	0.1676	46.714	soft	3	no_geox	Haplic Luvisols	499	fast_river	ET 1
C14	SC	Sc28313	20.20366	-11.0207	0.1689	0.3346	0.4965	22.645	soft	6	no_geox	Haplic Ferralsols	1280	fast_river	ET 4
C15	SC	Sc28336	20.91224	-11.52238	0.3891	0.3818	0.2293	28.975	soft	2	no_geox	Haplic Ferralsols	1223	slow_river	ET 4
C16	SC	Sc28336	20.91225	-11.52239	0.2629	0.465	0.2722	28.975	soft	2	no_geox	Haplic Ferralsols	1223	slow_river	ET 4
C17	SC	Sc28345	17.19536	-12.2502	0.4737	0.1765	0.3498	41.07	soft	4	no_geox	Haplic Acrisols	1284	slow_river	ET 1
C19	SC	Sc_H01	16.345	-9.547	0.2974	0.6288	0.0738	NA	NA	NA	NA	Haplic Ferralsols	NA	NA	NA
G01	SGG	Sgg01	22.65252	-14.88863	0.0985	0.6277	0.2736	27.2165	soft	12	no_geox	Haplic Podzols	974	dry	ET 2
G02	SGG	Sgg01	22.6524	-14.88773	0.1203	0.6486	0.2312	27.2165	soft	12	no_geox	Haplic Podzols	974	dry	ET 2
G03	SGG	Sgg02	22.7023	-14.61143	0.3851	0.16	0.4549	37.289	soft	13	no_geox	Haplic Podzols	984	dry	ET 2

G04	SGG	Sgg03	22.6555	-14.49308	0.1736	0.542	0.2842	29.9735	soft	11	no_geox	Haplic Podzols	986	dry	ET 2
G05	SGG	Sgg03	22.65407	-14.49405	0.6401	0.1822	0.1777	29.9735	soft	11	no_geox	Haplic Arenosols	986	dry	ET 2
G06	SGG	Sgg04	22.69927	-14.67135	0.2748	0.3627	0.3626	42.2125	soft	10	no_geox	Haplic Podzols	996	dry	ET 2
G07	SGG	Sgg05	22.67742	-14.82513	0.1805	0.4453	0.3742	19.1115	soft	14	no_geox	Haplic Podzols	979	dry	ET 2
G08	SGG	Sgg07	17.06932	-13.69258	0.4581	0.1399	0.4021	34.0875	soft	8	no_geox	Ferralic Arenosols	1121	dry	ET 2
G09	SGG	Sgg07	17.06873	-13.689	0.4375	0.1485	0.4137	NA	NA	NA	NA	Ferralic Arenosols	NA	NA	ET 2
G10	SGG	Sgg08	17.01387	-13.69912	0.1574	0.7214	0.1208	40.6105	soft	4	no_geox	Ferralic Arenosols	1132	dry	ET 4
G11	SGG	Sgg_H	13.533	-15.053	0.2548	0.6128	0.1326	NA	NA	NA	NA	Acric Ferralsols	NA	NA	NA
G12	SGG	Sgg28341	18.34317	-12.1673	0.2267	0.2826	0.4906	50.62	soft	8	no_geox	Ferralic Arenosols	1215	dry	ET 2
Gx01	SGGx	Sggx03	22.6546	-14.49407	0.4889	0.3348	0.1764	108.996	stiff	4	unk_geox	Haplic Podzols	986	dry	ET 5
Gx02	SGGx	Sggx03	22.65472	-14.49255	0.7568	0.0782	0.1649	108.996	stiff	4	unk_geox	Haplic Podzols	986	dry	ET 5
Gx03	SGGx	Sggx05	22.67732	-14.82335	0.4345	0.3865	0.1791	76.1575	stiff	2	unk_geox	Haplic Podzols	979	dry	ET 5
Gx04	SGGx	Sggx28311	20.89973	-11.52528	0.2755	0.3897	0.3343	76.1575	stiff	5	unk_geox	Acric Ferralsols	979	dry	ET 3
Gx05	SGGx	Sggx28311	20.89974	-11.52526	0.3789	0.436	0.1852	51.43	stiff	5	unk_geox	Acric Ferralsols	1218	s_flooded	ET 3
Gx06	SGGx	Sggx28313	20.20366	-11.0207	0.3627	0.3013	0.3363	62.805	stiff	6	unk_geox	Haplic Ferralsols	1280	fast_river	ET 3
Gx07	SGGx	Sggx28314	20.2058	-10.64443	0.4396	0.1748	0.3856	51.065	stiff	4	unk_geox	Haplic Ferralsols	1315	fast_river	ET 3
Gx08	SGGx	Sggx28337	20.91224	-11.52239	0.359	0.5504	0.0906	71.09	stiff	6	unk_geox	Haplic Ferralsols	1223	dry	ET 3
Gx09	SGGx	Sggx28552	16.55723	-14.48223	0.389	0.42	0.1911	42.595	stiff	7	unk_geox	Ferralic Arenosols	987	s_flooded	ET 3
Gx10	SGGx	Sggx28552	16.55724	-14.48221	0.3842	0.428	0.1878	42.595	stiff	7	unk_geox	Ferralic Arenosols	987	s_flooded	ET 3
H01	SGH	Sgh23935	17.30775	-13.59665	0.8217	0.033	0.1452	46.268	stiff	0.4	geoxyle	Haplic Ferralsols	1104	dry	ET 5
H02	SGH	Sgh23935	17.30776	-13.59666	0.7091	0.1279	0.1629	46.268	stiff	0.4	geoxyle	Haplic Ferralsols	1104	dry	ET 5
H03	SGH	Sgh23935	17.30774	-13.59664	0.7344	0.1168	0.1488	46.268	stiff	0.4	geoxyle	Haplic Ferralsols	1104	dry	ET 5
H04	SGH	Sgh23940	21.07199	-11.48048	0.8301	0.0254	0.1442	52.2115	stiff	0.4	geoxyle	Haplic Ferralsols	1234	s_flooded	ET 5
H05	SGH	Sgh23940	21.07198	-11.48047	0.8186	0.0322	0.1493	52.2115	stiff	0.4	geoxyle	Haplic Ferralsols	1234	s_flooded	ET 5
H06	SGH	Sgh23940	21.07197	-11.48046	0.7984	0.0377	0.1638	52.2115	stiff	0.4	geoxyle	Haplic Ferralsols	1234	s_flooded	ET 5

H07	SGH	Sgh23941	25.85778	-16.15886	0.8204	0.0307	0.1489	38.316	stiff	0.4	geoxyle	Haplic Ferralsols	784	s_flooded	ET 5
H08	SGH	Sgh23941	25.85777	-16.15887	0.6127	0.2083	0.179	38.316	stiff	0.4	geoxyle	Haplic Lixisols	784	s_flooded	ET 5
H09	SGH	Sgh23941	25.85779	-16.15888	0.6665	0.1623	0.171	38.316	stiff	0.4	geoxyle	Haplic Lixisols	784	s_flooded	ET 5
H10	SGH	Sgh23961	18.77962	-15.31175	0.2783	0.4127	0.3093	NA	stiff	0.4	geoxyle	Haplic Ferralsols	850	dry	ET 5
H11	SGH	Sgh23961	18.77963	-15.31176	0.274	0.4153	0.3109	NA	stiff	0.4	geoxyle	Haplic Ferralsols	850	dry	ET 5
H12	SGH	Sgh_H01	17.528	-15.76	0.7738	0.084	0.142	NA	NA	NA	NA	Haplic Fluvisols	NA	NA	ET 5
H13	SGH	Sgh01	23.28942	-15.5755	0.2898	0.5118	0.1985	44.411	stiff	0.4	geoxyle	Haplic Podzols	846	s_flooded	ET 5
H14	SGH	Sgh02	22.64578	-14.91278	0.4815	0.4177	0.1005	35.932	stiff	0.3	geoxyle	Haplic Arenosols	981	dry	ET 5
H15	SGH	Sgh02	22.64715	-14.91235	0.7063	0.1412	0.1527	35.932	stiff	0.3	geoxyle	Haplic Arenosols	981	dry	ET 5
H16	SGH	SGHs1	22.6523	-14.8875	0.4576	0.4279	0.1146	35.932	stiff	0.4	geoxyle	Haplic Podzols	981	dry	ET 5
H17	SGH	Sgh03	22.70215	-14.61315	0.8204	0.0429	0.1367	35.379	stiff	0.4	geoxyle	Haplic Podzols	984	s_flooded	ET 5
H18	SGH	Sgh03	22.70382	-14.61535	0.8209	0.0419	0.1373	35.379	stiff	0.4	geoxyle	Haplic Arenosols	984	s_flooded	ET 5
H19	SGH	Sgh04	22.69633	-14.61592	0.7439	0.1154	0.1407	41.7595	stiff	0.4	geoxyle	Haplic Arenosols	982	s_flooded	ET 5
H20	SGH	Sgh04	22.69652	-14.6151	0.8201	0.0425	0.1374	41.7595	stiff	0.4	geoxyle	Haplic Arenosols	982	s_flooded	ET 5
H21	SGH	Sgh05	22.57905	-14.355	0.8155	0.03	0.1547	39.9585	stiff	0.4	geoxyle	Haplic Arenosols	991	s_flooded	ET 5
H22	SGH	Sgh05	22.57913	-14.35443	0.7746	0.0688	0.1564	39.9585	stiff	0.4	geoxyle	Haplic Arenosols	991	s_flooded	ET 5
H23	SGH	Sgh06	22.68427	-14.81543	0.7208	0.1039	0.1756	38.936	stiff	0.4	geoxyle	Haplic Arenosols	977	s_flooded	ET 5
H24	SGH	SGHs2	22.6773	-14.8235	0.5632	0.3272	0.1097	39.9585	stiff	0.4	geoxyle	Haplic Podzols	991	s_flooded	ET 5
H25	SGH	Sgh07	17.11777	-13.69755	0.8086	0.0348	0.1567	50.7995	stiff	0.4	geoxyle	Haplic Ferralsols	1105	dry	ET 5
H26	SGH	Sgh09	17.07298	-13.7008	0.524	0.3194	0.1565	82.226	stiff	0.5	geoxyle	Haplic Ferralsols	1105	dry	ET 5
H27	SGH	SghGTN	16.70327	-13.00915	0.1542	0.7993	0.0465	NA	NA	NA	NA	Acric Ferralsols	NA	NA	ET 5
H28	SGH	Sgh10	17.66852	-16.20037	0.4514	0.4314	0.1172	52.035	stiff	0.4	geoxyle	Ferralic Arenosols	734	dry	ET 5
H29	SGH	Sgh11	17.70382	-16.33993	0.3118	0.5769	0.1114	66.6175	stiff	0.4	geoxyle	Petric Calcisols	718	s_flooded	ET 5
H30	SGH	Sgh28333	20.20111	-10.64027	0.7409	0.0429	0.2161	57.615	stiff	0.5	geoxyle	Haplic Ferralsols	1314	dry	ET 5
H31	SGH	Sgh28333	20.20113	-10.64026	0.1554	0.7736	0.0709	57.615	stiff	0.5	geoxyle	Haplic Ferralsols	1314	dry	ET 5

H33	SGH	Sgh28337	20.91224	-11.52239	0.5522	0.2599	0.1877	NA	stiff	0.4	geoxyle	Haplic Ferralsols	1223	dry	ET 5
H34	SGH	Sgh28337	20.91225	-11.52238	0.269	0.3809	0.3502	NA	stiff	0.4	geoxyle	Haplic Ferralsols	1223	dry	ET 5
H35	SGH	Sgh28337	20.91226	-11.52237	0.716	0.1114	0.1726	NA	stiff	0.4	geoxyle	Haplic Ferralsols	1223	dry	ET 5
H36	SGH	Sgh28338	21.13515	-11.62844	0.5584	0.2454	0.1963	44.33	stiff	0.4	geoxyle	Haplic Arenosols	1223	s_flooded	ET 5
H37	SGH	Sgh28338	21.13516	-11.62845	0.6981	0.1406	0.1613	44.33	stiff	0.4	geoxyle	Haplic Arenosols	1223	s_flooded	ET 5
H38	SGH	Sgh28344	17.83717	-11.96972	0.3884	0.4293	0.1824	51.975	stiff	0.4	geoxyle	Haplic Ferralsols	1189	dry	ET 5
H39	SGH	Sgh28349	17.57015	-15.8407	0.7991	0.0512	0.1497	53.405	stiff	0.4	geoxyle	Ferralic Arenosols	769	dry	ET 5
H40	SGH	Sgh28349	17.57014	-15.84069	0.8345	0.0347	0.1309	53.405	stiff	0.4	geoxyle	Ferralic Arenosols	769	dry	ET 5
H41	SGH	Sgh28349	17.57016	-15.84068	0.615	0.2235	0.1614	53.405	stiff	0.4	geoxyle	Ferralic Arenosols	769	dry	ET 5
H42	SGH	Sgh28349	17.57015	-15.84067	0.3561	0.4764	0.1674	53.405	stiff	0.4	geoxyle	Ferralic Arenosols	769	dry	ET 5
H43	SGH	Sgh28551	14.60148	-15.12613	0.5208	0.2796	0.1996	47.325	stiff	0.3	geoxyle	Haplic Arenosols	869	dry	ET 5
M01	SGM	Sgm23691	16.73154	-13.34144	0.1154	0.8509	0.0336	78.039	soft	4	no_geox	Haplic Ferralsols	1208	dry	ET 4
M02	SGM	Sgm23691	16.73155	-13.34143	0.1143	0.8549	0.0309	78.039	soft	4	no_geox	Haplic Ferralsols	1208	dry	ET 4
M03	SGM	Sgm23691	16.73156	-13.34145	0.1466	0.7988	0.0548	78.039	soft	4	no_geox	Haplic Ferralsols	1208	dry	ET 4
M04	SGM	Sgm23717	17.14019	-13.63721	0.3037	0.4095	0.2867	28.853	soft	8	no_geox	Ferralic Arenosols	1129	dry	ET 4
M05	SGM	Sgm23717	17.14032	-13.63722	0.1664	0.7009	0.1326	28.853	soft	8	no_geox	Ferralic Arenosols	1129	dry	ET 4
M06	SGM	Sgm23717	17.14018	-13.63723	0.1825	0.7012	0.1161	28.853	soft	8	no_geox	Ferralic Arenosols	1129	dry	ET 4
M07	SGM	Sgm_H01	16.074	-15.11	0.112	0.8033	0.0847	NA	NA	NA	NA	Haplic Arenosols	NA	NA	ET 4
M08	SGM	Sgm01	16.60492	-14.49627	0.1466	0.8182	0.035	109.6135	soft	6	no_geox	Ferralic Arenosols	1010	dry	ET 4
M09	SGM	Sgm01	16.60465	-14.49603	0.1391	0.7918	0.0691	109.6135	soft	6	no_geox	Ferralic Arenosols	1010	dry	ET 4
M11	SGM	Sgm02	14.76572	-12.9703	0.1338	0.8085	0.0578	106.7375	soft	4	no_geox	Haplic Ferralsols	1224	dry	ET 4
M12	SGM	Sgm02	14.76617	-12.97015	0.1305	0.8115	0.058	106.7375	soft	4	no_geox	Haplic Ferralsols	1224	dry	ET 4
M13	SGM	Sgm03	17.1137	-13.72255	0.1081	0.8001	0.0917	60.841	soft	6	no_geox	Haplic Ferralsols	1113	dry	ET 4
M14	SGM	Sgm03	17.11425	-13.72077	0.1347	0.8025	0.0627	60.841	soft	6	no_geox	Ferralic Arenosols	1113	dry	ET 4
M15	SGM	SGM	17.07407	-13.68257	0.1211	0.8365	0.0424	34.0875	soft	8	no_geox	Ferralic Arenosols	1121	dry	ET 4

M16	SGM	Sgm28310	19.35596	-10.11635	0.1353	0.7789	0.0859	142.35	soft	4	no_geox	Acric Ferralsols	1398	dry	ET 4
M17	SGM	Sgm28343	17.96609	-11.98638	0.133	0.538	0.3289	56.085	soft	3	no_geox	Haplic Ferralsols	1200	dry	ET 4
M18	SGMx	Sgm16	13.40637	-14.81457	0.1163	0.8316	0.052	57.5495	stiff	2	unk_geox	Acric Ferralsols	983	dry	ET 4
M19	SGMx	Sgm16	13.40087	-14.80043	0.1138	0.8573	0.029	57.5495	stiff	2	unk_geox	Haplic Ferralsols	983	dry	ET 4
M20	SGMx	Sgm16	13.4012	-14.80052	0.114	0.857	0.0292	57.5495	stiff	2	unk_geox	Haplic Ferralsols	983	dry	ET 4
M21	SGMx	Sgm08	17.118	-13.7007	0.1185	0.8485	0.0331	87.975	soft	1	geoxyle	Haplic Ferralsols	1111	dry	ET 4
M22	SGMx	Sgm08	17.11715	-13.70052	0.139	0.6542	0.207	87.975	soft	1	geoxyle	Haplic Ferralsols	1111	dry	ET 4
M23	SGMx	Sgm09	17.07183	-13.69963	0.1172	0.8504	0.0324	82.5345	soft	1.2	geoxyle	Haplic Ferralsols	1105	dry	ET 4
M24	SGMx	Sgm09	17.07117	-13.70245	0.1483	0.6682	0.1836	82.5345	soft	1.2	geoxyle	Haplic Ferralsols	1105	dry	ET 4
M25	SGMx	Sgm13	17.14155	-14.67065	0.1299	0.8238	0.0464	36.763	stiff	1.2	geoxyle	Ferralic Arenosols	959	dry	ET 5
M26	SGMx	Sgm13	17.1425	-14.67057	0.1507	0.7832	0.066	36.763	stiff	1.2	geoxyle	Ferralic Arenosols	959	dry	ET 5
M32	SGM	Sgm28346	15.21083	-12.89856	0.1362	0.8054	0.0587	71.465	soft	4	geoxyle	Acric Ferralsols	1291	dry	ET 4
T01	ST	St02	13.40215	-14.80738	0.208	0.1391	0.6529	20.082	stiff	6	no_geox	Ferralic Arenosols	983	dry	ET 1
T02	ST	St02	13.40203	-14.80455	0.3184	0.1137	0.5679	20.082	stiff	6	no_geox	Acric Ferralsols	983	dry	ET 1
T03	ST	St_H01	35.594	-7.326	0.4854	0.3048	0.2097	NA	NA	NA	NA	Haplic Cambisols	NA	NA	ET 1
T04	ST	St01	13.38075	-14.81618	0.4686	0.189	0.3427	14.205	stiff	4	no_geox	Haplic Ferralsols	865	dry	ET 1
T05	ST	St01	13.38076	-14.81616	0.3919	0.2065	0.4015	14.205	stiff	4	no_geox	Haplic Ferralsols	865	dry	ET 1
T06	ST	St01	13.38077	-14.81615	0.1084	0.1325	0.7593	14.205	stiff	4	no_geox	Haplic Ferralsols	971	dry	ET 1
T07	ST	St01	13.38078	-14.81619	0.5428	0.0823	0.3748	14.205	stiff	4	no_geox	Haplic Ferralsols	971	dry	ET 1
T08	ST	St_H02	13.377	-15.028	0.2846	0.4022	0.3132	NA	NA	NA	NA	Acric Ferralsols	NA	NA	ET 1
T09	ST	St_H03	13.38	-14.816	0.1554	0.2222	0.6224	NA	NA	NA	NA	Haplic Ferralsols	NA	NA	ET 1

Table S2: Detailed documentation of the outcomes from STRUCTURE analysis with 10 repeats per K. Simulations were run assuming the model allowing admixture, correlated allele frequencies, unknown allele dosage and no prior grouping. Results were interpreted according to Evanno et al. (2005) using the software STRUCTURE HARVESTER from Earl and von Holdt (2012). The first score was achieved at K = 3, and three genetic clusters were assumed in all subsequent analyses. Though K = 9 achieved the highest score, this was due to failed detection of genetic structuring (each individual shared the same ancestry from each cluster), which leads to seemingly high likelihood and probability.

# K	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	Delta K
1	-3830.74	0.45	-	-	-
2	-4119.93	406.33	-289.19	485.90	1.19
3	**-3923.21**	**147.79**	**196.71**	**925.06**	**6.25**
4	-4651.57	1764.62	-728.35	740.00	0.41
5	-4639.92	1209.54	11.65	78.71	0.06
6	-4549.55	1342.68	90.37	313.47	0.23
7	-4145.71	785.256	403.84	662.99	0.84
8	-4404.86	1350.08	-259.15	814.31	0.60
9	-3849.70	54.95	555.16	700.59	12.74
10	-3995.13	220.75	-145.43	-	-

Chapter IX Supplement

Table S9.1. Overview on families and species sampled for this study regarding life form, leaves type, height, leaf phenology, ectomycorrizal symbiosis and vouchers.

Species	Families	Life form	leaves	Height (m)	Leaf phenology	ECM	Vouchers (HBG)
Adenodolichos mendesii Torre	Fabaceae-Papilionoidae	geox.	c.t.	0.5	deciduous	N	140052
Annona stenophylla ssp *nana* Engl. & Diels	Annonaceae	geox.	s.	0.4	deciduous	N	140065
Brachystegia bakeriana Burtt Davy & Hutch	Fabaceae-Detarioidae	tree	c.p.	10+	deciduous	Y	135298; 139016
Brachystegia longifolia Benth.	Fabaceae-Detarioidae	tree	c.i.	10+	deciduous	Y	132957, 134288, 135621
Baphia bequaertii De Wild.	Fabaceae-Papilionoidae	tree	s.	4-7	semi-deciduous	N	135360; 139242; 133018
Brachystegia russelliae I.M.Johnst.	Fabaceae-Detarioidae	geox.	c.i.	0.4	deciduous	Y	132793, 143837
Brachystegia spiciformis Benth.	Fabaceae-Detarioidae	tree	c.p.	8-30	deciduous	Y	132676
Burkea africana Hook	Fabaceae-Caesalpinioidae	tree	c.p.	10+	deciduous	N	-
Combretum platypetalum Welw.	Combretaceae	geox.	s.	0.5	deciduous	N	135541
Combretum zeyheri Sond.	Combretaceae	tree	s.	10+	deciduous	N	132510
Cryptosepalum exfoliatum (Baker f.) P.A.Duvign. & Brenan. subsp. *pseudotaxus*	Fabaceae-Detarioidae	tree	c.p.	10+	deciduous	Y	135304
Cryptosepalum sp nov	Fabaceae	geox.	c.p.	0.3	semi-deciduous	Y	132481, 132754
Erythrophleum africanum (Welw. ex Benth.) Harms.	Fabaceae-Caesalpinioidae	tree	c.bp.	10+	deciduous	N	135333
Julbernardia paniculata (Benth.)	Fabaceae-Detarioidae	tree	c.p.	10+	deciduous	Y	-
Monotes africanus A.DC.	Dipterocarpaceae	tree	s.	10+	deciduous	(Y)	132917; 134160; 134228
Ochna arenaria De Wild. and T. Durand.	Ochnaceae	geox.	s.	0.2	deciduous	N	140070
Parinari capensis Harv.	Chrysobalanaceae	geox.	s.	0.1	deciduous	N	132664
Parinari curatellifolia Planch. ex Benth.	Chrysobalanaceae	tree	s.	10+	semi-deciduous	N	132671
Pterocarpus angolensis DC.	Fabaceae-Papilionoidae	tree	c.i.	10+	deciduous	N	-
Protea trichophylla Engl. & Gilg	Proteaceae	geox.	s.	0.5	deciduous	N	140095
Pygmaeothamnus zeyheri (Sond.) Robyns	Rubiaceae	tree	s.	0.2	deciduous	N	140075
Rhus exelliana Meikle	Anacardiaceae	geox.	c.t.	0.4	deciduous	N	140036
Syzygium guineense (Willd.) DC. subsp. *macrocarpum* (Engl.) F.White	Myrtaceae	geox.	s.	1	evergreen	N	135802, 143204
Syzygium guineense (Willd.) DC. subsp. *macrocarpum* (Engl.) F.White	Myrtaceae	tree	s.	5-6	evergreen	N	135805
Uapaca nitida Müll. Arg.	Euphorbiaceae	tree	s.	10+	evergreen	Y	135302
Uapaca nitida Müll. Arg.var. *suffrutescens* P.A.Duvign	Euphorbiaceae	geox.	s.	0.4	evergreen	Y	132490, 134199

Life form: geox.=geoxyle; Leaves: c.t.=compound trifoliate; s.= simple; c.p.=compound paripinnate; c.i.=compound imparipinnate; c.bp.= compound bipinnate. ECM: ectomycorrhizal symbiosis; N-non; Y-Yes.

Table S9.2: Mean values of plant functional traits for geoxyles. Adm-*Adenodolichos mendesii*; Ast- *Annona stenophylla*; Brs- *Brachystegia russelliae*; Ces- *Cryptosepalum* sp nov; Cpt- *Combretum platypetalum*; Oar-*Ochna arenaria*; Pcp- *Parinari capensis*; Ptr- *Protea trichophylla*; Pzh- *Pygmaeothamnus zeyheri*; Rex- *Rhus exelliana*; Shl-*Syzygium guineense* subsp. *huillensis*; Uns- *Uapaca nitida* var. *suffrutescens*.

	Adm	Ast	Brs	Ces	Cpt	Oar	Pcp	Ptr	Pzh	Rex	Shl	Uns
SLA	95.43	80.52	93.60	109.43	70.16	58.72	72.76	44.63	63.64	59.12	65.12	78.87
LT	0.53	0.40	0.22	0.20	0.35	0.27	0.26	0.53	0.33	0.37	0.37	0.39
LA	189.80	99.71	45.14	4.42	143.12	101.31	31.77	86.74	69.96	93.69	170.47	104.10
LDMC	0.20	0.31	0.49	0.47	0.40	0.63	0.53	0.43	0.52	0.45	0.41	0.32
WD	0.51	0.54	0.70	0.62	0.71	0.68	0.55	0.63	0.71	*	0.53	0.62
LN	2.20	1.61	1.93	2.22	1.12	1.33	1.35	0.75	1.38	1.60	1.17	1.52
LC	48.72	48.55	52.73	46.26	48.50	52.30	45.51	51.48	50.30	49.66	51.78	49.05
LP	1.33	1.03	1.54	1.52	0.75	0.63	0.75	0.50	0.64	1.01	0.81	0.82
LCa	7.20	9.59	9.36	6.91	3.39	4.20	3.07	2.34	5.27	13.91	4.44	2.19
LMg	6.93	0.21	5.05	5.77	0.15	0.13	0.15	0.10	0.13	0.20	4.58	0.16
LK	3.99	9.71	2.20	2.23	9.70	10.46	9.10	10.30	10.06	9.93	2.24	9.81
C/N	22.31	30.47	27.46	21.27	43.90	39.54	33.77	68.85	37.71	31.46	44.76	32.22
N/P	16.82	15.77	12.60	14.82	14.90	25.50	17.96	14.92	22.30	15.92	14.52	18.56
WP	-1.50	-4.18	-10.6	-10.60	*	-11.70	-10.7	-4.40	-7.60	-2.30	-9.23	-6.50

*-Not measured

Table S9.3: Mean values of plant functional traits for trees. Baf- Burkea Africana; Bbk- Brachystegia bakeriana; Bbq- Baphia bequaertii; Blf- Brachystegia longifolia; Bsp- Brachystegia spiciformis; Cef- Cryptosepalum exfoliatum subsp. pseudotaxus; Czh- Combretum zeyheri; Eaf- Erytrophleum africanum; Jpn-Julbernardia paniculata; Maf- Monotes africanus; Pcr- Parinari curatelifolia; Png- Pterocarpus angolensis; Szt-Syzyzgium guineense subsp. macrocarpum; Unt- Uapaca nitida subsp. nitida.

	Baf	Bbk	Bbq	Blf	Bsp	Cef	Czh	Eaf	Jpn	Maf	Pcr	Png	Szt	Unt
SLA	71.54	76.58	77.26	98.98	89.15	95.74	100.07	82.46	86.98	82.97	54.66	101.46	67.47	80.43
LT	0.30	0.26	0.36	0.20	0.23	0.25	0.30	0.24	0.25	0.24	0.38	0.21	0.32	0.35
LA	90.84	61.39	32.71	209.25	156.82	7.13	156.92	57.86	190.61	114.50	126.46	145.49	165.23	142.11
LDMC	0.47	0.51	0.37	0.50	0.50	0.42	0.34	0.52	0.46	0.52	0.49	0.48	0.46	0.36
WD	0.62	0.55	0.66	0.58	0.53	0.54	0.65	0.60	0.51	0.55	0.47	0.51	0.55	0.49
LN	2.07	1.95	2.70	2.09	2.01	2.40	2.25	1.99	2.24	1.49	1.05	2.81	0.96	1.60
LC	54.74	54.13	50.90	54.50	49.13	52.00	50.50	54.35	52.41	48.67	40.86	50.91	51.58	49.76
LP	0.81	1.16	1.27	1.44	1.44	1.12	1.51	0.84	1.18	1.01	0.58	1.42	0.71	1.14
Lca	3.32	4.98	3.64	4.91	5.13	2.47	7.86	3.54	6.31	3.41	6.57	7.31	6.40	4.96
LMg	0.16	0.23	0.25	0.82	0.29	0.22	0.30	0.17	0.24	0.20	0.12	0.28	0.14	0.23
LK	10.95	10.83	10.18	10.90	9.83	10.40	10.10	10.87	10.48	9.73	8.17	10.18	10.32	9.95
C/N	26.69	28.01	19.14	26.16	24.45	21.80	22.53	27.44	23.48	32.87	39.17	18.19	54.27	31.17
N/P	25.48	16.82	21.33	14.60	14.05	21.88	15.09	23.82	19.39	14.79	20.08	18.10	13.40	14.22
WP	-10.9	-11.0	-8.59	-11.0	-10.5	-10.3	-10.1	-10.9	-10.8	-19.4	-6.98	-1.74	-5.30	-2.75

Table S9.4: One-way ANOVA comparing means of traits between Fabaceae species and non-Fabaceae species within each group (geoxyles and trees).

	Traits	Mean±se		ANOVA	
		Fabaceae	non-Fabaceae	F	p(same)
Geoxyles	SLA (cm²/g)	99.49 ± 2.77	65.95 ± 1.82	90.023	***
	LT (mm)	0.32 ± 0.04	0.37 ± 0.05	2.535	n.s.
	LA (cm²)	79.79 ± 21.43	100.10 ± 5.92	1.622	n.s.
	LDMC (mg/g)	0.39 ± 0.04	0.45 ± 0.02	2.758	n.s.
	WD (g/cm³)	0.61 ± 0.05	0.62 ± 0.01	0.129	n.s.
	LN (%)	2.12 ± 0.06	1.31 ± 0.04	92.687	***
	LC (%)	49.23 ± 0.74	49.68 ± 0.40	0.308	n.s.
	LP (mg/g)	1.46 ± 0.046	0.77 ± 0.03	131.610	***
	LCa (mg/g)	7.82 ± 0.44	5.38 ± 0.60	5.227	**
	LMg (mg/g)	5.92 ± 0.26	0.65 ± 0.24	142.330	***
	LK (mg/g)	2.81 ± 0.52	9.03 ± 0.37	76.401	***
	C:N ratio	23.68 ± 0.83	40.30 ± 1.79	27.620	***
	N:P ratio	14.75 ± 0.78	17.82 ± 0.79	4.419	**
	WP (bar)	-7.59 ± 1.15	-7.07 ± 0.50	0.228	n.s.
Trees	SLA (cm²/g)	86.69 ± 1.78	77.12 ± 3.50	7.277	***
	LT (mm)	0.26 ± 0.01	0.32 ± 0.01	25.753	***
	LA (cm²)	105.79 ± 10.86	141.05 ± 5.06	5.457	**
	LDMC (mg/g)	0.47 ± 0.01	0.43 ± 0.02	4.693	**
	WD (g/cm³)	0.57 ± 0.01	0.54 ± 0.014	3.361	n.s.
	LN (%)	2.25 ± 0.06	1.471 ± 0.10	56.535	***
	LC (%)	52.56 ± 0.43	48.27 ± 0.80	26.733	***
	LP (mg/g)	1.19 ± 0.04	0.99 ± 0.07	6.939	**
	LCa (mg/g)	4.63 ± 0.28	5.84 ± 0.41	6.195	**
	LMg (mg/g)	0.30 ± 0.07	0.20 ± 0.014	1.015	n.s.
	LK (mg/g)	10.50 ± 0.09	9.66 ± 0.20	26.733	***
	C:N ratio	23.93 ± 0.58	36.00 ± 2.24	43.132	***
	N:P ratio	19.50 ± 0.6	15.52 ± 0.58	17.825	***
	WP (bar)	-9.51 ± 0.4	-8.91 ± 1.19	0.324	n.s.

(***-highly significant; **-significant; n.s.-not significant, p<0.05).

Table S9.5: One-way ANOVA showing traits variation in ectomycorrhizal (ECM) species and species without this association (non-ECM).

	Traits	Mean±se		ANOVA	
		ECM	non-ECM	F	p(same)
Geoxyles	SLA (cm²/g)	93.97 ± 3.89	67.79 ± 2.23	34.14	***
	LT (mm)	0.27 ± 0.02	0.38 ± 0.01	15.53	***
	LA (cm²)	51.22 ± 11.25	109.62 ± 7.3	16.83	***
	LDMC (mg/g)	0.43 ± 0.02	0.43 ± 0.02	0.01	n.s.
	WD (g/cm³)	0.65 ± 0.04	0.61 ± 0.01	1.36	n.s.
	LN (%)	1.89 ± 0.09	1.39 ± 0.06	18.37	***
	LC (%)	49.35 ± 0.7	49.64 ± 0.4	0.14	n.s.
	LP (mg/g)	1.29 ± 0.09	0.83 ± 0.04	26.44	***
	LCa (mg/g)	6.15 ± 0.80	5.94 ± 0.60	0.04	n.s.
	LMg (mg/g)	3.66 ± 0.70	1.40 ± 0.40	8.74	***
	LK (mg/g)	4.75 ± 0.96	8.39 ± 0.46	13.98	***
	C:N ratio	26.98 ± 1.26	39.20 ± 1.96	12.24	***
	N:P ratio	15.33 ± 0.79	17.62 ± 0.81	2.39	n.s.
	WP (bar)	-9.25 ± 0.50	-6.45 ± 0.60	7.73	***
Trees	SLA (cm²/g)	87.26 ± 1.66	79.27 ± 3.02	5.39	***
	LT (mm)	0.25 ± 0.01	0.30 ± 0.01	14.39	***
	LA (cm²)	125.97 ± 12.25	110.79 ± 8.52	1.04	n.s.
	LDMC (mg/g)	0.47 ± 0.01	0.45 ± 0.01	1.60	n.s.
	WD (g/cm³)	0.54 ± 0.01	0.58 ± 0.01	8.31	***
	LN (%)	1.97 ± 0.06	1.98 ± 0.12	0.00	n.s.
	LC (%)	51.51 ± 0.47	50.55 ± 0.81	1.08	n.s.
	LP (mg/g)	1.21 ± 0.03	1.02 ± 0.06	7.49	***
	LCa (mg/g)	4.60 ± 0.27	5.52 ± 0.39	3.78	n.s.
	LMg (mg/g)	0.32 ± 0.09	0.20 ± 0.01	1.52	n.s.
	LK (mg/g)	10.30 ± 0.09	10.11 ± 0.20	1.08	n.s.
	C:N ratio	26.85 ± 0.7	29.63 ± 2.10	1.56	n.s.
	N:P ratio	16.54 ± 0.57	19.61 ± 0.75	10.65	***
	WP (bar)	-10.80 ± 0.77	-7.78 ± 0.54	10.26	***

(***-highly significant; n.s.-not significant, p<0.05).

Declaration on oath

I hereby declare, on oath, that I have written the presented dissertation by my own and have not used other than the acknowledged resources and aids.

Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, der 27.09.2022

Paulina Meller