Analysis of vegetation and plant diversity patterns in the Okavango Basin at different spatial scales

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Integration of field based methods, remote sensing information and ecological modelling

Dissertation

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(4) Revermann, R. & Finckh, M. (2013) Cusseque - Microclimate. *Biodiversity and Ecology*, **5**, 47–50.

(5) Finckh, M., Revermann, R. & Aidar, M.P.M. (2016) Climate refugees going underground – a response to Maurin et al. (2014). *New Phytologist*, **209**, 904–909.

(6) Revermann, R., Finckh, M., Stellmes, M., Strohbach, B., Frantz, D. & Oldeland, J. (2016) Linking land surface phenology and vegetation-plot databases to model terrestrial plant α-diversity of the Okavango Basin. *Remote Sensing*, **8**, 370.

(7) Revermann, R., Wallenfang, J., Oldeland, J. & Finckh, M. (2016) Species richness and evenness respond to diverging land use patterns – a cross border study from dry tropical woodlands in southern Africa. *Journal of African Ecology*, doi: 10.1111/aje.12333.

(8) 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.

To increase the readability of the thesis, all figures, tables and supporting information have been renumbered in a consecutive manner. Moreover, one combined reference section is provided and one section containing all supporting information is given at the end of the thesis.

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Summary

The Okavango Basin is situated in south central Africa and shared among the three countries of Angola, Namibia and Botswana. The Okavango River has its source on the sub-humid Angolan Central Plateau where 95% of the runoff is generated. The river terminates in the endorheic Okavango Delta in the Kalahari Desert, forming a world renowned wetland ecosystem highly dependent on the annual inflow of water of the Okavango River. However, the upper reaches of the river in the Angolan Miombo belt are highly understudied; ecological data and understanding of ecosystem functioning are lacking. At the same time, the socio-ecological systems of the upper Basin are subject to rapid transformations and are regarded as a hot spot of accelerating land use change. However, the largely subsistence based economy of the rural communities is highly dependent on the continued delivery of a wide range of ecosystem services. Thus, the presented thesis aims to provide scientific data to contribute to a sustainable development and to safeguard plant diversity in the Okavango Basin.

The thesis focuses on three general aspects: a) the analysis of plant species composition and diversity and their underlying environmental drivers, b) the development of methodological tools to combine field data and remote sensing information to provide spatially explicit data, c) the investigation of the impact of land use on vegetation and plant diversity. The thesis hence combines methods of traditional vegetation ecology with the application of remote sensing information and the development of innovative ecological modelling approaches to upscale the knowledge gained in field studies at the local scale to the scale of the Okavango Basin.

The three core aspects are covered in six articles published in peer-reviewed journals and two submitted manuscripts. Moreover, summaries of the results from four co-author papers are presented and discussed in the synthesis chapter. Additionally, first results and a preliminary vegetation map of the Okavango Basin were published in a series of several short papers in a special issue of *Biodiversity and Ecology*. These articles are presented as pdf-files in the electronic appendix of the thesis. In the following, the main achievements of the thesis are summarised.

The thesis presented a comprehensive and quantitative account of the vegetation composition and the plant diversity of the Angolan part of the Okavango Basin for the first time. The established vegetation-plot database contains standardised plots of all common vegetation types of the study area ranging from Miombo woodlands and

forests, *Baikiaea* woodlands, and geoxylic grasslands to the wetlands of the Angolan Central Plateau (**Chapter 2**). During the vegetation survey carried out in the framework of the thesis approximately over 2,600 plant specimens were collected and deposited in herbaria of the host countries (Lubango, LUBA; Windhoek, WIND) and a new collection on plants from southeast Angola was established at the Herbarium Hamburgense (HBG). As reference for future studies, a check list of the woody species of the Cusseque study site was produced (**Chapter 2**). Furthermore, the vegetation classifications in **Chapter 3** and **7** contain detailed species lists. Thus, solid foundations for future work on the vegetation of southeast Angola have been laid and made available. As such, the vegetation plots were fed into the global vegetation-plot database sPlot and will be used in regional vegetation mapping of south central Africa within the SASSCAL project.

The thesis provided a first classification scheme of the woody vegetation of the Cubango Basin. One vegetation type, the *Combretum celastroides-Baikiaea plurijuga* community represents a unique vegetation type found only in the Cuando Cubango Province of Angola and was described for the first time in this thesis. Soil and other environmental conditions of the derived vegetation communities were quantified and compared among the different communities (**Chapter 3**).

A network of micro-climatic measurement stations was installed on the Angolan Central Plateau and air and soil temperatures were recorded over three years. The measurements provided insights in the role of night frost as a driving factor of current vegetation patterns and also identified frost as potential evolutionary driver of the development of geoxylic suffrutices in the Zambezian phytoregion (**Chapter 4**).

An ecological modelling framework was developed to provide spatially explicit data on vascular plant α-diversity of the Okavango Basin. The approach combined the information contained in the vegetation-plot database created during this thesis with landscape phenology metrics derived from moderate resolution satellite imagery (**Chapter 5**). It was shown that models using landscape phenology metrics produced more realistic maps and were better capable of depicting azonal vegetation types than models including climatic predictors. Instead, climate models predicted belts of homogenous plant α-diversity and ignored landscape level heterogeneity.

Two case studies investigated the impact of land use on vegetation and plant diversity (**Chapter 6** and **7)**. The unique situation of two contrasting land use intensities paired with similar physio-geographic settings and traditional land use practices along the Angolan and Namibian border allowed to assess the impact of diffuse, i.e. spatially not explicit

land use, on plant diversity. The cross border study revealed a negative impact of diffuse land use on plant diversity especially affecting woody species (**Chapter 6**).

In times of increasing shortage of agricultural land and increasing demand of agricultural products it is of high importance to understand how longer duration of usage for cropping in shifting cultivation affects diversity and regeneration of vegetation. The study in **Chapter 7** showed that nutrient contents are affected negatively by prolonged usage and that fallows with shorter time spans of land usage exhibit species composition more similar to the original state than fallows with longer spans of usage.

In **Chapter 8** the results of the preceding chapters are discussed in a wider context drawing also on knowledge gained in four co-authored studies and providing first insights from two manuscripts that are currently in preparation. These studies investigated the impact of road infrastructure on spatial dynamics of deforestation using chronosequences of satellite imagery, analysed the spatiotemporal patterns of the fire regime in the Okavango Basin and modelled the potential and realised distribution of the important timber species *Pterocarpus angolensis* DC. One highlight of the thesis was the discovery of a hitherto unknown grass species. Its placement in the subfamily of the Chloridoideae could be shown based on the anatomy and on molecular data. Further investigations will show weather it needs to be placed in a new genus or should be incorporated in an existing one.

In conclusion, the thesis filled important data gaps and produced new knowledge on vegetation composition and diversity patterns in southeast Angola. In combination with the studies on the impact of land use and the provision of spatial data the presented thesis hopes to make a strong contribution to allow spatial planning for a sustainable future of the Okavango Basin.

Zusammenfassung

Das Einzugsgebiet des Okavango liegt in Süd-Zentral-Afrika, in den Staaten Angola, Namibia und Botsuana. Der Okavango entspringt auf dem subhumiden, zentralen Hochland Angolas, wo 95% des Abflusses generiert werden. Der Fluss endet in dem endorheischen Okavango Delta, in der Kalahari Wüste. Das Ökosystem dieses weltbekannten Feuchtgebiets ist hochgradig abhängig vom jährlichen Zufluss des Wassers aus dem Okavango. Trotz seiner Bedeutung ist der Oberlauf des Okavango im Angolanischen Miombo Gürtel kaum erforscht. Es mangelt sowohl an ökologischen Daten, als auch an konkreten Erkenntnissen über die Funktionsweise des Ökosystems. Gleichzeitig unterliegen die sozioökologischen Systeme des Oberlaufs raschen Transformationsprozessen und werden als ‚hot spot' eines sich beschleunigenden Landnutzungswandels angesehen. Die Ökonomie im ländlichen Raum basiert vor allem auf Subsistenzwirtschaft und hängt stark von der kontinuierlichen Bereitstellung einer großen Zahl vielfältiger Ökosystemdienstleistungen ab. Die vorliegende Dissertation liefert essenzielle, wissenschaftliche Daten, die wesentlich zu einer nachhaltigen Entwicklung des Okavango Einzugsgebiets und zum Schutz seiner pflanzlichen Diversität beitragen.

Die Arbeit konzentriert sich auf drei Aspekte: a) die Analyse von Artenzusammensetzung und Diversität der Vegetation im Okavango Einzugsgebiet und den steuernden Umweltfaktoren, b) die Entwicklung von methodischen Werkzeugen um die im Feld gewonnenen Daten mit Fernerkundungsdaten zu kombinieren und räumlich explizite Daten zu generieren, c) die Erforschung des Einflusses der Landnutzung auf die Vegetation und auf die pflanzliche Diversität. Die Dissertation greift dafür auf den Methodenschatz der klassischen Vegetationsökologie zurück und kombiniert diesen mit Techniken der Fernerkundung und innovativen Ansätze ökologischer Modellierung. So wurde es möglich, die in Feldstudien erlangten Erkenntnisse von der lokalen Skala auf die Skala des Okavango Einzugsgebiets zu übertragen.

Die drei Kernaspekte werden in sechs Artikeln, die in wissenschaftlichen Fachzeitschriften mit "peer-review" Verfahren veröffentlicht wurden und in zwei zur Veröffentlichung eingereichten Manuskripten behandelt. Darüber hinaus werden die Ergebnisse von vier weiteren Artikeln, an denen ich als Coautor beteiligt war, in dem Synthese Kapitel

vorgestellt und diskutiert. Außerdem wurden erste Ergebnisse und eine vorläufige Vegetationskarte des Okavango Einzugsgebietes in einer Serie von mehreren kurzen Artikeln in einer Sonderausgabe von *Biodiversity and Ecology* veröffentlicht. Diese Artikel sind im elektronischen Anhang der Arbeit enthalten. Im Folgenden werden die wichtigsten Erfolge der Arbeit zusammengefasst und vorgestellt.

Die Dissertation präsentiert zum ersten Mal eine umfassende und quantitative Analyse der Artenzusammensetzung, der Vegetation und der pflanzlichen Diversität im angolanischen Teil des Okavango Einzugsgebiets. Die erstellte Vegetationsdatenbank enthält standardisierte Vegetationsaufnahmen aller häufigen Vegetationstypen des Untersuchungsraumes und umfasst u.a. die Miombo Wäldern, die *Baikiaea* Baumsavannen sowie die Zwergstrauch-Grasländer und tropischen Feuchtgebiete des Angolanischen Zentralplateaus (**Kapitel 2**). Während der Vegetationskartierung, die im Rahmen der Dissertation durchgeführt wurde, wurden über 2600 Herbarbelege gesammelt. Diese wurden den Herbarien der Herkunftsländer zur Verfügung gestellt (Lubango, LUBA; Windhoek, WIND). Mit den Doubletten wurde eine neue Sammlung von Pflanzen aus dem Südosten Angolas am Herbarium Hamburgense (HBG) aufgebaut. Als Referenz für zukünftige Arbeiten wurde eine „Checkliste" der holzigen Arten des Untersuchungsgebietes Cusseque zur Veröffentlichung eingereicht (**Kapitel 2**). Außerdem enthalten die Vegetationsklassifikationen in **Kapitel 3** und **7** weitere detaillierte Artenlisten. Diese Daten bilden eine solide und wertvolle Basis für weitere Forschung zu Ökologie und Vegetation im Südosten Angolas. Alle Daten der Vegetationsaufnahmen wurden der globalen Datenbank für Vegetationsaufnahmen, sPlot, hinzugefügt und sind damit zugänglich für die zukünftige Forschung. Die Vegetationsaufnahmen werden weitere Verwendung in der im Rahmen von SASSCAL durchgeführten Vegetationskartierung Südzentral Afrikas finden.

Im Zuge dieser Arbeit wurde erstmalig eine Klassifikation der holzigen Vegetation des Cubango Einzugsgebietes erstellt. In diesem Zusammenhang wurde die Pflanzengemeinschaft *Combretum celastroides-Baikiaea plurijuga* erstmals beschrieben, welcher ausschließlich in der Provinz Cuando Cubango vorkommt. Die Boden- und weitere Umwelteigenschaften der abgeleiteten Pflanzengemeinschaften wurden analysiert und zwischen den Gemeinschaften verglichen (**Kapitel 3**).

Ein Netzwerk von mikroklimatischen Messstationen wurde auf dem Angolanischen Zentralplateau eingerichtet. Dort wurden über den Zeitraum von drei Jahren Luft- und Bodentemperatur gemessen. Aufgrund dieser Messungen konnte die zentrale Rolle von

Nachtfrösten in tropischen Hochländern als wichtiger, steuernder Faktor der rezenten Vegetationsmuster gezeigt werden. Darüber hinaus lieferten die Messungen starke Hinweise dafür, dass Frost ein möglicher Treiber der Evolution der für die Zambesiche Phytoregion typischen Zwergsträucher, den sogenannten „geoxylic suffrutices", gewesen sein könnte (**Kapitel 4**).

Im Rahmen der Dissertation wurde ein ökologischer Modellierungsansatz entwickelt, der die Informationen aus der Vegetationsdatenbank mit sog. „landscape phenology metrics" kombiniert. Diese beschreiben die Entwicklung der Vegetation im Jahresgang und wurden aus dichten Zeitreihen von Satellitenbildern abgeleitet. Auf diese Weise konnten Karten der pflanzlichen α-Diversität für das Okavango Einzugsgebiets erstellt werden. Die Modelle, die „landscape phenology metrics" als Prädiktoren nutzten, produzierten realistischere Karten und bildeten azonale Vegetationstypen besser ab als Modelle, die klimatische Prädiktoren beinhalteten. Die Modelle mit klimatischen Prädiktoren sagten Gürtel mit einheitlicher α-Diversität vorher und ignorierten die Heterogenität der Landschaft (**Kapitel 5**).

In zwei Fallstudien wurde der Einfluss von Landnutzung auf die Vegetation und auf die pflanzliche Diversität erforscht (**Kapitel 6** und **7**). Die besondere Situation von zwei gegensätzlichen Landnutzungsintensitäten gepaart mit ähnlichen pyhsio-geographischen Voraussetzungen und traditionellen Landnutzungspraktiken entlang der angolanisch-namibianischen Grenze erlaubten den Einfluss von diffuser, also räumlich nicht expliziter, Landnutzung, auf die pflanzliche Diversität zu erforschen. Der Vergleich der beiden Seiten der Grenze zeigte, dass diffuse Landnutzung einen negativen Effekt auf die Diversität der Gefäßpflanzen hat, und dass insbesondere die holzigen Arten davon betroffen waren (**Kapitel 6**).

Vor dem Hintergrund von zunehmendem Mangel an ackerbaulicher Nutzfläche und steigendem Bedarf an ackerbaulichen Produkten ist es besonders wichtig zu verstehen, wie längere ackerbauliche Nutzungsdauer von Feldern im Wanderfeldbau die Diversität und die Regeneration der Vegetation beeinflussen. Die Studie in **Kapitel 7** zeigt, dass Nährstoffgehalte negativ durch längere Nutzung beeinflusst werden. Außerdem konnte gezeigt werden, dass Brachen mit einer kürzeren Dauer ackerbaulicher Nutzung eine Artenzusammensetzung zeigen, die dem ursprünglichen Zustand näher ist als bei Brachen, die länger genutzt wurden.

In **Kapitel 8** werden die Ergebnisse der vorangegangenen Kapitel im Gesamtkontext diskutiert. In diese Diskussion fließen auch die Erkenntnisse aus vier weiteren Studien ein,

die ich als Coautor mitverfasst habe sowie auch Ergebnisse von zwei Manuskripten, die derzeit in Vorbereitung sind. Diese Studien untersuchten a) den Einfluss von Straßeninfrastruktur auf die räumlichen Dynamiken von Entwaldung, basierend auf Chronosequenzen von Satellitenbildern, b) die räumlichen und zeitlichen Muster des Feuer Regimes im Okavango Becken und c) die potenzielle und realisierte Verbreitung der ökonomisch wichtigen Baumart *Pterocarpus angolensis* DC anhand von Habitatmodellen. Ein Höhepunkt der Arbeit war außerdem die Entdeckung einer bislang unbekannten Gras Art. Eine Einordnung in die Unterfamilie der Chloridoideae war mittels anatomischer Untersuchungen und aufgrund von molekularen Daten möglich. Weitere Untersuchungen werden zeigen, ob die Art in eine neue Gattung eingeordnet werden muss oder ob sie in eine bereits existierende eingegliedert werden kann.

Abschließend lässt sich sagen, dass die vorliegende Dissertation wichtige Datenlücken geschlossen hat und viele neue Erkenntnisse über die Vegetationszusammensetzung und die Diversitätsmuster in Südost Angola erbracht hat. In Kombination mit den Studien zum Einfluss der Landnutzung und der Bereitstellung von räumlich expliziten Daten hat die vorliegende Arbeit einen wichtigen Beitrag geleistet, um die räumliche Planung für eine nachhaltige Zukunft des Okavango Einzugsgebietes zu ermöglichen.

Resumo

A Bacia do Cubango/Okavango situa-se à sul da África Central e é partilhada entre três países Angola, Namíbia e Botswana. O rio Cubango/Okavango tem a sua nascente na região sub-húmida do Planalto Central Angolano, onde 95% de escoamento são gerados. O rio termina no Delta endorreico do Okavango no Deserto do Kalahari, formando um ecossistema de zonas úmidas altamente dependente no fluxo anual de água do rio Cubango/Okavango. Contudo, o curso superior do rio na faixa do Miombo Angolano é pouco estudado; dados ecológicos e a compreensão do funcionamento dos ecossistemas estão em falta. Ao mesmo tempo, o sistema socio-ecológico da parte superior da bacia estão sujeitas à transformações rápidas e são considerados como um hotspot de alterações aceleradas de uso de terras. Contudo, a economia das comunidades rurais, em grande parte de subsistência, é altamente dependente do fornecimento contínuo de uma grande variedade de serviços de ecossistemas.

A tese centra-se em três aspectos gerais: a) Analizar a composição e diversidade de espécies e seus factores ambientais subjacentes, b) O desenvolvimento de ferramentas metodológicas para combinar dados de campo com a informação de deteção remota para proporcionar dados espacialmente explícitos, c) A investigação do impacto do uso de terras na vegetação e na diversidade de plantas. A tese consequentemente combina métodos de ecologia vegetal tradicionais com a aplicação de informação de deteção remota e o desenvolvimento de abordagens inovativas de modelação ecológica para tranferir o conhecimento ganho em estudos de campo a escala local para a escala da Bacia do Cubango/Cuvango.

Os três aspectos principais são abordados em seis artigos publicados em revistas e jornais e dois manuscritos submetidos. Além disso, os resumos dos resultados duns quatro artigos em co-autoria são apresentados e discutidos no capítuto síntese. Adicionalmente, os primeiros resultados e o mapa preliminar de vegetação da Bacia do Okavango foram publicados numa série de vários artigos curtos na edição especial do Jornal *Biodiversity and Ecology*. Estes artigos são apresentados como ficheiros-pdf no apêndice eletrônico da tese. Em seguida, os principais realizações da tese são resumidas.

A tese apresenta em primeira mão uma abordagem abrangente e quantitativa da vegetação e diversidade de plantas da parte Angolana da Bacia do Cubango/Kuvango. A base de dados estabelecida de parcelas de vegetação contém parcelas padronizadas de

todos tipos de vegetação comuns da área de estudo, que vão desde as savanas de Miombo e florestas, savanas de *Baikiaea*, e Anharas de ongote às zonas úmidas do planalto central de Angola (**Capítulo 2**). Durante o levantamento da vegetação levado a cabo no contexto da tese mais de 2600 espécimes de plants foram colhidas e depositadas nos herbários dos países acolhedores (Lubango, LUBA; Windhoeck, WIND) e uma nova coleção de plantas do sudoeste de Angola foi estabelecida no Herbário Hamburgense (HGB). Como referência para futuros estudos, uma checklist de espécies lenhosas da área de estudo do Cusseque foi produzida (**Capítulo 2**). Além disso, a classificação da vegetação no **Capítulo 3** e **7** contém listas de espécies detalhadas. Assim, bases sólidas para futuros estudos sobre a vegetação do sudoeste de Angola foram estabelecidas e estão disponibilizadas. Como tal, as parcelas de vegetação foram incluidas na base de dados global para parcelas de vegetação sPlot e serão usadas no mapeamento da vegetação regional do sul da África central no projecto SASSCAL.

A tese fornece o primeiro esquema de classificação da vegetação lenhosa da Bacia do Cubango/Kuvango. Um tipo de vegetação, a comunidade de *Combretum celastroides-Baikiaea plurijuga* representa um tipo único de vegetação encontrado só na Província do Cuando Cubango de Angola e foi descrita pela primeira vez nesta tese. O solo e outras condições ambientais derivado das comunidades vegetais foram quantificados e comparados entre as diferentes comunidades (**Capítulo 3**).

Uma rede de estações de medidas micro-climáticas foram instaladas no Planalto Central de Angola e as temperaturas do solo e do ar foram registadas ao longo de três anos. As medidas fornecem informações sobre as geadas nocturnas como factores determinantes do padrão da vegetação e também identifica as geadas como potencial factor evolucionário do desenvolvimento das 'geoxylic suffrutices' na phytoregião Zambeziaca (**Capítulo 4**).

Uma estrutura de modelação ecológica foi desenvolvida para fornecer dados espacialmente explícitos da α-diversidade das plantas vasculares da Bacia do Cubango/Okavango. A abordagem combina a informação contida na base de dados da vegetação criada durante a tese com "landscape phenology metrics" derivada das imagens de satélites da resolução moderada (**Capítulo 5).** Demonstrou-se que modelos que usam landscape phenology metrics produzem mapas mais realísticos e são mais capazes de descrever tipos de vegetação azonal em relação aos modelos que incluem predictores climáticos. Em vez disso, os modelos climáticos prevêem faixas homogéneas de α-diversidade de plantas e ignoram o nível de heterogeneidade da paisagem.

Dois estudos de caso investigaram o impacto do uso do solo na vegetação e diversidade de plantas (**Capítulo 6** e **7**). A situação particular em que dois tipos contrastantes de intensidade de uso de terras pareados com similares cenários fisico-geografico e práticas tradicionais de uso da terra ao longo da fronteira Angolana-Namibiana permitiu investigar o impacto difuso, i.e. especialmente uso da terra não explícito, na diversidade de plantas. O estudo transfonteiriço revelou um impacto negativo do uso de terras difuso na diversidade de plantas, especialmente afectando as espécies lenhosas (**Capítulo 6**).

Em tempo de crescente excassez de terras agrícolas e o aumento da procura de produtos agrícolas é de elevada importância entender como a longa duração da utilização dos solos para cultivo na agricultura itinerante afeta a diversidade e regeneração da vegetação. O estudo no **Capítulo 7** mostrou que o teor de nutrientes é negativamente afetados pelo uso prolongado e que os pousios com períodos de curtos intervalos de tempo de uso exibem uma composição de espécies mais similar ao estado original em relação aos pusios com maior período de uso.

No **Capítulo 8** os resultados dos capítulos precedentes são discutidos num contexto mais amplo e do contexto sobre os conhecimentos adquiridos nos quatro estudos em co-autoria e dos dois manuscritos que estão actualmente em preparação. Estes estudos investigaram o impacto das infraestruturas das estradas na dinâmica espacial da desflorestação, usando uma cronosequência de imagens de satélites, analizando os padrões de espaço-temporal do regime de fogo na Bacia do Cubango/Okavango e modelado o potencial e realizada distribuição de *Pterocarpus angolensis* DC, uma espécie das árvores com alto valor economica. Um destaque da tese foi a descoberta de uma nova espécie de gramínea. Mostrou-se que a espécie pertenece á subfamília Chloridoideae basado na anatomia e nos dados moleculares. Novas investigações mostrarão sim a espécie deve ser colocada num novo género ou ser incorporada num género já existente.

Em conclusão, a tese preencheu lacunas de dados importantes e produziu novo conhecimento sobre a composição da vegetação e padrões de diversidade no sudoeste de Angola. Em combinação com os estudos sobre o impacto do uso das terras e o fornecimento de dados espaciais, a tese apresentada espera fazer uma forte contribuição para permitir o planeamento espacial para um futuro sustentável da Bacia do Okavango.

CHAPTER 1

General Introduction

Rasmus Revermann

Rational of the study

Globally, sustainable land management becomes paramount for safeguarding human livelihoods and to ensure continued ecosystem functioning and the delivery of ecosystem services. However, for many regions of the world adequate scientific data on the impact of land use practices on natural resources, spatial information on ecosystem properties, species distributions and diversity patterns are missing but urgently needed for sustainable land use planning and management.

The Okavango Basin is situated in south-central Africa and shared by the countries of Angola, Namibia and Botswana (Figure 1). It is a hotspot of accelerating change and looming land use conflicts. At the same time, the Basin harbours a rich plant and animal diversity and its ecosystems are, to a large extent, still in (near) natural state. Yet, there are high indices of poverty and underdevelopment, e.g. a high degree of illiteracy or limited access to clean water (Pröpper et al. 2015). Thus, there is an urgent need for a socio-economic development accompanied with sustainable land management. However, data on the socio-ecological system are scarce and ecological system understanding is limited. This is especially true for the Angolan part of the Basin where almost four decades of civil war lead to a stagnation of development. The armed conflict started already in the years preceding independence in 1975 and lasted, with short interludes, until 2002 (Pycroft 1994; Windeler 2008). This impeded not only socio-economic development but also any kind of research in the country and, therefore, the most recent scientific studies often date back to the pre-independence era (Huntley & Matos 1994).

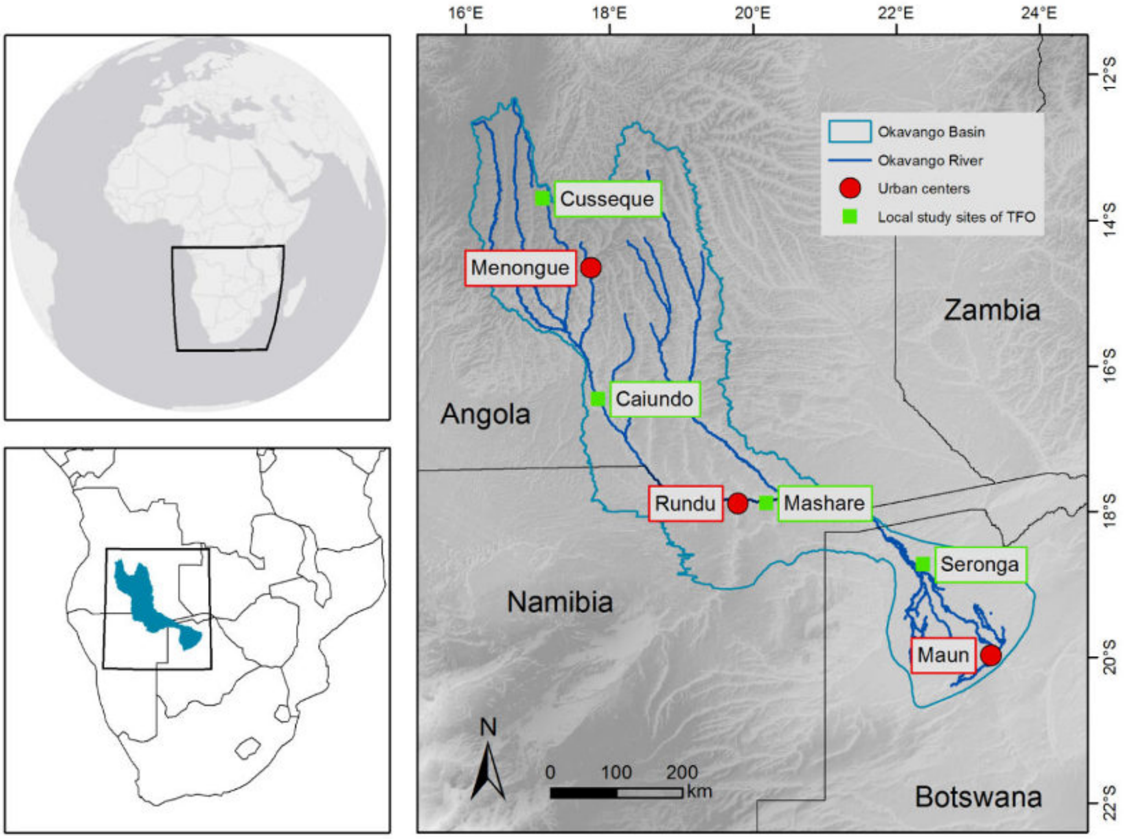

Figure 1 Location of the Okavango Basin in southern Africa and the location of the local study sites of The Future Okavango Project (TFO). The delimitation of the Okavango Basin follows the definition of TFO (Wehberg & Weinzierl 2013). It comprises the area of the active catchment, the Delta in Botswana and the hinterland in the Kavango Regions in Namibia that is closely linked to the socio-ecological system of the Okavango River. The background shows the relief based on the digital elevation model SRTM at 90 m-resolution (Jarvis et al. 2008).

Since the ceasing of turmoil at the turn of the millennium, Angola has started to recover. Fuelled by high state revenues from the petroleum sector and backed by Chinese credit lines, the country has strongly invested in infrastructure projects (Power 2012). Concurrently, global drivers exert more and more influence on the development in southcentral Africa. As such, Gasparri et al. (2015) outline the potential new 'soybean production frontier' evolving in the dry forest ecosystems of southern Africa. They draw parallels to the past development in South America and forecast detrimental effects for the natural environment. Laurance et al. (2015) sketch the environmental costs of new development corridors criss-crossing the African continent, also in the Okavango region. They come to the conclusion that economic benefits may be low but will come at a high price for the natural environment. Foreign direct investment may foster economic development but is often coupled with a multitude of conditions and in some cases entailing the expropriation of land of local communities as shown by Power (2012) for Angola. One example of how new agro-industrial projects may transform the near natural ecosystems of the Okavango Basin in the near future is the "Longa rice scheme" established on the floodplains of the Longa River in 2013 (Pröpper et al. 2015).

As a regional phenomenon, deforestation and degradation of forests in southern Africa is up to now primarily driven by the expansion of agricultural land by smallholders and by the production of charcoal. In all countries with dry tropical woodlands in southern Africa the growing demands for energy of a steadily increasing urban population largely contribute to deforestation or forest degradation (Kutsch et al. 2011). Cabral et al. (2010) observed a slight recovery of the Miombo woodlands in the Province of Huambo on the Angolan Central Plateau during the war torn 1990ies. With the end of civil war in the following decade they detected again advancing deforestation, especially around the urban centres. As evident from the study on global deforestation rates by Hansen et al. (2013) the frontier of deforestation is advancing on the rural areas approaching the Okavango Basin from a north-western direction (Figure 2).

Although southeast Angola has always been considered as "terras do fim do mundo" ('land at the end of the world', Gois 1973 cited in Bereslawski 1997) even here rapid changes in rural areas are evident. Pröpper et al. (2013) nicely portrayed the impact of rapid global change on urban and rural societies in the Namibian Kavango Region. Transition from traditional subsistent economy to modern consumerism changes aspirations and economic strategies, thus thoroughly changing rural and urban societies alike. In Angola, a similar process has started in recent years: new tar roads facilitate the exploitation and trading of natural resources, installation of cell phone network and the availability of cash transform the Angolan (rural) society at a high pace.

Facing these rapid transformations, adequate socio-economic and ecological data are essential for developing sustainable land management strategies. This thesis aimed to make a contribution from the perspective of vegetation ecology in providing relevant data on vegetation composition and plant diversity patterns, as well as providing analyses of their environmental drivers. Furthermore, the impact of land use on the vegetation and the regeneration after land used had ceased was investigated. Modern ecological research methods were combined using studies on local field sites, regional surveys and ecological modelling to enable system understanding and the provision of spatial data. The presented work focused on the Angolan part of the Okavango Basin as here the largest changes of land use are projected and almost no current data exist on vegetation composition and plant diversity.

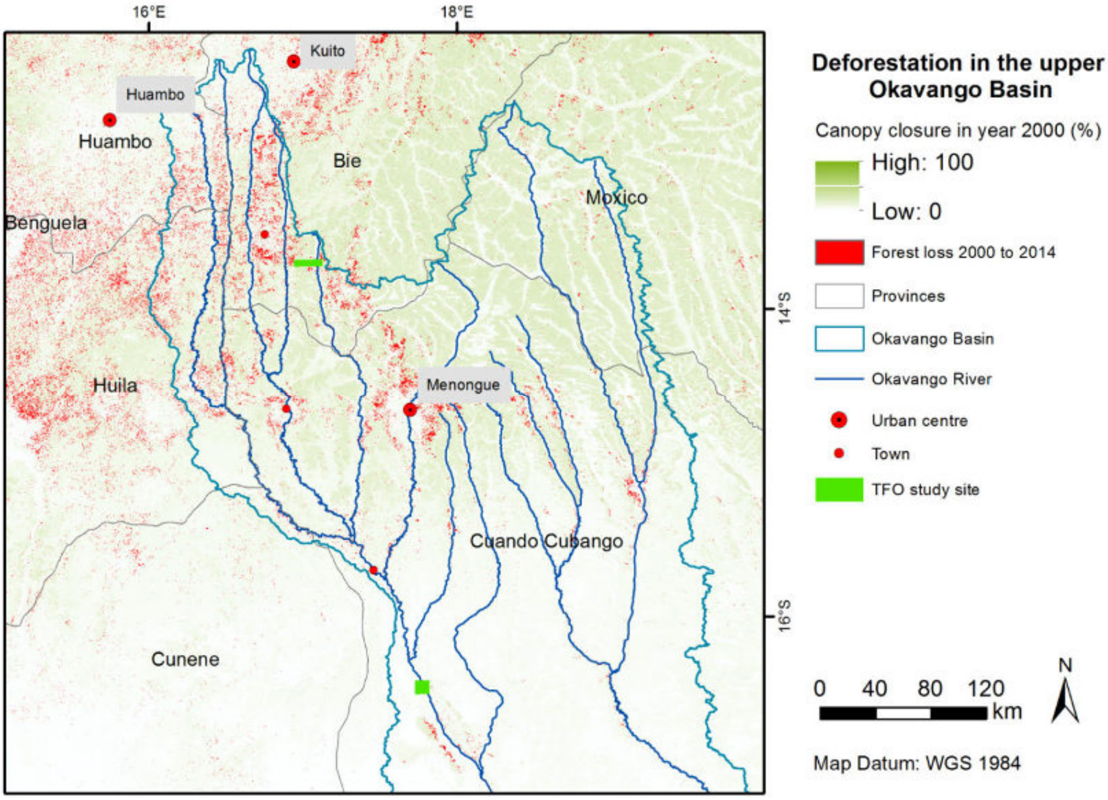

Figure 2 Deforestation on the Angolan Central Plateau in the time period 2000 to 2014 according to Hansen et al. (2013, available online: http://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.2.html (accessed on 04 May 2016). Note that the *Baikiaea* woodlands of the southern parts of the Okavango Basin did not fall under the forest definition applied by Hansen et al. (2013), except for some very dense tracts south of the TFO core site Caiundo.

The Future Okavango project (TFO)

The research was carried out within the framework of The Future Okavango project (TFO). TFO was embedded in the global program on 'Sustainable Land management' (LaMa) by the German Federal Ministry of Education and Research (BMBF) under the umbrella initiative 'Research for sustainable development' (FoNa). Aim of TFO was to gather scientific data to support an integrated transboundary management of the Okavango Basin and to develop visions for sustainable use of natural resources. A multidisciplinary team of scientist analysed the impact of land use on natural resources from multiple perspectives. An important part of the research agenda was also to close knowledge gaps and to understand ecosystem functioning within the Okavango Basin (Jürgens 2013). First results on the current status of the socio-ecological system were presented in a special volume of Biodiversity and Ecology, Vol. 5 (Oldeland et al. 2013). Finally, scenarios for future land use options were developed (Pröpper et al. 2015).

Study area

Physio-geographic setting of the Okavango Basin

The following section provides an overview of the socio-ecological system of the Okavango Basin with a focus on data relevant for analyses of vegetation and process of change influencing vegetation. For this purpose I will make use of the results obtained by various researchers working in the TFO project.

The Okavango River originates on the Angolan Central Plateau. From there, the river flows south-eastwards forming the border between the countries Angola and Namibia, crossing the Caprivi Strip in Namibia and finally entering Botswana where it forms a large, endorheic delta in the Kalahari desert. While the Okavango Delta itself is a world famous tourist destination, acknowledged as ecologically highly important ecosystem and listed as world heritage site, the upper reaches of the river where the vast majority of the runoff is generated remains under studied.

The delimitation of the Okavango Basin used in this study follows the definition of The Future Okavango project (TFO, see below). In total the Basin covers an area of 228,106 km^2. The area actively contributing to the runoff generation accounts for 170,029 km^2 and the delta for 39,476 km^2 (Wehberg & Weinzierl 2013).

Climate

The climate is characterised by two opposing gradients of temperature and precipitation. Mean annual temperature is lowest on the Angolan Central Plateau with 18°C in the extreme northwest and highest in the Delta reaching 24°C. Inversely, mean annual precipitation decreases from the northwest with an annual precipitation of approximately 1400 mm in the north to less than 500 mm in the in the southeast (Figure 3a and b, Weber 2013a). In the sub-humid upper reaches rainfall concentrates on the months October to April (Weber 2013b). The length of the vegetation period steadily decreases southwards and in Seronga, located at the northern margin of the delta, it lasts from December to March only (Weber 2013c). From 1950 to 2009 there was a high inter-annual variability in mean annual precipitation and neither a positive nor negative trend was observed during this time period. In contrast, mean annual temperature showed a low variability and an

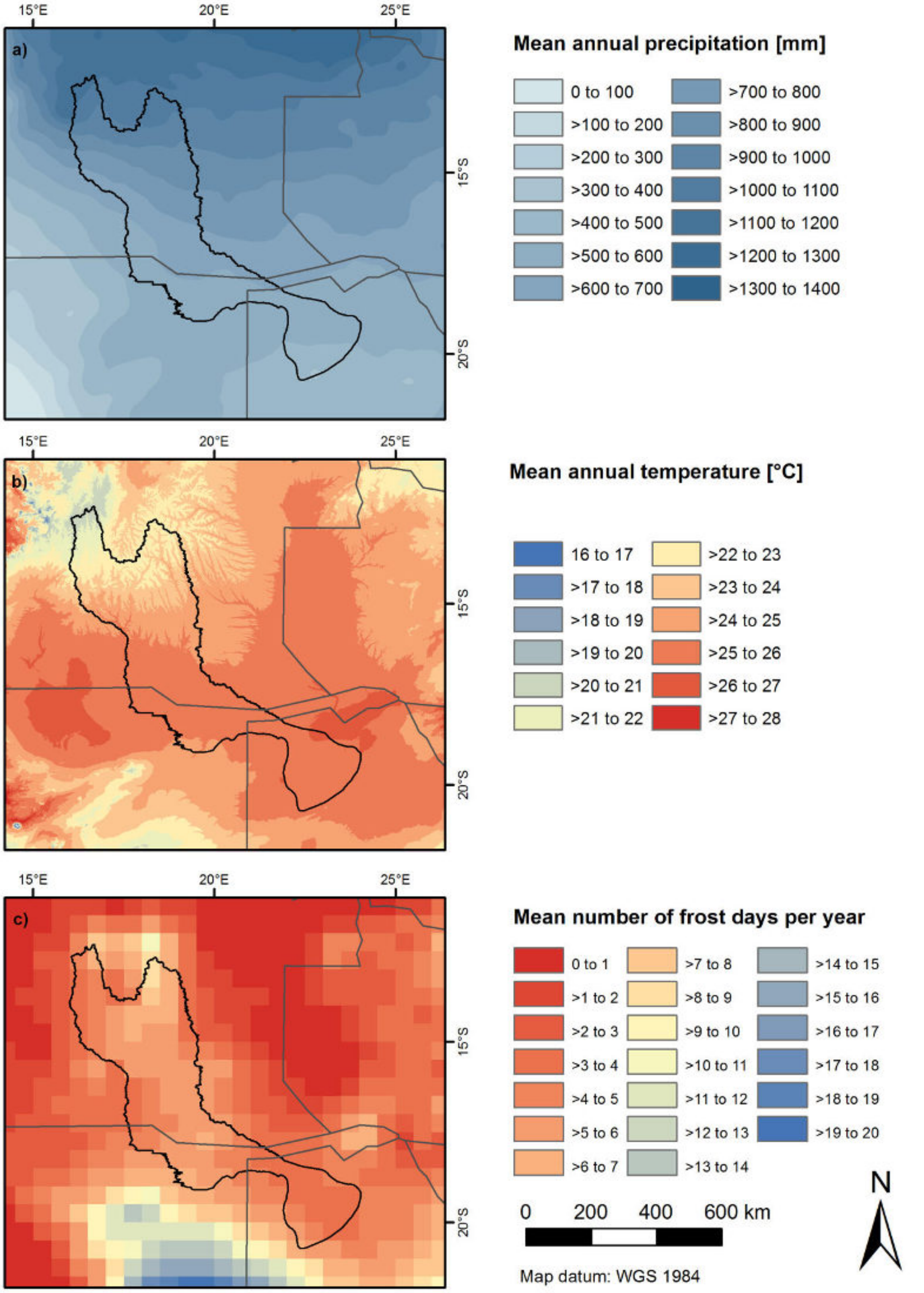

Figure 3 Climate of the Okavango Basin, a) mean annual temperature b) mean annual precipitation c) number of frost days. Data sources: a) and b) were compiled from the regionalised climatologies with 1-km spatial resolution; they were based on the regional climate model REMO that was forced with the Global Circulation Model ECHAM for the time period 1950-2000 (Weinzierl et al. 2013); c) was compiled from the CRU TS v3.22 data set (Harris et al. 2014).

increasing trend was recorded starting in the late 1970s and continuing until today (Weber 2013a). Frost occurs primarily in the subtropical region to the south of the Basin but also on the Angolan Central Plateau (Figure 3c).

Hydrology

The Okavango River originates on the Angolan Central Plateau where 95% of the runoff is generated. In contrast, most of the tributaries of the middle reaches in the extreme South of Angola, in Namibia and Botswana are either ephemeral or fossil, i.e. currently do not carry surface water. The two main tributaries are the Cubango and Cuito Rivers forming the Okavango River at the confluence in Dirico. The hydrological system of both tributaries is characterised by one flood pulse reaching the peak discharge towards the end of the rainy season in April and baseflow conditions occur in October. However, the flow regime throughout the year differs strongly. The Cubango shows fast runoff generation due to the underlying geology and the steeper topography. Consequently, the Cubango exhibits faster water travel times and a higher amplitude in the annual discharge than the Cuito. In contrast, the flow of the Cuito is moderated by wider floodplains and the water is retained for longer periods of time leading to a smoother hydrograph and higher baseflow is sustained during the dry season. However, considering the contribution over the course of the year, both tributaries contribute similar amounts to the mean annual discharge of the Okavango River (Steudel et al. 2013a).

Just after entering Botswana, the river widens to the so called ‘Panhandle’, a large floodplain 12 km wide. After the 120 km long Panhandle the river fans out into the alluvial plains of the Delta. Once reaching the Delta area the water flow is slowed down drastically. It takes between three to four month for the water to traverse the Delta spanning 250 km. Depending on the inflow and the inflow of the previous years the flooded area of the delta ranges from 6,000 km^2 to 12,000 km^2. 95% of the inflow into the Delta is lost to evapotranspiration (Steudel et al. 2013b). The functioning of the Delta ecosystem is highly depended on continued inflow of water from the Angolan Central Plateau. Thus, changes affecting the upper reaches strongly impact on the downstream systems via teleconnections.

Geology and soils

Two major fault lines control the flow of the river. The first one directs the Cubango and Cuito Rivers, but also the Kwando and the Zambezi Rivers south-eastwards. The second set, extensions of the East African Rift Valley, determines the position of the Panhandle and the Delta in Botswana (Mccarthy & Ellery 1989).

To a large extent the Okavango Basin is covered by deposits of the Kalahari system resting on top of the basement rock formations (Figure 4). The Kalahari Group sediments are of fluviatile origin and were in part redeposited by aeolian processes during drier periods (Haddon & McCarthy 2005). As a result, in the south of the Kavango regions of Namibia and to the West of the Delta extensive areas of parallel, longitudinal paleo dune systems were formed. In the area to the east and north of the delta they have been eroded (Ringrose et al. 2008). The north western part of the Basin is not entirely covered by Kalahari deposits. Here, the bedrock is of Precambrian origin comprising igneous rocks such as granite and metamorphic rocks such as gneiss (Direcção Provincial dos Serviços de Geologia e Minas Angola 1969).

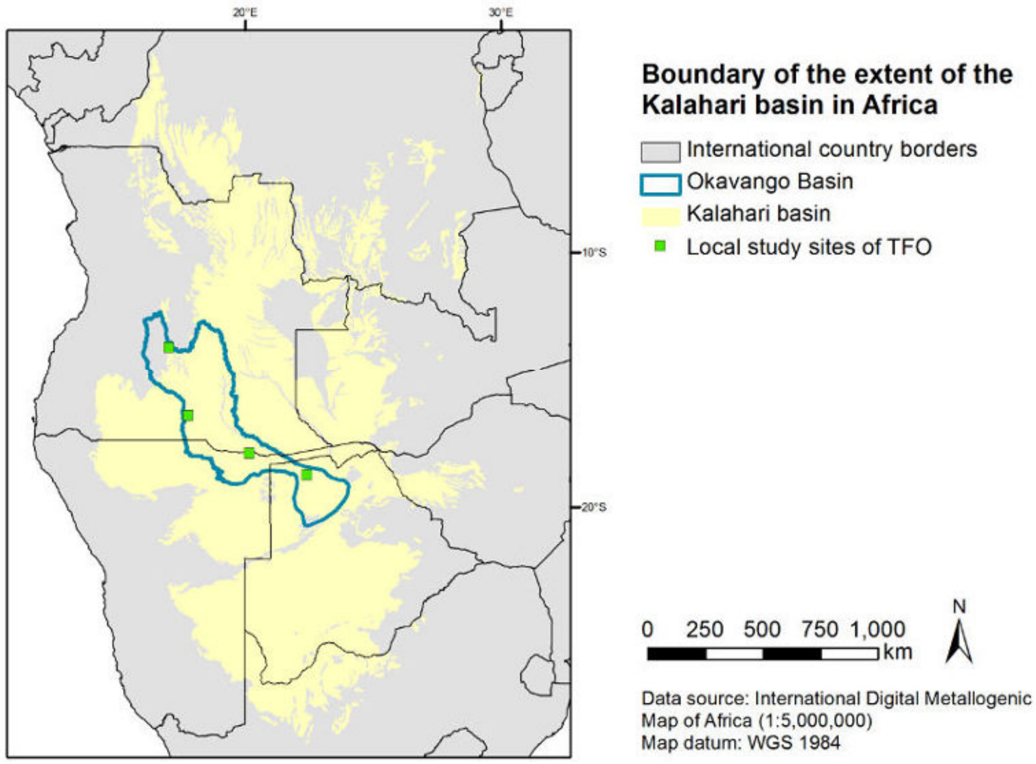

Figure 4 Extent of the Kalahari Basin in southern Africa according to the International Digital Metallogenic Map of Africa (Data available online: http://leutra.geogr.uni-jena.de/obis/metadata/view.php?view=geodata&id=162, accessed on 24.05.2016)

Due to the deposits of Kalahari sands in large parts of the Basin (Figure 4), the most common soil types according to WRB (2015) are Arenosols. They have less than 10% silt and clay content, are nutrient poor and very porous allowing for rapid drainage of precipitation. Within the extent of the deposits of the Kalahari system soils with higher content of fine material and rich in carbonate are restricted to the river valleys, dry riverbeds (Omiramba) and the Delta (Gröngröft et al., 2013a). Furthermore, in the area of the eroded and still existing longitudinal paleo dunes systems a striking difference between (former) dune valleys and dune tops can be observed. The dune valleys accumulated fine particles and consequently, the content of silt and clay is much higher (Wisch et al. 2010).

In the absence of Kalahari sands the upper Basin displays a different pedogenesis and features a high pedodiversity. Again, highly leached and acidic Arenosols are common on the elevated areas. However, on sloping areas shallow Plinthosols on granitic bedrock can be found. Along the tributaries of the upper reaches riverine peatlands with peat layers reaching several meters have formed, Histosols in the centre and Gleysols along the margins are the corresponding soil types (Gröngröft et al. 2013b).

Socio-economic setting and land use systems

The Okavango Basin is home to more than 1 million people with half of the population living in urban centres. Annual population growth is estimated to be approximately 2%. In Angola, a remigration to rural areas occurred after the end of the civil war in 2002 (Abdelli & Jouen 2012). However, in general a migration to urban centres is observed as a result of 'push and pull factors' of the conditions in the poor rural areas and the seemingly attractive urban centres (Pröpper et al. 2015).

Customary law exists in all three countries but only in Namibia and Botswana it is recognized by statutory law. In Botswana, land is administered by state run 'land boards' since the 1960s. In contrast, in Namibia and Angola allocation of land to community members follows customary law. Whereas in Namibia traditional authorities usually are able to enforce the land rights, in Angola community land is designated state land leaving local farmers without a legal land title. Thus, there is a high risk of acquisition of land by powerful entities, i.e. so called 'land grabbing'. In all three countries environmental legislation exists but is hardly enforced (Pröpper et al. 2015).

Rain-fed subsistent agriculture is the main form of land use in the Basin. At present large scale industrialized irrigation schemes cover only 1,100 ha in Angola, 2,200 ha in Namibia and 34 ha in Botswana (Pröpper et al. 2015). Consequently, smallholders are the back bone of food security. In the upper Basin where land is still available, traditional slash-and-burn agriculture is practised with cultivation periods of five to ten years followed by fallow periods of several decades (Domptail et al. 2013). In face of decreasing land abundance also short term rotation systems are practised on the Angolan Central Plateau (Abdelli & Jouen 2012). Main crops are maize (*Zea mays*), pearl millet (*Penisetum glaucum*) and Manioc (*Manihot esculenta*) cultivated together with a variety of legumes, sweet potatoes (*Ipomea batata*) and Cucurbitaceae (Domptail et al. 2013). During the dry season, horticulture (onions, tomatoes, cabbage) is practised in the peat lands (Abdelli & Jouen 2012). Livestock is not abundant and labour on the field is done by hand.

Farming along the middle reaches of the Okavango is semi-permanent and mixed cropping of millet (*Penisetum glaucum*) and a variety of secondary crops is practiced by small holders. However, due to variable precipitation and low soil fertility farming rarely meets household needs. In contrast to the upper Basin, small herds of livestock form part of the system and oxen are used for preparing land for cultivation (Kowalski et al. 2013). In the panhandle area the situation is similar but aggravated by human wild life conflicts leading to harvest loss (Große et al. 2013).

Next to agricultural land use, there are multiple forms of how the natural environment is used by rural populations. Fishery plays an essential role in the diet along the larger streams. Charcoal and honey play a primary role for cash income in the upper Basin (Domptail et al. 2013). Furthermore, a variety of other forest products are used such as wild fruits or medicinal plants and make an important contribution to nutrition and health (Piedade 2013). In fact, non-agricultural products and benefits from non-cleared woodlands outweigh short-term return by agriculture (Pröpper et al. 2015).

Vegetation of the Okavango Basin

The Okavango Basin belongs to the Zambezian phytoregion (White 1983) and is strongly shaped by the climatic gradient of decreasing precipitation from the northwest to the southeast (see above).

The vegetation map of Africa by White (1983) listed six coarse vegetation types. To a large extent the terrestrial ecoregions defined by Olson et al. (2001) correspond to the vegetation units delimited by White. In the context of the TFO project a new land cover map of the Okavango Basin was elaborated in order to fill these rather coarse units with content (Figure 5). The map was based on satellite images from the Moderate Resolution Imaging Spectroradiometer (MODIS) with a 250-m spatial resolution. Using a time series of 16-day-composites of the enhanced vegetation index (EVI) land surface phenology metrics were derived. These were subject to an unsupervised classification. The resulting classes were interpreted using the vegetation-plot database of the Okavango Basin

(Revermann et al. 2016b) and cross-checked during subsequent field work. In total, six major vegetation units containing 20 subunits were identified: a) Miombo woodlands and forests, b) woodlands on Kalahari sand c) other woodlands d) Thornbush savanna, e) shrub- and grasslands, and f) wetlands. The largest units were "Woodlands on Kalahari Sands" and "Miombo woodlands and forest" covering one third and one quarter of the land surface of the Okavango Basin respectively. "Wetlands" were the smallest unit comprising 7% of the area (Table 1).

Short description of the vegetation units of the Okavango Basin

In the following section I will provide a summary of the identified vegetation units based on our publications by Stellmes, Frantz, Finckh & Revermann (2013a) and Revermann & Finckh (2013a) in *Biodiversity and Ecology* Vol. 5.

a) **Miombo forests and woodlands** are the dominant vegetation in the upper reaches of the Basin forming part of the tropical dry forest ecosystem stretching over large parts of south-central Africa. The Miombo region typically shows seasonal climate with a wet season lasting 5-7 month. Mean annual precipitation ranges from 650 mm to 1,400 mm and soils are generally nutrient poor. Species composition is characterised by the dominance of Caesalpinoid tree species from the genera *Brachystegia*, *Cryptosepalum*, *Julbernardia* or *Isoberlinia*, and meso- and microphyllous, compound leaves (Campbell 1996). In the Okavango Basin three subunits were identified. **Miombo forests with *Cryptosepalum exfoliatum* ssp. *pseudotaxus*, Miombo forests dominated by deciduous tree species,** and **Miombo forests dominated by *Julbernardia paniculata*.** The latter vegetation unit represents the transition zone to the *Baikiaea* woodlands of the middle reaches and forms the southern limit of Miombo *sensus stricto*.

b) **Woodlands on Kalahari sand**

The dominant vegetation type of the middle reaches are drier woodlands often referred to as *Zambezian Baikiaea* woodlands (Olson et al. 2001). Vegetation structure changes profoundly, from a rather closed canopy in Miombo to a more savanna like structure with large crowns of individual trees leaving enough light for a more or less continuous shrub and herbal layer. Although *Baikiaea plurijuga* is the eponymous species, these **Woodlands on Kalahari sand** are composed of several dominant tree species such as *Burkea africana*, *Pterocarpus angolensis*, *Erythrophleum africanum*, *Schinziophyton rautanenii*, and *Guibourtia coleosperma.* Four different subunits were differentiated:

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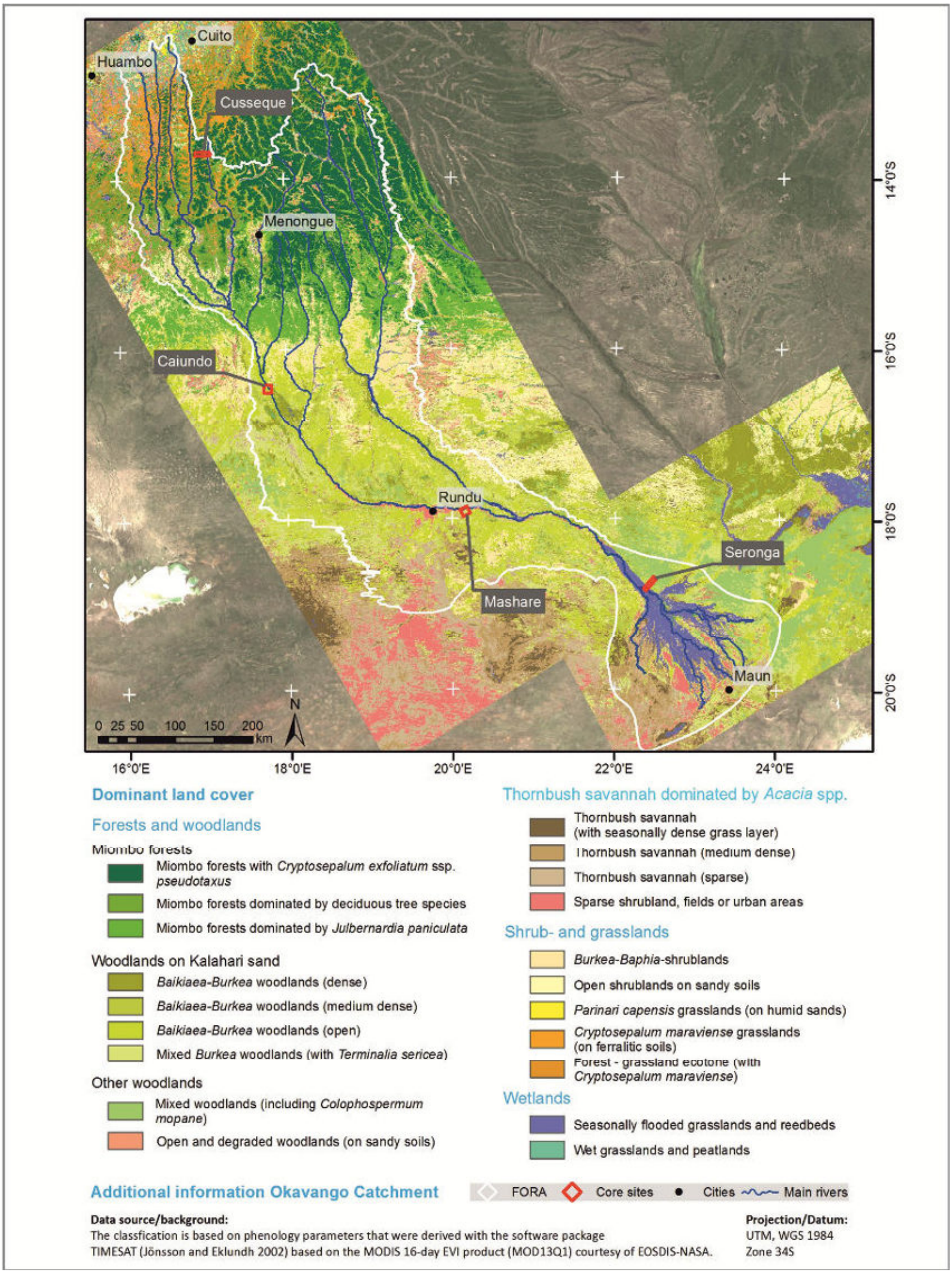


Data source/background:
The classfication is based on phenology parameters that were derived with the software package TIMESAT (Jönsson and Eklundh 2002) based on the MODIS 16-day EVI product (MOD13Q1) courtesy of EOSDIS-NASA.

Figure 5 Dominant land cover classes produced by an unsupervised classification approach which was based on phenology metrics derived from 16-day MODIS EVI time series covering the observation period 2000 to 2011 (source: Stellmes, M., Frantz, D., Finckh, M. & Revermann, R. (2013a).

Table 1 Proportions of dominant land cover types within the Okavango Basin (source: Stellmes, M., Frantz, D., Finckh, M. & Revermann, R. (2013a).

Land cover class	Area (km²)	Per cent
Miombo forests	**58,752**	**25.76**
Miombo forest with *Cryptosepalum exfoliatum* ssp. *pseudotaxus*	29,811	13.07
Miombo forest dominated by deciduous tree species	13,805	6.05
Miombo forest dominated by *Julbernardia paniculata*	15,135	6.64
Woodlands on Kalahari Sands	**68,046**	**29.83**
Baikiaea-Burkea woodlands (dense)	3,417	1.5
Baikiaea-Burkea woodlands (medium dense)	16,512	7.24
Baikiaea-Burkea woodlands (open)	28,377	12.44
Mixed *Burkea* woodlands (with *Terminalia sericea*)	19,741	8.65
Other woodlands	**15,365**	**6.74**
Mixed Kavango woodlands (including *Colophospermum mopane*)	7,526	3.3
Open and degraded woodlands (on sandy soils)	7,839	3.44
Thornbush savanna	**29,177**	**12.79**
Thornbush savanna (with seasonally dense grass layer)	3,641	1.6
Thornbush savanna (medium dense)	9,612	4.21
Thornbush savanna (open)	10,161	4.45
Sparse shrublands, fields or urban areas	5,763	2.53
Shrub- and grasslands	**40,098**	**17.58**
Burkea-Baphia shrublands	7,069	7.48
Open shrublands on sandy soils	13,141	5.76
Parinari capensis grasslands (on humid soils)	738	0.32
Cryptosepalum maraviense grasslands (on ferralitic soils)	4,595	2.01
Forest grassland ecotone (with *Cryptosepalum maraviense*)	4,555	2
Wetlands	**16,667**	**7.31**
Seasonally flooded grasslands and reedbeeds	12,906	5.66
Wet grasslands and peatlands	3,761	1.65
Total	**228,104**	**100**

dense, **medium dense** and **open *Baikiaea-Burkea* woodlands** and **Mixed *Burkea* woodlands (with *Terminalia sericea*)** (for more details see Revermann & Finckh 2013a).

c) The group **Other woodlands** includes the ***Colophospermum mopane* woodlands** the dominant vegetation unit to the east of the Panhandle and the Delta. In the Delta area *Colophospermum mopane* is often associated with comparatively clay rich soils while the sandier parts are usually covered by stands of *Terminalia sericea* (Murray-hudson, Finckh & Revermann 2013). The *Colophospermum mopane* woodlands occupy only a small fraction of the Basin but have a wide distribution throughout the semi-arid parts of southern Africa

d) **Thornbush savanna dominated by *Acacia* spp.** occur to the west of the Okavango Delta and to the south of the Kavango Regions in Namibia marking the shift to the "regional transition zone of the Kalahari Highveld" (White 1983). Depending on local soil conditions and land use, species composition and vegetation structure change from **Thornbush savanna with seasonally dense grass layer**, to a **medium dense Thornbush savanna** and to a **sparse Thornbush savanna.**

e) **Shrubs- and grasslands**

A unique feature of the Zambezian phytoregion are dwarf-shrub communities with a high underground woody biomass. Often the dwarf-shrub species have close relatives growing as trees in neighbouring woodlands and forests. In his paper "The underground forest of Africa" White (1976) termed this specialized growth form "geoxylic suffrutex". Herbivory, unfavourable edaphic conditions, frost and fire have been discussed as the driving factors for the development of the geoxyles (Davy 1922; White 1976; Pennington & Hughes 2014; Maurin et al. 2014; Davies et al. 2016; Finckh, Revermann & Aidar 2016). However, no final consensus has been reached, yet.

On the Angolan Central Plateau two types can be differentiated. The ***Cryptosepalum maraviense* grasslands**, locally referred to as "Anhares de Ongote" or "Cassamba", cover the mid- and foot slopes on ferralitic soils leading down to the stream network. Woodlands cover the elevated areas and are separated by a **Forest grassland ecotone (with *Cryptosepalum maraviense*)**. The second type is referred to as ***Parinari capensis* grasslands (on humid sands)** or as "Anharas de Borracha" in Portuguese (Barbosa 1970). They occur on sandy plains in the larger valleys of southern Bié and northern Cuando Cubango featuring deep, sandy, leached soils exhibiting hydromorphic features in the lower soil horizons. Similar grasslands cover large surfaces in Moxico (e.g. the Cameia National Park) and Zambia (e.g. Liuwa Plains National Park) west of the Zambezi River.

Not further specified shrublands include ***Burkea-Baphia*** **shrublands** and **Open shrublands on sandy soils.**

f) **Wetlands**

The unit **Seasonally flooded grasslands and reed beds** subsumes the various wetland types along permanently flowing water courses, ranging from seasonally flooded grasslands to permanently flooded *Cyperus papyrus* and *Phragmites* swamps and the open water of the channels within the Okavango Delta. In this region vegetation patterns are governed by the prevailing flood regime and therefore small differences in topography can lead to compositional changes over short horizontal distances. **Wet grasslands and peatlands** occur on the Angolan Central Plateau. On the one hand, this unit comprises tropical, riverine peatbogs with peat layers of several meters depth. They are usually located at valley bottoms of small, perennial tributaries and dominated by Cyperaceae but also feature other genera typical to temperate peatbogs, i.e. *Drosera* spp. On the other hand, this unit comprises edaphic grasslands with peaty mineral soils on elevated plains. Due to impeded drainage and high precipitation in the rainy season soils are temporarily waterlogged. No woodlands can establish under these conditions but humid grasslands with dwarf-shrubs of the genera *Protea*, *Parinari*, or *Syzygium* have formed.

Within The Future Okavango (TFO) project four core research sites were chosen to represent the different socio-ecological systems of the Basin. A detailed descriptions of the vegetation for each of the core sites and a land cover map based on multi-seasonal Landsat imagery is available in the publications in Biodiversity and Ecology Vol. 5 (De Cauwer 2013; Frantz et al. 2013; Murray-hudson, Finckh & Revermann 2013; Revermann & Finckh 2013b; Revermann et al. 2013; Röder et al. 2013; Schneibel et al. 2013a; b).

Flora of Angola and historical, botanical explorations of south-central Angola

After having characterised the vegetation units of the Okavango Basin I will now briefly review the flora of Angola and the history of the botanical exploration of the country. The systematic botanical exploration of Angola started in the mid-19th century with the Austrian born botanist Friedrich Weltwitsch. His collection included over 8000 specimen containing more than 1000 species new to science (Figueiredo & Smith 2008). However, Weltwitsch’s journey focused on the western part of the country. In contrast, the German expedition of Hugo Baum traversed the southern part of the country, the provinces of Cunene and Cuando Cubango (Baum 1903) and the specimen collected by Baum are therefore of higher relevance for this study. The most important collector of the 20th century was with no doubt John Gossweiler collecting over 14,000 specimen (Figueiredo & Smith 2008). Furthermore, he provided a first national vegetation map of the country (Gossweiler & Mendonça 1939). A detailed list of all collectors of Angola can be found in Figueiredo and Smith (2008).

The flora of Angola was not included in the major regional Floras of the region such as the *Flora Zambesiaca* or the *Flora of Tropical East Africa*. In contrast, the Angolan Flora was dealt with separately in the *Conspectus Florae Angolensis* (CFA). Work on CFA was initiated by Exell and Mendonça in the 1930ies and several volumes were published subsequently (Exell & Mendonça 1937, 1951, 1954, 1955; Exell & Fernandes 1962, 1966; Exell, Fernandes & Mendes 1970; Schelpe, Jermy & Launert 1977; Fernandes 1982; Diniz 1993). However, the CFA was never completed and important families such as the Rubiaceae are still missing until today (Figueiredo 2008).

As former Portuguese colony, the best collections of specimens from Angola are housed at herbaria in Portugal namely LISC (Instituto de Investigação Científica Tropical), LISU (University of Lisbon) and COI (University of Coimbra). Moreover, Angolan plant material is represented in the major herbariums of Europe (Figueiredo & Smith 2008). In Angola three herbaria do exist. However, only the herbarium in Lubango (LUBA) is currently fully functional.

Checklists detailing the known species present within a country or regions are an essential basis for studies on the ecology of vegetation and also for many natural resource management applications (Huntley & Matos 1994). However, for Angola such a list did not exist until recently. The gap was finally filled after a concerted effort of an international team of researchers and "Plants of Angola – Plantas de Angola" was published in 2008 (Figueiredo & Smith 2008). The list contains 7,296 taxa whereof 1,069 are considered endemic and thus the flora of Angola is the second richest in southern Africa (Figueiredo, Smith & César 2009).

A first map of the vegetation of Angola was published by Gossweiler (Gossweiler & Mendonça 1939) followed by a refined version of Barbosa (1970). On a provincial level there are maps available for Bié Province (Monteiro 1970) and for Cuando Cubango (dos Santos 1982). These maps predate modern satellite imagery and were expert drawn and not based on vegetation-plots, with the exception of the map of Bié. The vegetation units delimited in the national vegetation map of Barbosa served as the main basis for White's vegetation map of Africa (1983) and also for the terrestrial ecoregions of the world (Olson et al. 2001).

The global biodiversity information facility (GBIF) is the largest database storing biodiversity information for all organismic groups listing records of specimen as well as species observations. For Angola, GBIF currently holds 12,724 entries for vascular plants with a spatial reference (GBIF.org 2016). However, for about one third the exact locality is missing and instead the geographic centre of Angola is given. The map in Figure 6 shows the density of records per 0.2° grid cells. Records of vascular plants cluster around cities and major road axis; yet, vast parts of Angola are not covered at all. As such, the east, southeast and the extreme north of the country do not show any records at all. Although the information stored in GBIF clearly does not include all available information, e.g. the number of existing herbarium specimen is many times higher than the number of GBIF entries, the low number of records illustrates how understudied the flora of Angola still is and how little effort is put into digitizing available (historic) information.

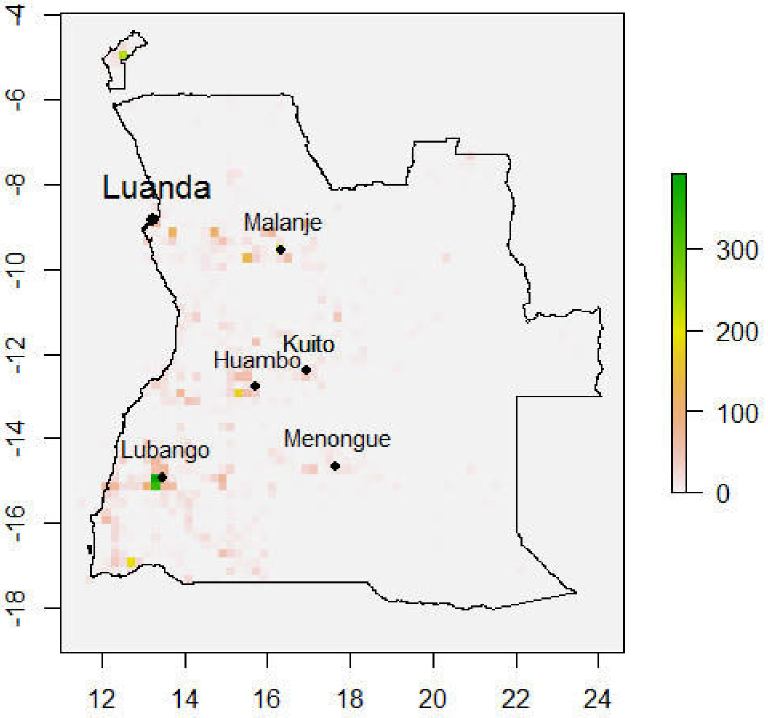


Figure 6 Density of records of vascular plants stored in the global biodiversity information facility (GBIF) for Angola. The density is given in observations per 0.2° grid cells. In total, 12,724 records with a spatial reference are listed in the database (GBIF.org 2016). However, about one third had no exact spatial reference but instead the locality was set to the geographic centre of Angola in the GBIF database. For the spatial analysis, these entries were not considered. The map was produced using the 'count.points' function of the R package adehabitatMA (Calenge 2006) and topographic information from the maps package; map Datum: WGS 1984.

General methodological considerations and constraints

Some general considerations shaped the methodological approach of the thesis. The largest share of the Okavango Basin is located in Angola and almost all the runoff sustaining the sensitive ecosystem of the Okavango Delta is generated there. At the same time, the most rapid socio-economic transformations among the countries sharing the Okavango Basin are currently occurring in Angola. However, scientific knowledge on the upstream ecosystems was very scarce and due to several decades of civil war no scientific research had been carried out for a long time. Therefore, I chose to concentrate my work on southeast Angola.

Although Angola is now quickly recovering, several issues still make research in the country a challenging task. A limited road network and land mines, a legacy of the civil war, put restrictions on the choice of field sites. Furthermore, visa policies and quality of roads especially during the rainy season when studies on the vegetation need to take place increase the necessary time to carry out field work. All in all, the difficult conditions as well as language barriers have hampered research in Angola also after the armed conflict had ceased.

One aim of the thesis was to provide ecological data that allow thorough, quantitative analyses of the ecology of the vegetation of the Okavango Basin. Furthermore, the data was supposed to be useful for future studies and regional analyses such as phytosociological classifications of the Miombo belt or contribute to the vegetation mapping project of south central Africa. Hence, the approach needed to follow a standardized methodology accepted in the region. Therefore, vegetation plots followed the design established in the BIOTA project (Jürgens et al. 2012) and in the Vegetation Survey of Namibia (Strohbach 2001): A nested design of one 100 m^2 plot situated in the centre of a 1,000 m^2 plot.

In all relevés the entire spectrum of vascular plants was recorded. However, due to the incomplete treatment of the Angolan flora and the lack of current identification keys (see above) as well as the high plant diversity the identification of the collected plant material was very time consuming. Therefore, I chose to restrict some analyses on woody species only. However, once the identification of the remaining specimen is completed, the data will allow further in depth analyses of the full species pool.

In a short time frame a large spatial extent needed to be covered with many areas being inaccessible due to the lack of access routes or the danger of land mines. As such, some areas had to be exclude *a priori* from the sampling scheme, e.g. the road to Cuito Carnavale, the main access to the central Cuito catchment.

Next to the scientific community, the main addressee of outcomes of this thesis were stakeholders of the administrational level responsible for spatial planning, i.e. OKACOM or government departments. Therefore, there was a need to upscale results from the local vegetation plot to the extent of the Okavango Basin. In order to generate spatially explicit data, suitable remote sensing data were identified and ecological modelling frameworks developed.

Objectives and chapter outline

The overall aims of the thesis are (1) to analyse species composition of the understudied woodlands of the upper reaches of the Okavango Basin in Angola and to identify representative vegetation communities, (2) to investigate environmental drivers of vegetation patterns, (3) to quantify plant diversity and to analyse spatial patterns of plant diversity in the Okavango Basin, (4) to explore methodological tools to link ecological field data to continuous remote sensing data in order to predict ecosystem properties of unsurveyed areas, (5) to assess the impact of land use on vegetation composition, plant diversity and regeneration of dry tropical woodlands.

Chapter 2: Baseline survey of the Vegetation of the Okavango Basin

As described above, there was hardly any published, quantitive information on vegetation composition and on the distribution of plant species for southeast Angola. Therefore, a vegetation survey aiming at covering all major vegetation types in the Angolan part of the Okavango Basin was initiated. In the first part of this chapter the vegetation-plot database of the Okavango Basin is shortly presented. In the second part a checklist of the woody species of the Cusseque study site and an analysis of the dominant botanical families is presented.

Chapter 3: Dry tropical forests of the Cubango Basin in southern Africa - A first classification and assessment of their woody species diversity.

Vegetation units serve as the basic entities in resource management and conservation planning. Therefore, woody vegetation communities of the Cubango Basin were identified based on the vegetation survey carried out within the framework of this thesis. 12 woody vegetation communities were derived using the ISOPAM algorithm. The communities were described regarding their species composition and their environmental characteristics were quantified. Furthermore, the size of the species pool of woody species was estimated using species accumulation models.

The study had the following aims:

(i) to estimate woody species diversity and the size of the species pool
(ii) to characterise the woody vegetation communities of the Cubango Basin in terms of their floristic composition
(iii) to analyse the underlying abiotic drivers of the distribution of woody vegetation communities

Chapter 4: Environmental drivers of vegetation patterns – frost as a driver of vegetation patterns on the Angolan plateau

The Zambezian Phytoregion is the centre of diversity of the so called geoxylic suffrutex – dwarf shrubs with an enormous underground woody biomass. Characteristic for the geoxyles is the fact that they have tree relatives growing the close by woodlands as tall trees. In the rolling landscape of the Angolan Central Plateau the geoxylic suffrutex dominate the open vegetation types located on the lower slopes in between the woodlands on the elevated area and the riverine wetlands at the valley bottoms. Unfavourable edaphic conditions, herbivory, frost and fire have been discussed as the environmental driver of their evolution.
The aim of this chapter was:

(i) to provide, for the first time, microclimatic data from the Angolan Central Plateau documenting the occurrence of frequent night frosts
(ii) to bring frost as a potential driver back on to the scientific discussion and to raise attention for the regular occurrence of frost during the dry season in tropical, elevated areas promoted by local topography

Chapter 5: Linking land surface phenology and vegetation-plot databases to model terrestrial plant α-diversity of the Okavango Basin.

Spatial data on diversity are urgently needed for spatial conservation planning in many regions of the globe – but often are not available. Bringing together ecological field data, the vegetation survey of the Okavango Basin, and state of the art remote sensing data allowed making predictions of diversity for unsurveyed areas.

The aim of this study was:

(i) to test the suitability of MODIS EVI land surface phenology metrics to predict vascular plant α-diversity derived from the vegetation-plot database
(ii) to compare the performances of statistical models using a) only phenological metrics and topography, b) only climate data, and c) the entire set of predictor variables
(iii) to provide a modelling framework transferable to other regions

Chapter 6: Species richness and evenness respond to diverging land use patterns – a cross border study of dry tropical woodlands in southern Africa

At its middle reaches the Okavango River forms the border among Angola and Namibia. Traditional land use practices as well as the physio-geographic settings are very similar on either side of the river. However, during the last decades Namibia underwent strong socio-economic changes whereas in Angola development was rather stagnant. Hence, the exciting opportunity arises to study in situ the impact of two diverging land use regimes on plant diversity.
The purpose of this study was

(i) to investigate whether diverging land use in the cross border region of Angola and Namibia has caused detectable differences in plant diversity patterns (species richness, Shannon index, and evenness) over the last decades.
(ii) to analyse if different life forms, i.e. woody species, herb and forb species, and grass and sedge species respond in the same way.

Chapter 7: Impact of shifting cultivation on dense tropical woodlands in southeast Angola

As illustrated above, subsistent agriculture by smallholders is the main form of land use. Studying the impact of this type of land use is a key to anticipate changes invoked by increasing demands for agricultural area. Along the lower Cubango River a distinct vegetation type of very dense *Baikiaea* woodland with thicket like understorey exists. It is preferred for farming and since the year 2000 clearance for new fields has increased exponentially. However, this vegetation type had never been described before and the underlying environmental factors and the regeneration dynamics are unknown.

The major goals of this study are to:

(i) describe the species composition, diversity, and structure of the dense woodland and compare it to the surrounding open woodland matrix;
(ii) determine whether abiotic conditions in the dense woodland differ from the open woodland, and why the dense woodland is preferred for agriculture;
(iii) determine whether the duration of agricultural use has a negative impact on the regeneration, species composition, vegetation structure, and soil properties of the fallows.

Chapter 8: Syntheses

This chapter discusses the results of the preceding chapters in the light of the overarching objectives of the thesis outlined above. Furthermore, four co-authored papers not included in the preceding chapters are briefly presented and used to underpin the discussion of the key findings of the thesis.

CHAPTER 2

Baseline survey of the Vegetation of the Okavango Basin

a) Vegetation Database of the Okavango Basin

Rasmus Revermann, Amândio Luis Gomes, Francisco Maiato Gonçalves, Johannes Wallenfang, Torsten Hoche, Norbert Jürgens and Manfred Finckh
Phytocoenologia (2016) **46**: 103-104

b) Checklist of the woody vegetation of the Cusseque study site

Rasmus Revermann, Francisco Maiato Gonçalves, Amândio Luis Gomes and Manfred Finckh
Checklist (submitted)

2a) Vegetation Database of the Okavango Basin

Abstract

The Okavango River Basin, located in southern Africa and shared by the countries Angola, Namibia and Botswana, harbours large extents of natural and semi-natural ecosystems. At the same time, it is a hot spot of accelerating land-use change causing transformation of vegetation in many regions of the Basin. However, knowledge on vegetation composition and plant diversity is very limited, especially of the upper reaches of the river in Angola. The Future Okavango (TFO) project aimed at closing this gap and initiated a plot-based vegetation survey in 2011. Here we present the resulting Vegetation Database of the Okavango Basin (GIVD ID:AF-00-009; http://www.givd.info/ID/AF-00-009). We used unsupervised classification of MODIS land surface phenology metrics to identify existing major vegetation units forming the basis of a random, stratified sampling design. However, sampling was largely constrained by limited access and the hazard of land mines, a legacy of the civil war in Angola. Furthermore, detailed sampling on four local study sites of 100 km^2 representing the different macro-ecosystems of the Basin was carried out. Vegetation plots followed a nested design of a 100-m$_2$plot resting in the centre of a 1,000-m$_2$ plot. In every plot, we recorded all vascular plant species with their estimated, projected cover, vegetation height, cover of vegetation strata, topography, and intensity of land-use activities. Furthermore, soil samples were taken, and diameters of trees measured. Currently, the database has a focus on terrestrial vegetation, including Miombo woodlands and forests, geoxylic grasslands, *Baikiaea-Burkea* woodlands, and *Colophospermum mopane* woodlands. However, the database also includes plots of the tropical wetlands and peat bogs of the Angolan Central Plateau. The specific vegetation of the Okavango Delta is not yet included. The collected vegetation data will feed into a phytosociological classification and ecological modelling applications. Another objective is the identification of successional pathways after disturbance through land use. Ultimately, it will provide the basis for a vegetation map of the Okavango region.

Keywords: Angola; Botswana; Cubango; geoxylic suffrutex; Kavango; Miombo; Namibia; The Future Okavango (TFO)

GIVD Database ID: AF-00-009 **Last update:** 2016-01-06

Vegetation Database of the Okavango Basin

Web address: http://www.future-okavango.org/

Database manager(s): Rasmus Revermann (rasmus.revermann@uni-hamburg.de); Manfred Finckh (manfred.finck@uni-hamburg.de)

Owner: Working group Biodiversity, Ecology and Evolution of Plants, Biocentre Klein Flottbek, University of Hamburg, Germany

Scope: The vegetation database covers the Okavango River Basin located in the countries of Angola, Namibia and Botswana. Sampling aims at covering all major vegetation types present in the Basin. Additionally, detailed investigations are carried out at four research areas sized 100 km^2. Vegetation plots are sized 20 m × 50 m with a 10 m × 10 m plot nesting in the centre. Grassland and wetland plots are in many cases sized 10 m × 10 m. On every plot all vascular plants species present including their estimated projected cover were recorded. Currently, the database holds vegetation-plots from semi-humid to semi-arid tropical woodlands (Miombo woodlands, *Baikiaea-Burkea* woodlands, *Colophospermum mopane* woodlands, and Thornbush savanna) as well as from geoxylic grasslands and Cyperaceae dominated wetlands of the Angolan Central Plateau. So far no plots of the wetlands of the Okavango Delta have been included but contributions from other researchers are welcome.

Availability: according to a specific agreement **Online upload:** no **Online search:** no

Database format(s): BIOTA Base **Export format(s):** MS Access, Excel, CSV file, plain text file

Plot type(s): normal plots; nested plots **Plot-size range:** 100-1000 m²

Non-overlapping plots: 404 **Estimate of existing plots:** [NA] **Completeness:** [NA] **Status:** ongoing capture

Total no. of plot observations: 661 **Number of sources (biblioreferences, data collectors):** 3 **Valid taxa:** 456

Countries: AO: 78.0%; BW: 11.0%; NA: 11.0%

Forest: 39% — **Non-forest:** aquatic: 0%; semi-aquatic: 11%; arctic-alpine: 0%; natural: 45%; semi-natural: 5%; anthropogenic: 0%

Guilds: all vascular plants: 100%

Environmental data: altitude: 100%; slope aspect: 100%; slope inclination: 100%; microrelief: 100%; soil depth: 100%; surface cover other than plants (open soil, litter, bare rock etc.): 100%; soil pH: 100%; other soil attributes: 100%; land use categories: 100%

Performance measure(s): cover: 100%; measurements like diameter or height of trees: 100%

Geographic localisation: GPS coordinates (precision 25 m or less): 100%

Sampling periods: 2010-2019: 100.0%

Information as of 2016-01-06; further details and future updates available from http://www.givd.info/ID/AF-00-009

2b) Checklist of the woody vegetation of the Cusseque study site

Abstract

We provide a detailed account of the woody flora of the Miombo woodlands and geoxylic grasslands of the Cusseque study site of "The Future Okavango" (TFO) project in south central Angola. In total, we documented 154 woody species belonging to 99 genera of 37 botanical families on 100 km^2. The study represents the first comprehensive account of the woody vegetation of the area including all habitats and growth forms.

Key words: Angola; Bié; geoxylic suffrutex; Miombo; The Future Okavango

INTRODUCTION

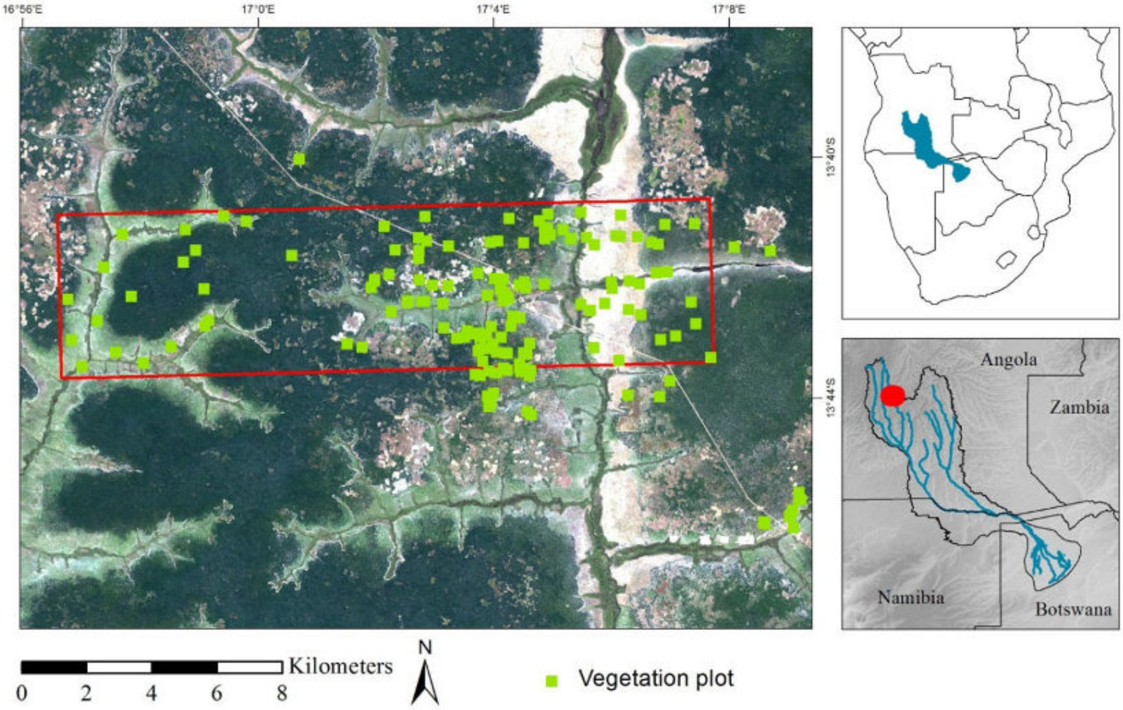
In spite of the early works mapping the vegetation of Angola by Gossweiler (1939) and Barbosa (1970), detailed studies of the species composition of the coarse vegetation units delineated by these authors is still lacking. However, for the province of Bié Monteiro (1970) provided an excellent overview and his work was a valuable starting point for this study. Until recently, a countrywide checklist of the flora of Angola was missing until this gap was filled in 2008 with the publication of "Plants of Angola – Plantas de Angola" by Figueiredo and Smith (2008). But at the local and regional scale inventories of vascular plants are still lacking. Such inventories are indispensable for any kind of natural resource management planning, conservation measures or ecological studies (Figueiredo, Smith & César 2009).

The interdisciplinary research project 'The Future Okavango' (TFO) aimed at providing a scientific basis for strategic resource management planning for the Okavango Basin. The Okavango River originates on the Angolan Central Plateau and terminates in a large inland delta in the Kalahari Desert in Botswana. Detailed studies were carried out at four research sites representing the different parts of the river basin. In this study, we present results of the vegetation survey carried out within the TFO project at the research site 'Cusseque' in the province of Bié situated at the upper reaches of the Okavango River.

MATERIALS AND METHODS

Study site

The study site Cusseque is situated on the Angolan Central Plateau in the province of Bié (13.6985°S, 17.0382°E) and has a size of 100 km^2 (Figure 7, Wehberg & Weinzierl 2013). The landscape can be described as a gently rolling plain with a perpendicular river network. Three major landscape units can be identified: the elevated areas, the sloping areas leading down to the valley bottoms and the valley floor (Gröngröft et al. 2013c). The mean elevation is 1,575 m above sea level while the height difference between the valley bottom of the main river and the surrounding elevated areas is about 100 m (Gröngröft et al. 2013c). The climate of the Cusseque area can be described as semi-humid with a pronounced wet season lasting from November to April with a mean annual precipitation of 987 mm. The mean annual temperature is 20.4°C (Weber 2013b). The climate can be categorized as 'Cwa' according to the climate classification of Köppen-Geiger (Peel, Finlayson & Mcmahon 2007). The study area harbours a high pedodiversity. The elevated areas are characterised by deep and developed slightly loamy Arenosols. The slopes of the smaller valleys of the tributaries and at the western side of the Cusseque River show shallow Plinthosols on granitic bedrock. In contrast, the soils along the eastern part of the Cusseque River are characterised by very deep and leached Arenosols. The centre of the valleys support Histosol with peat layers exceeding 1 m in depth while at the edges of the wetlands Gleysols are the common soil type (Gröngröft et al. 2013b).



Projection: WGS 1984; background: RapidEye high resolution satellite imagery, recorded 1st May 2013. We acknowledge the DLR for the provision of the data from the RapidEye Science Archive.

Figure 7 Location of the Okavango Basin in southern Africa and the study site "Cusseque" denoted in red. Okavango Basin follows the definition of the "The Future Okavango" project (www.future-okavango.org, Wehberg & Weinzierl 2013).

The main vegetation types covering south central Angola are brevi-deciduous Miombo woodlands and forests. These woodlands are interspersed with open vegetation types termed 'anharas de ongote' in Portuguese. The unique feature of these vegetation types are dwarf shrubs with an enormous underground woody biomass described by White (1976) as 'geoxylic suffrutex'. In the Cusseque area geoxylic suffrutex occur on two different soil types: on deep, leached sandy soils and on shallow, compact ferritic soils. In the following we will refer to these vegetation types as 'geoxylic grasslands on sandy soils' and 'geoxylic grasslands on ferralitic soils'. Woodlands and forests are confined to the elevated areas and top-slopes. The mid- and foot-slopes feature 'geoxylic grasslands' and the valley bottoms exhibit wetlands dominated by Cyperaceae (Figure 8,Figure 9, Revermann et al. 2013; Schneibel et al. 2013a).

Data collection

Plot based vegetation surveys were carried out during the vegetation period in the years 2011 to 2014. In order to evenly map all present vegetation units sampling followed a random, stratified design. Based on an image segmentation algorithm using all bands of a Landsat 7 scene seven major vegetation units were identified. In these vegetation units random points were created in the GIS and transferred to a hand held GPS for localisation in the field. Furthermore, additional vegetation plots were placed in different successional stages of Miombo forest to analyse successional pathways. We used a nested plot design with a smaller 10 m x 10 m plot resting in a larger 20 m x 50 m plot. In total, we sampled 148 vegetation plots. Due to the unique character of the geoxylic grasslands these were subject to an additional field campaign. Data collection was made using 10 m × 10 m plots with two subplots sized 3.3 m x 3.3 m situated in diagonally opposite corners (adapted from Dengler 2009b). The plots were established randomly along the valleys where the geoxylic grasslands occur. In every plot all vascular plants found were registered and their projected cover estimated. Unknown plants were photographed and herborised according to botanical methods lined out by Victor *et al.* (2004). Voucher specimens were deposited in the herbaria of the Instituto Superior de Ciências da Educação in Lubango (LUBA) and the Herbarium Hamburgense (HBG, CITES register DE 205-01). In addition to the species recorded on vegetation plots, species found elsewhere while working at the study area are also included in this checklist.

Taxonomy and plant identification

We followed the taxonomy of the checklist "Plants of Angola – Plantas de Angola" by Figueiredo and Smith (2008). We are aware of recent changes in the taxonomy but decided to stick to the national checklist of Angola to be consistent. There is no current, comprehensive work on the flora of Angola. For identification we consulted the Conspectus Florae Angolensis (Exell & Mendonça 1937) where possible, and the flora of neighbouring countries, especially the Flora Zambeziaca (Exell & Wild 1960). Identification was double checked with herbarium collections at LUBA and online data bases such as JSTOR Plant Science. We also consulted experts for some specimen at Kew Botanical Garden (K).

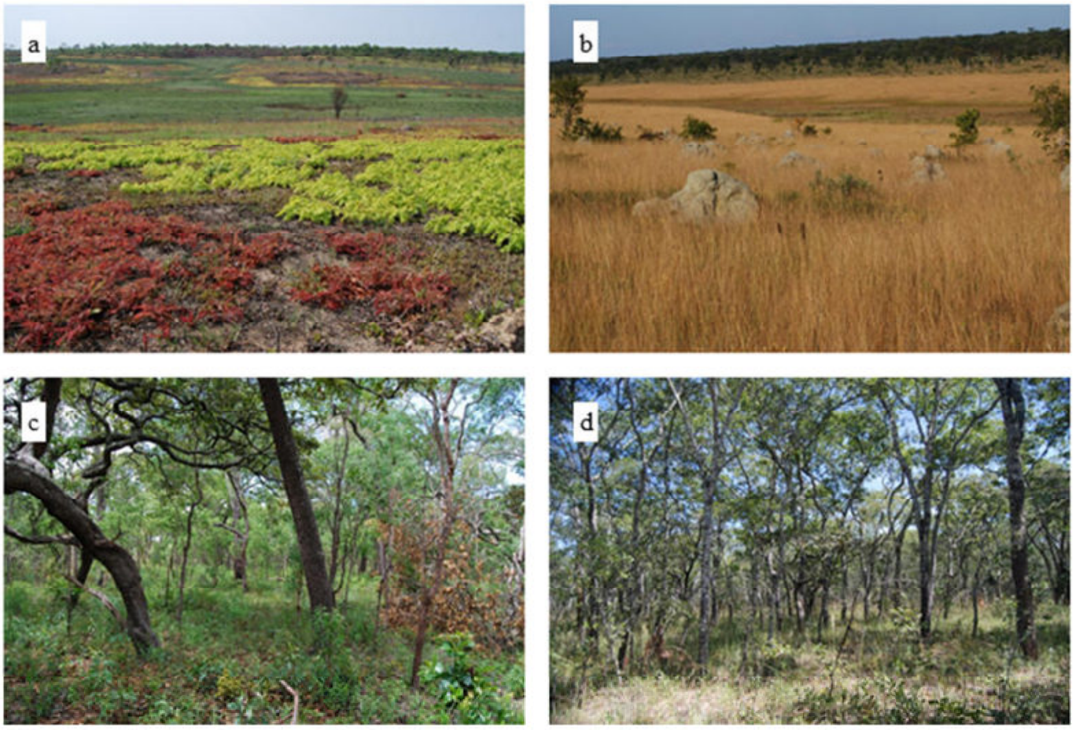


Figure 8 Landscape of the Cusseque study area. a) geoxylic grasslands dominated by *Cryptosepalum maraviense* at the start of the wet season in October, b) geoxylic grassland on sandy soils at the start of the dry season in May, in the background wetland at the valley bottom and Miombo woodlands, c) Miombo woodland, and d) Miombo woodland.

Permits

Permits for plant collection and transfer of biological material in Angola for scientific purposes was arranged based on the framework of bilateral agreement between Angola, represented by the Instituto Superior de Ciências de Educação da Huíla (ISCED - Huíla), Lubango and Germany, represented by the University of Hamburg (UHH) as the collection of biological material for the country is still not regulated by specific legislation. All International Conventions, on which Angola is signatory country such as Convention on International Trade in Endangered Species of Wild Fauna and Flora (1973), Convention on Biological Diversity (1992), International Treaty on Plant Genetic Resources for Food and Agriculture (2004), and all other national and international relevant instruments concerning biodiversity were taken into account.

Data analysis

We visualised the number of species per family of all species belonging to one family using the package ‘wordcloud’ (Fellows 2014) in the statistical software R (R Development Core Team 2015). Data on frequency, habitat and life form was compiled from vegetation plot data. We assigned frequency according to the following categories: very rare (1-2 observations), rare (3-5 observations), occasional (6-10 observations), frequent (11-30 observations), common (>30 observations).

Figure 9 Typical plants of the Cusseque area. a) Copaifera baumiana, 7b) Uvaria angolensis, c) Fadogia fuchsioides, d) Warneckea sapinii, e) Ochna arenaria, f) Combretum platypetalum ssp. platypetalum, g) Cryptosepalum maraviense, h) Brachystegia longifolia, i) Cryptosepalum exfoliatum ssp. Pseudotaxus.

RESULTS

At the Cusseque study site in south central Angola, we documented 154 woody species on 100 km^2 belonging to 99 genera and 37 botanical families (Table 2). The majority of species belonged to the Family of Fabaceae, followed by Rubiaceae, Euphorbiaceae, Proteacea and Combretacea (Figure 10). While the species of the Rubiaceae are occurring only with low frequencies, many of the species belonging to the Fabaceae family showed high frequency and included the dominant species of the area. The woodlands and forests showed higher species richness than the geoxylic grasslands: 110 species belonging to 32 families occurred in the woodlands while 33 woody species of 14 families were found in the geoxylic grasslands (Table 2). One species, *Combretum schumannii* Engl., was recorded but is not listed in the current checklist of Angola (Figueiredo & Smith 2008).

Figure 10 Wordcloud showing the families of woody plants found at the Cusseque research site, south central Angola. The size of the letters corresponds to the number of species belonging to that family. In total 37 families of woody plant species occur, summing to 154 species of 99 genera.

DISCUSSION

The presented study is the first comprehensive account of the woody flora of the vegetation of the Angolan Central Plateau in the province of Bié covering all habitats. The only previous study in the area documented larger shrubs and trees of the woodland only (Monteiro 1970). Monteiro (1970) documented 166 woody species in the entire province of Bié. Our study almost reached the same number on only 100 km^2.

The provided list of woody species of the Cusseque area can be expected to reflect the present species pool well. All major vegetation units of the study site have been covered more or less evenly. Furthermore, botanical collections made while on site further augmented the collection. However, this list does not contain any specimen that could not be identified to at least genus level. Therefore, the actual number of woody species can be expected to be slightly higher.

Most of the species occurred either in the geoxylic grasslands or in the woodlands and forests. However, many of the geoxyles have close tree relatives in the woodlands. Furthermore, the geoxylic grasslands on the two soil types had a distinct species pool and vegetation composition showed only a very small overlap.

Acknowledgements

Research was funded by the German Federal Ministry of Education and Research (BMBF) in the context of The Future Okavango (TFO) project, grant number 01LL0912A. We are thankful for the support of the staff at Kew Royal Botanical gardens that aided in the identification, in particular David John Goyder and Iain Darbyshire. Furthermore, we thank the people of the villages Kahololo, Sovi, Cusseque and Calomba and especially the traditional authorities (sobas) for their support of our study.

Table 2 List of species sorted according to family. Voucher specimen have been deposited in the herbaria of Lubango (LUBA) and Hamburg (HBG). Frequency was assigned according to the following categories: very rare (1-2 observations), rare (3-5 observations), occasional (6-10 observations), frequent (11-30 observations), common (>30 observations).

Species name	**Frequency**	**life form**	**habitat**	**Collection number(s)**
ANACARDIACEAE				
Ozoroa cf. xylophylla (Engl. &Gilg) R.Fern. & A.Fern.	very rare	shrub	geoxylic grassland (sandy soils)	133057B
Ozoroa stenophylla Engl. &Gilg.	frequent	shrub	woodland / grassland (ferralitic soils)	140123
Rhus arenaria Torre, A.R.	frequent	dwarfshrub / geoxyle	geoxylic grassland (ferralitic soils)	140101
Rhus exelliana Meikle	frequent	dwarfshrub		135250; 134275
Rhus gracilipes Exell	frequent	dwarfshrub	woodland / forest	139227; 132483
Rhus kirkii Oliv.	frequent	dwarfshrub	woodland / forest	139253
ANISOPHYLLEACEAE				
Anisophyllea boehmii Engl.	frequent	tree	woodland / forest	134316; 139018; 135297
Anisophyllea quangensis Engl. ex Henriq.	rare	dwarfshrub	geoxylic grassland (sandy soils)	133044; 134116; 140109
ANNONCACEAE				
Annona stenophylla subsp. *nana* Engl. & Diels	rare	dwarfshrub	woodland / forest	133058; 134218; 140065
Uvaria angolensis Welw. ex Oliv.	frequent	shrub	woodland / forest	135323; 134240
Xylopia odoratissima Welw. ex Oiv.	frequent	shrub	woodland / forest	133057A; 134263
Xylopia tomentosa Exell	common	shrub	woodland / forest	135279; 132956; 132986; 139177
APOCYNACEAE				
Chamaeclitandra henriquesiana (Hallier f.) Pichon	common	dwarfshrub / geoxyle	geoxylic grassland (sandy soils)	140121
Diplorhynchus condylocarpon (Müll. Arg.) Pichon	frequent	shrub / tree	woodland / forest	135300
Landolphia camptoloba (K.Schum.) Pichon	frequent	liana	woodland / forest	132537

Species name	**Frequency**	**life form**	**habitat**	**Collection number(s)**
Landolphia gossweileri (Stapf) Pichon	rare	dwarfshrub	geoxylic grassland (sandy soils)	133048
Strophanthus welwitschii (Baill.) K.Schum.	frequent	shrub / liana	woodland / forest	135336; 135378; 134091
ASPARAGACEAE				
Asparagus sp. 135286	frequent	shrub	woodland / forest	135286
Asparagus cf. *africanus* Lam.	very rare	shrub	woodland / forest	134115
ASTERACEAE				
Helichrysum kraussii Sch.Bip	occasional	shrub	woodland / forest	132695
CRYSOBALANACEAE				
Parinari capensis Harv.	frequent	dwarfshrub / geoxyle	geoxylic grassland (sandy soils)	132664; 132898; 140068
Parinari curatellifolia Planch. exBenth.	common	tree	woodland / forest	132444
COMBRETACEAE				
Combretum acutifolium Exell	very rare	liana / shrub	woodland / forest	135306
Combretum collinum Fresen.	common	tree	woodland / forest	139176
Combretum elaeagnoides Klotzsch	very rare	tree	woodland / forest	132538
Combretum engleri Schinz	frequent	shrub	woodland / forest	133216
Combretum platypetalum subsp. *platypetalum* Welw. ex M.A.Lawson	occasional	dwarfshrub	geoxylic grassland (sandy soils)	132639; 134114; 140113
Combretum schumannii Engl.	rare	shrub	woodland / forest	139048
Combretum zeyheri Sond.	frequent	shrub / tree	woodland / forest	135280; 132510
Pteleopsis anisoptera (Welw.) Engl. & Diels	frequent	shrub / tree	woodland / forest	135365; 134110; 139066
Terminalia brachystemma Welw. ex Hiern	frequent	tree	woodland / forest / grassland (sandy and ferralitic soils)	132997; 134088; 134131
DICHAPETALACEAE				
Dichapetalum cymosum (Hook.) Engl.	frequent	dwarfshrub / geoxyle	geoxylic grassland (sandy soils)	140165
DIPTEROCARPACEAE				
Monotes africanus A.DC.	common	tree	woodland / forest	132917; 134160; 134228

Species name	**Frequency**	**life form**	**habitat**	**Collection number(s)**
Monotes angolensis de Wild.	very rare	tree	woodland / forest	132443
Monotes caloneurus Gilg.	rare	tree	woodland / forest	134820
Monotes dasyanthus Gilg	common	tree	woodland / forest	132907; 132961; 139228
EBENACEAE				
Diospyros batocana Hiern	occasional	shrub / tree	woodland / forest	139247
Diospyros chamaethamnus Dinter ex Mildbr.	frequent	dwarfshrub / geoxyle	geoxylic grassland (sandy soils)	140179
Diospyros pseudomespilus subsp. *brevicalyx* Mildbr.	frequent	shrub	woodland / forest	135379
Diospyros virgata (Gürke) Brenan	occasional	shrub	woodland / forest	132941
Euclea crispa subsp. *crispa* (Thunb.) Gürke	frequent	dwarfshrub		135413
ERICACEAE				
Erica benguellensis (Welw. ex Engl.) E.G.H. Oliv.	very rare	shrub / tree	woodland / forest	139235
EUPHORBIACEAE				
Bridelia sp. 139095	occasional	shrub / tree	woodland / forest	139095
Hymenocardia acida Tul.	frequent	shrub / tree	woodland / forest	134099; 134135; 139068
Maprounea africana Müll. Arg.	rare	shrub / tree	woodland / forest	139113
Phyllanthus angolensis Müll. Arg.	rare	dwarfshrub	woodland / forest	139256
Phyllanthus sp. 139238	common	dwarfshrub	woodland / forest	139238
Phyllanthus welwitschianus Müll. Arg.	common	dwarfshrub	woodland / forest	139237
Pseudolachnostylis maprouneifolia Pax	occasional	tree	woodland / forest	132555; 134232; 139038
Sclerocroton oblongifolius (Müll.Arg.) Kruijt&Roebers	frequent	dwarfshrub	woodland / forest	132990; 134185
Uapaca sp. 134199	common	dwarfshrub / geoxyle	geoxylic grassland (ferralitic soils)	132490; 134199
Uapaca kirkiana Müll.Arg.	common	tree	woodland / forest	-
Uapaca nitida var. *nitida* Müll.Arg.	common	tree	woodland / forest	132691; 132912; 132998

Species name	**Frequency**	**life form**	**habitat**	**Collection number(s)**
FABACEAE				
Abrus melanospermus subsp. s*uffruticosus* (Boutique) D.K.Harder	occasional	dwarfshrub / geoxyle	geoxylic grassland (sandy soils)	140167
Albizia antunesiana Harms	frequent	tree	woodland / forest	134156; 135318; 139223
Albizia gummifera (J.F.Gmel) C.A.Sm.	occasional	shrub / tree	woodland / forest	139065; 135342; 132967
Baphia bequaertii De Wild.	frequent	shrub / tree	woodland / forest	135360; 139242; 133018
Bauhinia petersiana Bolle	common	shrub	woodland / forest	135311
Bobgunnia madagascariensis (Desv.) J.H.Kirkbr. &Wiersema	frequent	shrub / tree	woodland / forest	132963; 139128
Brachystegia bakeriana Hutch. & Burtt Davy	common	tree	woodland / forest	135298; 139016
Brachystegia longifolia Benth.	occasional	tree	woodland / forest	132957; 139255
Brachystegia spiciformis Benth.	common	tree	woodland / forest	132676
Burkea africana Hook.	common	tree	woodland / forest	-
Copaifera baumiana Harms	common	shrub	woodland / forest	132900; 135335; 139233
Crotalaria amoena Welw. ex Baker	rare	dwarfshrub	woodland / forest	139121
Crotalaria cistoides Welw. ex Baker	rare	dwarfshrub	woodland / forest	139257
Crotalaria florida Welw. ex Baker	rare	dwarfshrub	woodland / forest	139196
Cryptosepalum exfoliatum subsp. *pseudotaxus* (Baker f.) P.A.Duvign. & Brenan	common	tree	woodland / forest	135304; 139023
Cryptosepalum exfoliatum subsp. *suffruticans* (P.A.Duvign.) P.A.Duvign. & Bre	common	dwarfshrub	geoxylic grassland (ferralitic soils)	132754; 132825
Cryptosepalum maraviense Oliv.	common	dwarfshrub	geoxylic grassland (ferralitic soils)	135308B; 135620
Dalbergia nitidula Welw. ex Baker	rare	shrub / tree	woodland / forest	139236
Dialium englerianum Henriq.	frequent	shrub / tree	woodland / forest	133147; 139034
Dolichos sp. 140088	frequent	dwarfshrub / geoxyle	geoxylic grassland (ferralitic soils)	140088
Entada arenaria Schinz	very rare	dwarfshrub	geoxylic grassland (sandy soils)	134147
Eriosema sp. 133109 Pseudo-species	rare	dwarfshrub	geoxylic grassland (ferralitic soils)	133109

Species name	**Frequency**	**life form**	**habitat**	**Collection number(s)**
Eriosema sp. 132895 Pseudo-species	rare	dwarfshrub	geoxylic grassland (ferralitic soils)	132753; 132895
Erythrina abyssinica Lam. ex DC.	very rare	tree	giant termite mounds	-
Erythrophleum africanum (Welw. ex Benth.) Harms	common	tree	woodland / forest	135333
Guibourtia coleosperma (Benth.) J.Léonard	occasional	tree	woodland / forest	139054
Humularia welwitschii (Taub.) P.A.Duvign.	common	dwarfshrub	woodland / forest	139146
Indigofera baumiana Harms	frequent	shrub	woodland / forest	132530
Indigofera congesta Welw. ex Baker	occasional	dwarfshrub	woodland / forest	139237
Kotschya strobilantha (Welw. ex Baker) Dewit & P. A. Duvign. var. *strobilantha*	rare	dwarfshrub / geoxyle	geoxylic grassland (ferralitic soils)	139141
Mucuna sp. 140052	frequent	dwarfshrub / geoxyle	geoxylic grassland (sandy soils)	140052
Pericopsis angolensis (Baker) Meeuwen	frequent	shrub / tree	woodland / forest	139181
Pterocarpus angolensis DC	occasional	tree	woodland / forest	
HYPERICACEAE				
Psorospermum febrifugum Spach.	rare	shrub / tree	woodland / forest	139036
Psorospermum tenuifolium Hook.f.	rare	shrub / tree	woodland / forest	132958
IXONANTHACEAE				
Phyllocosmus lemaireanus (De WIld. &T.Durand) T.Durand&H.Durand	common	shrub	woodland / forest	132968; 133005; 133149
LAMICACEAE				
Alvesia rosmarinifolia Welw.	occasional	shrub	woodland / forest	134776; 132533
Tinnea sp. 133121	frequent	dwarfshrub	geoxylic grassland (ferralitic soils)	133121
Vitex doniana Sweet	occasional	shrub	woodland / woodland ecotone	132915
Vitex madiensis Oliv.	frequent	shrub	woodland / woodland ecotone	132996; 139069
MELASTOMATACEAE				
Memecylon flavovirens Baker	frequent	shrub / tree	woodland / forest	132519; 133161; 139240
Warneckea sapinii (De WIld.) Jacq.-Fél.	occasional	tree	woodland / forest	135309; 139140

Species name	**Frequency**	**life form**	**habitat**	**Collection number(s)**
MELIACEAE				
Ekebergia benguelensis Welw. ex C.DC.	occasional	shrub	woodland / forest	132546; 133000; 133096
MORACEAE				
Ficus pygmaea Welw. ex Hiern	rare	dwarfshrub	riverine	141510
Ficus sp. 141539	rare	dwarfshrub	riverine	141539
MYRICACEAE				
Morella serrata (Lam.) Killick		dwarfshrub / geoxyle		
MYRSINACEAE				
Myrsine africana L.	common	shrub	woodland / forest	134107; 134278; 139024
MYRTACEAE				
Syzygium guineense subsp. *barotsense* F.White	occasional	tree	woodland / forest	135813
Syzygium guineense subsp. *macrocarpum* (Engl.) F.White	common	shrub / tree	woodland ecotone	135800; 135796
Syzygium guineense subsp. *huillense* (Hiern) F.White	frequent	dwarfshrub	geoxylic grassland (sandy soils)	133072; 135614; 135882
OCHNACEAE				
Ochna afzelii subsp. *mechowiana* R.Br. ex Oliv.	rare	dwarfshrub / geoxyle	woodland / grassland	133128
Ochna arenaria De Wild. &T.Durand	frequent	dwarfshrub	woodland, geoxylic grassland (sandy and ferralitic soils)	132947; 133024; 140016
Ochna manikensis De Wild.	frequent	dwarfshrub	geoxylic grassland (sandy soils)	132654; 132803
Ochna pulchra Hook.	common	shrub / tree	woodland / forest	135381; 139064
Ochna pygmaea Hiern	common	dwarfshrub / geoxyle	woodland / forest, grassland (sandy soils)	139239; 140154
OLACACEAE				
Jasminum pauciflorum Benth.	rare	liana / shrub	woodland / forest	139238

Species name	**Frequency**	**life form**	**habitat**	**Collection number(s)**
Schrebera trichoclada Welw.	rare	shrub / tree	woodland / forest	139189
OROBANCHACEAE				
Sopubia karaguensis Oliv.	rare	dwarfshrub	woodland / forest	139033
PASSIFLORACEAE				
Paropsia brazzaeana Baill.	common	shrub	woodland / forest	135299; 139242
PICODENDRACEAE				
Oldfieldia dactylophylla (Welw. ex Oliv.) J.Léonard	rare	shrub / tree	woodland / forest	139208
POLYGALACEAE				
Securidaca longepedunculata Fresen	occasional	tree	woodland / forest	133017
POLYGONACEAE				
Oxygonum fruticosum Dammer ex Milne-Redh.	frequent	shrub	woodland / forest	135322; 133032; 139164
PROTEACEAE				
Faurea intermedia Engl. &Gilg	occasional	shrub / tree	woodland / forest	132720; 139072
Faurea rochetiana (A.Rich.) Chiov. ex Pic.Serm.	frequent	tree	woodland / forest / ecotone	135307
Faurea saligna Harv.	occasional	tree	geoxylic grassland (ferralitic soils)	132549; 132980; 134205
Protea baumii Engl. &Gilg.	occasional	dwarfshrub	woodland / forest	132501; 133019; 134225
Protea gaguedi J.F.Gmel.	frequent	tree	woodland / forest	132918
Protea angolensis var *divaricarta* (Engl. & Gilg.) Beard	rare	dwarfshrub	geoxylic grassland (ferralitic soils)	134200
Protea micans subsp. *trichophylla* Welw.	occasional	dwarfshrub		132607; 140096
Protea petiolaris subsp. *petiolaris* (Hier) Baker &C.H.Wright	frequent	tree	woodland / forest	132982
Protea cf. *welwitschii* Engl.	rare	dwarfshrub	geoxylic grassland (ferraliticsoils)	132480
Protea sp. 133045	rare	dwarfshrub	geoxylic grassland (sandy soils)	133045
RHAMNACEAE				

Species name	**Frequency**	**life form**	**habitat**	**Collection number(s)**
Ziziphus mucronata Willd.	rare	shrub	woodland / forest	133093; 135285
RUBIACEAE				
Ancylanthos rubiginosus Desf.	rare	dwarfshrub	geoxylic grassland (on sandy soils) & woodland ecotone	136003
Fadogia cf. *chrysantha* K.Schum.	very rare	shrub	woodland ecotone	134257
Fadogia cf. *triphylla* var. *triphylla* Baker	very rare	shrub	woodland / forest	132987; 133081
Fadogia fuchsioides Welw. exOliv.	occasional	shrub	woodland / forest	132524
Fadogia homblei De Wild.	rare	dwarfshrub / geoxyle	geoxylic grassland	
Fadogia monticola Robyns	rare	dwarfshrub / geoxyle	geoxylic grassland	
Fadogia sp. 134097	occasional	shrub	geoxylic grassland (ferralitic soils), woodland ecotone	132453; 134097; 134167
Gardenia brachythamnus (K.Schum.) Launert	very rare	dwarfshrub	woodland ecotone	135338
Keetia cf. *gracilis* (Hiern) Bridson	very rare	shrub	woodland / forest	132442; 133148
Keetia venosa (Oliv.) Bridson	rare	shrub	woodland / forest	132534A
Leptactina benguellensis (Welw. ex Benth. &Hook.f.) R.D.Good	rare	dwarfshrub	woodland / forest	135313; 135353; 133153
Leptactina prostrata K.Schum	very rare	dwarfshrub	geoxylic grassland (ferralitic soils)	134181
Pachystigma pygmaeum (Schltr.) Robyns	frequent	dwarfshrub / geoxyle	geoxylic grassland (sandy soils)	140138
Pygmaeothamnus cf. *chamaedendrum* (Kuntze) Robyns	very rare	dwarfshrub	geoxylic grassland (sandy soils)	132723
Pygmaeothamnus sp. 132552	very rare	dwarfshrub	woodland / forest	132552
Pygmaeothamnus zeyheri (Sond.) Robyns	rare	dwarfshrub	geoxylic grassland (sandy soils)	132798; 133033; 134089
Rytigynia orbicularis (K.Schum.) Robyns	frequent	shrub	woodland / forest	132925; 134127; 139056
Tapiphyllum cf. *psammophilum* (S.Moore) Robyns	very rare	shrub	woodland / forest	134279

Species name	**Frequency**	**life form**	**habitat**	**Collection number(s)**
Tricalysia angolensis A.Rich. ex DC.	very rare	shrub	woodland / forest	132500;133012
Tricalysia sp. 134221	rare	shrub	woodland / forest	134221
Tricalysia coriacea subsp. *nyassae* (Benth.) Hiern	occasional	shrub	woodland / forest	133008; 134095; 134170
Tricalysia sp. 135367	very rare	shrub	woodland / forest	135367
SANTALACEAE				
Thesium sp. 139228	rare	dwarfshrub		139228
SAPOTACEAE				
Chrysophyllum bangweolense R.E.Fr.	rare	tree	woodland / forest	135359
Englerophytum magalismontanum (Sond.) T.D.Penn.	common	shrub	woodland / forest	135320; 133151; 139109
SMILACACEAE				
Smilax anceps Willd.	rare	shrub		135308A
STRYCHNACEAE				
Strychnos cocculoides Baker	frequent	shrub / tree	woodland / forest	139070
Strychnos pungens Soler.	common	shrub / tree	woodland / forest	139254
Strychnos spinosa Lam.	occasional	tree	woodland / forest	135301

CHAPTER 3

Dry tropical forests of the Cubango Basin in southern Africa - A first classification and assessment of their woody species diversity.

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Ready to be sumbitted to *Phytocoenologia*

Abstract

The socio-ecological systems of the Cubango Basin in south east Angola are subject to rapid socio-economic transformations. However, sustainable land management planning is hampered by the lack of ecological information. In this study, we present a first comprehensive overview of the vegetation types and species composition of the dry tropical forests and woodlands of the Cubango Basin and provide estimates of the size of the woody species pool.

Based on a plot-based vegetation survey covering all major vegetation types of the Cubango Basin we used the woody species data to carry out a classification of 190 relevés sized 1,000 m^2 applying a numerical classification approach. We compared the vegetation properties and the environmental characteristics of the derived communities using an ANOVA and a Tukey HSD post-hoc test. The number of woody species was estimated using four non-parametric species richness estimators.

We provided a detailed description of the twelve derived woody plant communities in terms of species composition, structure and habitat characteristics. At the scale of the Basin, climate was the most important driver. Topsoil properties did not vary much throughout the study area but higher contents of silt and clay in the lower soil horizons governed species composition in the Miombo woodlands. Additionally, we showed how the usage of remotely sensed land surface phenology metrics can add value to and support the interpretation of ecological properties of plant communities. The number of woody species in the entire Cubango Basin was estimated at 471±29 species, for the Miombo woodlands at 302±11 and for the *Baikiaea* woodlands at 262±20.

The presented classification scheme, the analysis of the environmental requirements provide a solid basis for future investigations of the vegetation of southeast Angola and will provide a robust basis for conservation planning and sustainable natural resource management.

Key words: Angola; *Baikiaea* woodlands; geoxylic suffrutex; Miombo

Introduction

The urgent need to halt loss of biodiversity is an important challenge which requires detailed knowledge of the species and the systems involved. While diversity hot spots and tropical rainforests have been in the focus of research, dry tropical forests have received much less attention (Miles et al. 2006). The dry tropical forest of sub-Saharan Africa harbour a rich biodiversity and at the same time safeguard the daily livelihoods of millions of people in rural areas (Chidumayo & Gumbo 2010). They provide important regulating functions e.g. for the water cycle and regional climate as well as provisioning ecosystem services such as fuel wood, charcoal, and a plethora of other woody and non-woody products (Chidumayo & Gumbo 2010). Currently, many rural societies in sub-Saharan Africa depend on subsistence agriculture and rely on the provision of ecosystem services of dry tropical forest ecosystems. At the same time population growth (United Nations, Department of Economic and Social Affairs 2015), industrialised agricultural schemes, e.g. the 'emerging soybean frontier' (Gasparri et al. 2015), and new development corridors (Laurance et al. 2015) pose enormous challenges for sustainable land management in sub-Saharan Africa.

All dry tropical forests are currently subject to a large array of anthropogenic threats (Miles et al. 2006). The global analysis of patterns of deforestation revealed that central Angola has become a hot spot of recent deforestation (Hansen et al. 2013). Yet, extensive tracts of pristine forests and woodlands still exist in Angola. According to a FAO report from 2010 Angola had at this time a forest cover of 58 million hectares equalling 47% of its land surface (FAO 2010). However, with the end of the decades of civil war in 2002 rapid economic development started, igniting intensive transformation and deforestation processes. In spite of the urgent need of natural resource management with a long term perspective, relevant environmental and ecological information is mostly unavailable for decision makers. A national forest inventory is lacking and floristic data is mostly limited to the literature of the pre-independence era. It is primarily based on the works of early botanists exploring Angola such as Welwitsch (1869) and Baum (1903). The first attempt to compile a Flora for Angola, the 'Conspectus Florae Angolensis', was started in the 1930ies but never reached completion (Exell & Mendonça 1937); important botanical families remain untreated. The first countrywide vegetation map was created by (Gossweiler & Mendonça 1939) and a more detailed map produced by Barbosa (1970). However, these maps delimit large scale vegetation units only and are based on expert knowledge; no quantitative data was involved in the process of map making. On a regional level, for the province of Bié Monteiro (1970) mapped the woodlands of the province based on over hundred vegetation-plots. For the Cuando Cubango province no similar work is available; the vegetation map of Cuando Cubango by Dos Santos (1982) is solely based on floristic itineraries. In comparison to southern Angola, the vegetation of northern Namibia is well covered by the country wide mapping scheme and the phytosociological database of Namibia contains many relevés of the Kavango regions (Strohbach & Kangombe 2012). Furthermore, detailed, local studies based on vegetation relevés were carried out (Strohbach & Petersen 2007; Strohbach 2013).

Thus, there is an urgent need to generate base line data on the floristic composition of the dry forest ecosystems of south east Angola including the underlying environmental drivers governing their distribution. In the context of the Future Okavango project (TFO, www.future-okavango.org, Oldeland et al. 2013) we aimed at closing this gap by initiating a plot-based vegetation survey in 2011. The Okavango River Basin, situated in south-central Africa and shared by the countries of Angola, Namibia and Botswana, constitutes an ideal study system. It comprises pristine Miombo and *Baikiaea* woodlands but is starting to come increasingly under pressure from land use change. As evident from the global study on deforestation by Hansen et al. (2013) the frontier of deforestation is currently advancing exactly on this region. In order to understand trade-offs of future developments a sound understanding of the socio-ecological systems and ecological base line data are urgently needed. In order to gather a first comprehensive overview on woody vegetation and the diversity of woody species in the Cubango Basin, this study aims at

(i) estimating the diversity of woody species and the size of the species pool.
(ii) characterising the woody vegetation communities of the Cubango Basin in terms of their floristic composition.
(iii) analysing the underlying environmental factors that drive the distribution of woody vegetation communities.

Methods

Study site

The Okavango Basin is formed by its two main tributaries the Cubango and the Cuito. However, for reasons of accessibility, this study concentrates in the following on the Cubango Basin located mainly in south east Angola. The river originates on the Angolan Central Plateau at elevations of 1850 m asl. and terminates at the confluence with the Cuito River in Dirico at an elevation of 1068 m. Together with the Cuito River, the Cubango River forms the Okavango River that terminates in the famous endorheic delta in the Kalahari Desert in Botswana. The Basin is shaped by a strong environmental gradient of decreasing precipitation and increasing temperature from the northwest to the southeast. While the upper reaches are sub-humid receiving a mean annual precipitation of over 1400 mm the lower reaches are classified as semi-arid with only 570 mm mean annual precipitation (Weber 2013a; d). The mean annual temperature shows an inverse pattern and rises from 18°C in the northwest to 23°C in the southeast (Weber 2013a). Large areas of the Basin are covered by sandy deposits of the Kalahari system. Thus, nutrient poor and acidic Arenosols are the most common soil type. However, soils with higher content of silt and clay are located on recent and old floodplains (Gröngröft et al. 2013a). The upper Basin exhibits the highest pedodiversity and includes Histosols at the valley bottoms, shallow Plinthisols on the sloping areas, but also here deep and permeable, nutrient poor Arenosols are otherwise dominant (Gröngröft et al. 2013b).

Two major vegetation belts cover the Cubango Basin. The more mesic areas in the north are dominated by Miombo forests and woodlands (Figure 11). At the foot slopes of the Angolan Central Plateau where climate progressively becomes drier the Miombo gives way to more open *Baikiaea-Burkea* woodlands (Revermann & Finckh 2013a; Stellmes et al. 2013a). Next to woodlands there exist various open vegetation types such as edaphic grasslands in the extreme north, tropical peat bogs at the valley bottoms in the Miombo region and anthropogenic shrub- and grasslands. Typically, the footslopes of the gently rolling landscape of the Miombo region are not covered by woodlands, but instead by dwarf shrub-grasslands. These vegetation types, locally referred to as "anharas de ongote", are dominated by geoxylic suffrutices. These dwarf shrubs have an enormous underground woody biomass, in many cases have closely related tree species growing in the neighbouring woodlands, and are a unique feature of the Zambezian Phytoregion

(White 1976). All vegetation types mentioned were included in the study, only the wetland vegetation was excluded.

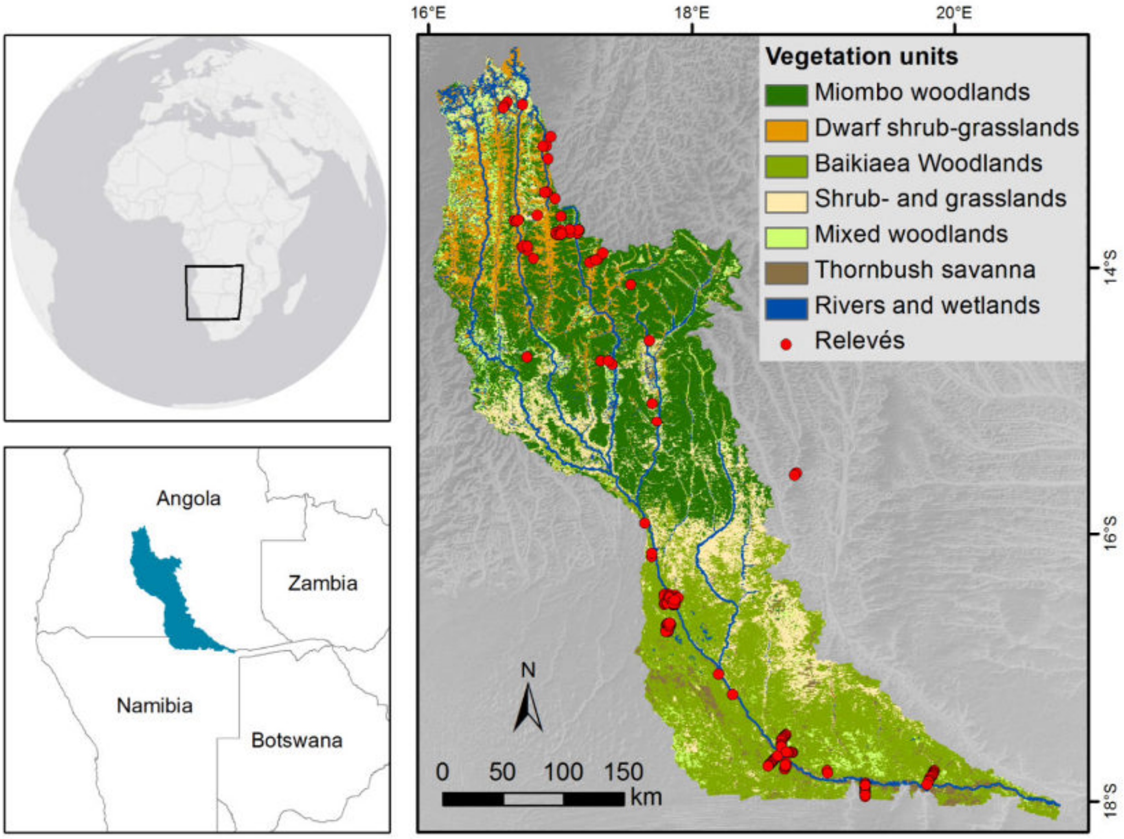

Figure 11 The location of the Cubango Basin in south central Africa and its major vegetation units (modified from Stellmes et al. 2013b). Locations of the 191 relevés surveyed for this study are denoted as red dots.

Vegetation data

Vegetation-plots followed a nested design of a 20 m x 50 m plot with 10 m x 10 m plot resting in the centre (Figure S1). However, for the classification we used the larger plot size only. The sampling aimed at covering all major vegetation types of the Cubango Basin and followed a random stratified sampling design. However, limited access routes and the danger of land mines put serious constraints on the sampling. Plots were distributed randomly in the major vegetation types as mapped by (Stellmes et al. 2013a) in the GIS and coordinates were transferred to a hand held GPS for localisation in the field. Furthermore, vegetation plots from local in depth studies were also included (Revermann & Finckh 2013b; Revermann et al. 2013, 2016c; Wallenfang et al. 2015). All 191 vegetation plots are stored in the Vegetation Database of the Okavango Basin (GIVD ID AF-00-009, Revermann et al. 2016b).

At every relevé, all vascular plant species present were noted and their projected cover estimated (in %). Furthermore, we assessed the relevé based vegetation parameters listed in Table 3. The taxonomy followed the current Checklist of the Angolan Flora (Figueiredo & Smith 2008). We are aware of recent taxonomic changes but for consistency retained the taxonomy of the national checklist. For the classification we considered the woody vegetation including trees, shrubs, suffrutices and shrublets emerging from a woody rootstock. All species occurring only once or twice were removed for classification, but retained for the analysis of woody plant diversity. In total, 191 plots were used in this classification. One plot, the only one from the gallery forest fringing the Cubango River, was removed after first inspection with detrended correspondence analysis (DCA) as it was a complete outlier and had no species in common with the other plots.

Table 3 Vegetation parameters of the relevés. In the formulas of the diversity indices Shannon and Simpson p_i refers to the abundance of species i / total abundance.

variable	description	method / unit
richness	number of woody species (S)	
shannon	Shannon index (H)	$H = -\text{sum}\ (p_i \ln(p_i))$
simpson	Simpson index (D)	$D = \text{sum}\ (p_i^2)$
shannon.evenness	Shannon Evenness index	$J = H / \ln(S)$
soft.litter	cover of litter	estimated [%]
lichens	cover of lichens	estimated [%]
mosses	cover of mosses	estimated [%]
termitePA	presence (1) or absence (0) of termite mounds	binary
total.cover	ground covered by vegetation (bird's eye view)	estimated [%]
herb	cover in herbal layer (0-0.5 m)	estimated [%]
shrub1	cover in lower shrub stratum (0.5-2 m)	estimated [%]
shrub2	cover in lower shrub stratum (2-5 m)	estimated [%]
tree1	cover in lower tree stratum (5-10 m)	estimated [%]
tree2	cover in upper tree stratum (10-20 m)	estimated [%]
max.height	maximum height in vegetation plot	[m]
main.height	highest point of 90% of vegetation	[m]

Environmental data

At every relevé, three soil samples were taken using an Edelman corer at a depth of 45–55 cm and 70–90 cm. Furthermore, a mixed sample from the upper 10 cm of the soil was taken. All samples were analysed for the physical and chemical soil properties listed in Table 4. We compiled bioclimatic variables from regionalised climatologies of a regional climate model for current climate (Weinzierl et al. 2013). Micro-climatic differences related to the topography play an important role and determine vegetation patterns in the rolling landscape of the upper Basin (Revermann & Finckh 2013c; Finckh, Revermann & Aidar 2016). Thus, we included three topographic attributes calculated from the global digital elevation model SRTM with a 90-m resolution (Shuttle Radar Topography Mission, Jarvis et al. 2008) in the open source GIS SAGA (Conrad et al. 2015): a) the topographic position index (TPI, Wilson & Gallant 2000), b) the topographic wetness index (TWI, Beven & Kirkby 1979), and c) the topographic ruggedness index (TRI, Riley, DeGloria & Elliot 1999). To assess season length as well as start and end of the vegetation period we used land surface phenology (LSP) metrics calculated from time series of the remotely sensed enhanced vegetation index (EVI). The LSP metrics also give an indication of standing biomass and biomass growth. As such, the 'LargeIntegral' serves as a proxy for the total above ground biomass, the 'BaseValue' for the share of biomass remaining after senescence of the vegetation and the 'Amplitude' for the accumulation of life biomass during the growing season (Table 4, Revermann et al. 2016a).

Statistical analyses

To explore the variation within the vegetation data set, we calculate a detrended correspondence analysis (DCA). The length of the first axis of the DCA, measured in standard deviation units (SD), gives an estimation of the species turnover. A length of SD = 4 indicates one complete turnover (McCune, Grace & Urban 2002). Prior to classifying and visualising vegetation data using ordination we performed a Hellinger transformation. This transformation is known to avoid the horseshoe effect where sites that have no species in common are close to each other in ordination space. Furthermore, Hellinger transformation gives low weight to rare species (Legendre & Gallagher 2001). In order to preserve metric distances we used Euclidean dissimilarities in ordination and classification (Legendre & Gallagher 2001). For visualisation of vegetation data we calculated a Nonmetric Multidimensional Scaling (NMDS). For the classification we chose the

Table 4 Environmental variables used in the analysis of the vegetation data. Soil variables were recorded in three depth. The depth is indicated by a letter following the variable name: U for 0-10 cm depth, M for 45-55cm and 70-90 cm depth.

variable	Description	method / data set
Topography		
elevation	elevation above sea level [m]	recorded in field with handheld GPS
TPI	topographic position index	SRTM 90 m; (Wilson & Gallant 2000)
TRI	topographic ruggedness index	SRTM 90 m; (Riley, DeGloria & Elliot 1999)
TWI	topographic wetness index	SRTM 90 m; (Beven & Kirkby 1979)
Land surface phenology		
Amplitude	maximum EVI - minimum EVI	Derived from 12 year long time series of MODIS EVI; image interval 16 day; MOD13Q1 product with 250 m-resolution (Jönsson & Eklundh 2004; Stellmes et al. 2013a; Revermann et al. 2016a)
BaseValue	lowest value of EVI in the year	
LargeIntegral	total integral of EVI in the year	
SeasonLength	duration of the vegetation period [days]	
Climate		
MAT	mean annual temperature [K]	1-km resolution (Weinzierl et al. 2013)
TDR	mean diurnal range [K]	1-km resolution (Weinzierl et al. 2013)
TAR	tem annual range [K]	1-km resolution (Weinzierl et al. 2013)
MAP	mean annual precipitation [mm]	1-km resolution (Weinzierl et al. 2013)
fire	Number of years with fire	MODIS Burned Area, 250-m spatial resolution (Stellmes et al. 2013c)
frost	number of day with frost	CRU TS3.22, 0.5° spatial resolution (Harris et al. 2014)
Soil roperties		
pHCaCl2	pH in 0.01 M $CaCl_2$	Preparation of soil suspensions by addition of 0.01 M CaCl2 in a 1:2.5 ratio; measurement with a pH electrode after 1 h of repeated stirring
pHdelta	difference between pH in $CaCl_2$ and aq. dest.	pH in aq. dest: preparation of soil suspensions in aq. dest. in a 1:2.5 ratio; measurement with a pH electrode after 1 h of repeated stirring
EC	electrical conductivity	Measurement in an aquademin solution (1:5 ratio) with a conductivity sensor.
sand	sand fraction [%]	(AG Boden 2005)
silt	silt fraction [%]	(AG Boden 2005)

variable	Description	method / data set
clay	clay fraction [%]	(AG Boden 2005)
CEC	cation exchange capacity	1 M NH4–acetate–EDTA extraction
CaCO3	Carbonate content [cat.]	Field method with 12% HCl (AG Boden 2005)

algorithm ISOPAM (isometric feature mapping and partitioning around medoids) introduced by Schmidtlein et al. (2010) and implemented in the R package 'isopam'. ISOPAM is based on the ordination method Isomap (isometric feature mapping, Tenenbaum, de Silva & Langford 2000) and the subsequent classification of the ordination scores of Isomap using partitioning around mediods (PAM, Kaufman & Rousseeuw 1990). The algorithm repeatedly searches for high quality and quantity of indicator species to groups of sites. Compared to other statistical methods ISOPAM has the advantage that it is capable of analysing long gradients and non-linear relationships. The approach searches for the optimal combination of the number of clusters in PAM, the number of neighbours used in ISOMAP and the number of ISOPAM dimensions (Schmidtlein et al. 2010). The maximum number of classes for ISOPAM was set to 20. However, if the algorithms does not find as many as specified as the maximum, the remainder is left empty.

For preparing a synoptic vegetation table the result of the ISOPAM classification was exported to Juice 7.0 (Tichý 2002). As fidelity measure we used the phi value (De Cáceres & Legendre 2009). Species were considered as diagnostic if phi value exceeded > 20 and as highly diagnostic for phi values > 50; the maximum p-value was set to 0.05. Calculation of the phi values were adjusted for unequal group sizes. To assess the quality of the classification we calculated the sharpness in Juice defined as the proportion of diagnostic species in relation to the average species richness (Chytrý & Tichý 2003). The group of clusters at hierarchy level one were considered as major vegetation units and the terminal clusters of the dendrogram (Figure 13) were considered as woody vegetation communities. In some cases neighbouring terminal clusters were joined if this increased overall sharpness of the classification. The derived communities were named after one diagnostic and one dominant species.

Analysing environmental conditions of woody vegetation communities

We compared the diversity, vegetation structure and environmental properties of the derived woody vegetation communities using an analysis of variance (ANOVA). Significant differences were assessed by a Tukey HSD *post-hoc* test (Mendiburu 2015). Canonical correspondence analysis (CCA) was calculated to analyse species-environment relationships using the R package 'vegan' (ter Braak 1987; Oksanen et al. 2015). Furthermore, we partitioned the variance of the vegetation explained by the environmental factors grouped into four categories a) land surface phenology, b) topography, c) climate, and d) soil properties (Table 4). The variance partitioning is based on redundancy analysis and uses adjusted R^2 to assess the contributions of groups of explanatory variables (Borcard, Legendre & Drapeau 1992; Oksanen et al. 2015).

Diversity and estimate of the regional species pool

Any biodiversity survey can never capture all species present in a given ecosystem. The observed number of species is a non-linear function of sampling effort and sampling area (and the number of encountered individuals, Chao et al. 2014). We used sample based rarefaction and extrapolation curves to assess the completeness of our samples of the vegetation. The point where the extrapolated curve reaches the asymptote gives an indication of the size of the species pool. However, it has been shown that non-parametric estimators, making use of detection probabilities of species or the frequency of rare species, i.e. species occurring only once or twice, outperform curve extrapolations in estimating the number of undetected species. Therefore, we calculated four non-parametric richness estimators: a) the improved Chao2 estimator (iChao2, Chiu et al. 2014), b) Incidence-based Coverage Estimator (ICE, Lee & Chao 1994), c) 1st order jackknife (Burnham & Overton 1978), and d) 2nd order jackknife (Burnham & Overton 1978). We did all calculations for the entire data set of the Cubango Basin and also in accordance to the major floristic groups identified at cluster hierarchy level one. Rarefaction curves were constructed using the R package 'iNEXT' (Hsieh, Ma & Chao 2016) and species richness estimators were calculated using the R package 'SpadeR' (Chao, Ma & Hsieh 2016).

In order to compare woody plant diversity of the derived major vegetation units, we calculated Reyni's diversity profiles. The profiles provide a more complete picture of the multifaceted term diversity compared to the calculation of a few arbitrary selected diversity indices (Tóthmérész 1995). The scale parameter α can be mathematically converted to common diversity indices. Low α values represent diversity indices focusing on species richness, while with an increasing α value more weight is given to the aspect of evenness, e.g. α=0 is related to species richness, α=1 to the Shannon diversity index, and α=2 to the inverse Simpson index (Kindt & Coe 2005). One vegetation unit is considered to have higher diversity than another one if the graph is constantly higher and never intersects. The diversity profiles were calculated with the R package 'BiodiversityR' (Kindt & Coe 2005). All statistical analysis were done in R (R Development Core Team 2015).

Results

Results of ISOPAM clustering

The DCA featured a length of 8.62 standard deviation units indicating more than two complete species turnovers within the study area. The ISOPAM cluster algorithm split the vegetation data into three major floristic groups (hierarchy level one of the dendrogram) and yielded 16 terminal clusters with one cluster containing only one relevé (Figure 13). The first group contained the relevés from the Miombo region (terminal clusters 1-5) and the remaining two major groups included relevés belonging to the Zambezian *Baikiaea* woodlands *sensu* White (1983) with two exceptions. In the following, we will refer to these three groups as 'Miombo' (terminal clusters 1-5), wooded grasslands and *Baikiaea* woodlands on Kalahari sands (BW1, terminal clusters 6-9) and *Baikiaea* woodlands on Arenosols with higher nutrient status (BW2, terminal clusters 10-16).

The NMDS (Figure 12) showed a grouping of the relevés from the Miombo region in the upper left corner; the wooded grasslands and *Baikiaea* woodlands on Kalahari sands (BW1) were located at the bottom centre and the *Baikiaea* woodlands on Arenosols with higher nutrient status (BW2) on the right hand side of the NMDS plot. Within the Miombo group terminal cluster 1 composed of relevés from the geoxylic-grasslands formed a well-defined cluster. Within BW2 a well separated cluster containing the terminal clusters 12-14 was recognised in the upper right corner. Terminal cluster six and eleven contained relevés with special site conditions such as giant termite mounds and sites from the floodplains. The relevés of these clusters were widely dispersed in the NMDS plot and overlapped with other clusters. Every terminal cluster was considered as one woody plant community. However, the NMDS (Figure 12) showed strong overlapping among some terminal clusters and they were therefore merged to form one woody plant community.

The following terminal clusters were merged: a) eight and nine, b) 12, 13 and 14, c) 15 and 16. Furthermore, one relevé was shifted from terminal cluster 11 to 6. These measures increased the overall sharpness of the classification from 41.0% to 48.7%.

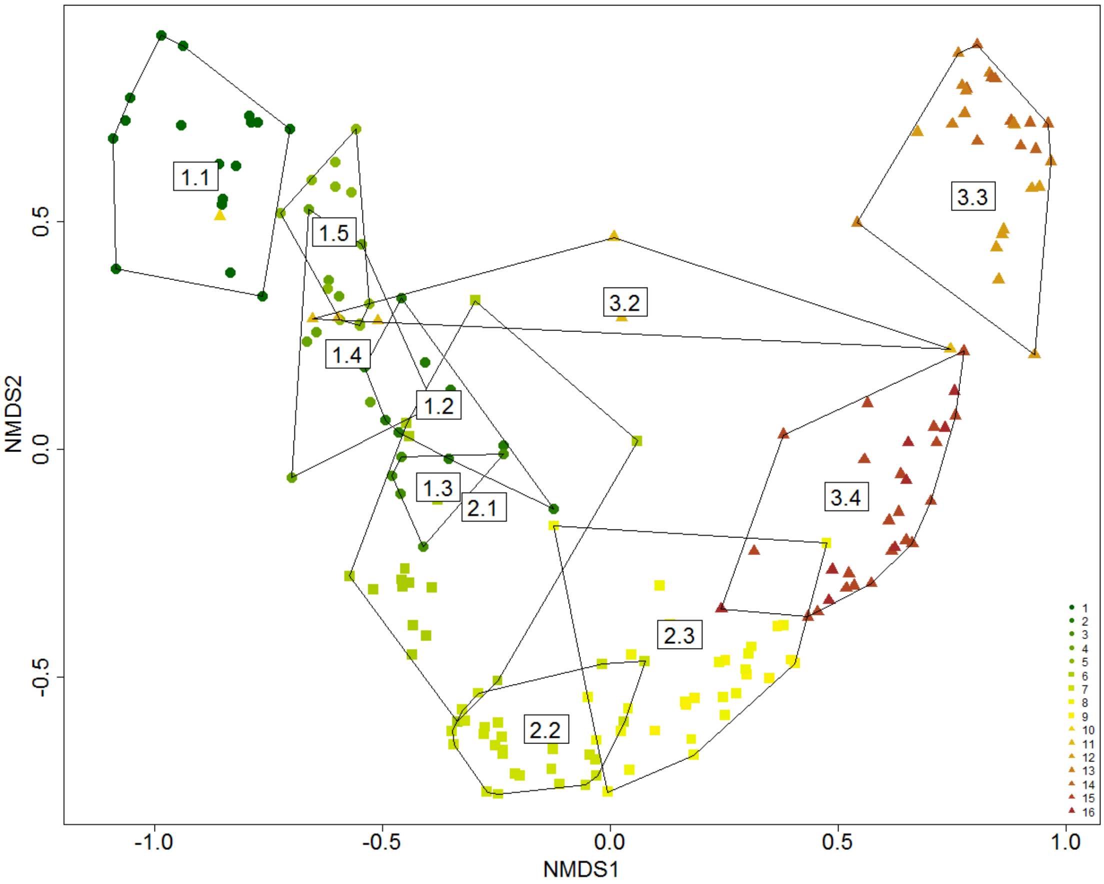

Figure 12 NMDS of vegetation data set using Euclidian dissimilarity matrix of Hellinger transformed vegetation cover. Symbols denote cluster hierarchy 1 (1=squares, 2=circles, 3=triangles), colours denote the 16 different classes of highest hierarchical cluster level five and range from dark green over yellow to brown.

Description of the derived woody vegetation communities

In the following, we provide a detailed description of the derived woody vegetation communities according to the three major floristic groups 1) Miombo woodlands and geoxylic grasslands, 2) wooded grasslands and *Baikiaea* woodlands on Arenosols, and 3) *Baikiaea* woodlands on Arenosols with higher nutrient status in terms of character species based on the synoptic vegetation table (Table 6). Vegetation structure and habitat characteristic are described based on the CCAs in Figure 16 and Figure S4, the geographical distribution in Figure S2 and the results of the ANOVAs in Figure S3. Exemplary photographs of the 12 described communities are displayed in Figure 14.

The tree species *Burkea africana*, *Erythrophleum africanum*, *Pterocarpus angolensis*, *Guibourtia coleosperma*, and *Ochna pulchra* occurred almost in all vegetation communities and can therefore be considered as characteristic for the woody vegetation of the Cubango Basin as a whole.

Group one: Miombo woodlands and geoxylic grasslands of the Angolan Central Plateau

The major vegetation unit one containing the Miombo woodlands was clearly set apart by 74 exclusively diagnostic species. Species frequently cited as typical Miombo species formed the tree layer: *Brachystegia spiciformis*, *B. longifolia*, *Julbernardia paniculata* and *Cryptosepalum exfoliatum* subsp. *pseudotaxus*. Smaller trees included species of the genera *Monotes* and *Uapaca*. Diagnostic shrub species were *Phyllocosmos lemaireanus*, *Sclerocroton oblongifolius*, *Myrsine africana*, *Xylopia tomentosa* and the vine *Landolphia camptoloba*. Only *Erythrophleum africanum*, diagnostic for Miombo woodlands, was also characteristic for vegetation unit two (Table 6).

1.1 (terminal cluster 1): ***Cryptosepalum maraviense-Cryptosepalum exfoliatum ssp. suffruticans***

Characterisation: This plant community is very well defined and contains 27 diagnostic species. Geographically it is confined to the Angolan Central Plateau. Vegetation is open and trees and shrubs are very rare. Instead, geoxylic suffrutices (White 1976) with high underground woody biomass shape this plant community. The geoxylic suffrutices *Cryptosepalum maraviense* and *Cryptosepalum exfoliatum* subsp. *suffruticans* are highly diagnostic and dominant. Geoxylic shrubs of various families enrich the flora of this plant community. Colourful resprouting of the geoxyles at the end of the dry season lends this plant community a unique appearance.

Structure: trees and larger shrubs absent, dominated by dwarf shrubs and Poaceae, the latter becoming dominant in the second half of the wet season.

Habitat: This vegetation unit usually occurs on footslopes leading down to the stream network but characteristic species may also occur on regenerating fallows. Soils are mostly shallow and ferralitic, rarely also occurring on deep, sandy and leached soils.

1.2 (terminal cluster 2): ***Cryptosepalum exfoliatum ssp. pseudotaxus-Copaifera baumiana***

Characterisation: typical Miombo woodland with a high share of evergreen species, geographical at the centre and southern part of the Miombo belt under study.

Cryptosepalum exfoliatum subsp. *pseudotaxus* and *Brachystegia bakeriana* are both highly characteristic and dominant tree species in this plant community. Characteristic shrubs and small trees: Warneckea sapinii, Psorospermum tenuifolium, Baphia bequaertii, Ekebergia benguellensis. This plant community shares many characteristic shrub species with plant community 1.4 including *Englerophytum magalismontanum*, *Phyllocosmus lemaireanus*, *Uvaria angolensis*, *Chrysophyllum bangweolense* and the liana *Landolphia camptoloba*. *Copaifera baumiana* and *Rytigynia orbicularis* are a linkage to plant community 1.3.

Structure: Herb, shrub and tree layer equally contribute to a high total vegetation cover. It ranges among the highest in the study area and the canopy height is among the highest. High values of 'LargeIntegral' indicate a high above ground biomass.

Habitat: A high ground cover by mosses and presence of lichens indicate that this plant community rarely burns. Many evergreen species contribute to a more humid microclimate also in the dry season. The soils are sandy throughout the entire soil profile. In contrast to the communities 1.4 and 1.5, the *Cryptosepalum exfoliatum ssp. pseudotaxus-Copaifera baumiana* community does not show a higher content of fine material in the lower soils horizon and thus indicates a lower nutrient level of the sites occupied by this community.

1.3 (terminal cluster 3): ***Diospyros batocana-Julbernardia paniculata***

This cluster represents the transition of the Miombo to the *Baikiaea* woodlands of the southern reaches of the Cubango Basin. It still contains species usually associated with Miombo; however, typical trees of wetter Miombo are absent, i.e. *Brachystegia spiciformis* and *Cryptosepalum exfoliatum* ssp. *pseudotaxus*.

Structure: The canopy is more open than in the other vegetation communities of the Miombo woodlands and the canopy is mostly restricted to the tree layer below 10 m.

Habitat: Mean annual temperature is significantly higher than in the rest of the Miombo area and the mean annual precipitation with only 700 mm is significantly lower (Figure S3b). Therefore, this unit represents the transition to the drier *Baikiaea* woodlands of the middle reaches of the Cubango River. Similarly, soils are often deep Arenosols and hence closer related to the ones of the more southern relevés with a low proportion of fine material.

1.4 (terminal cluster 4): ***Brachystegia spiciformis-Phyllocosmus* lemaireanus**

Characterisation: Mature stands of Miombo woodland dominated by typical Miombo species *Brachystegia spiciformis, Brachystegia longifolia, Julbernardia paniculata* and

Cryptosepalum exfoliatum ssp. *pseudotaxus*. It resembles the core area of the Miombo region and features, together with 1.2, the highest species richness. It shares many character species with 1.2 and 1.5.

Structure: High tree coverage but still enough light is reaching the ground to support a rich shrub and herbal layer.

Habitat: Soils have a substantial share of clay and silt. However, they are still classified as rubic Arenosols. Fire usually does not affect the woodlands, due to the dense canopy and the more humid micro-climatic conditions, this vegetation unit is rather fire resistant, indicated also by high coverage with soft litter and the presence of lichens and mosses.

1.5 (terminal cluster 5): ***Uapaca kirkiana-Julbernardia paniculata***

Characterisation: Open Miombo woodland characterised by smaller tree species such as *Uapaca kirkiana*, *U. nitida* var. *nitida*, *Protea gaguedii* and *Faurea rochetiana*. Shrubs include *Myrsine africana*, *Mucuna stans* and *Rothmania engleriana*. Often found in ecotone situations or in areas with strong human impact.

Structure: This community has a more open character with slightly lower vegetation cover in the upper tree canopy and generally slightly lower vegetation height if compared to the other Miombo communities. A low 'BaseValue' and a high 'Amplitude' in comparison to the other Miombo communities suggests that more biomass dies off during the dry season.

Habitat: Mostly ferralitic soils with a higher silt and clay content. Underlying laterite was observed in some occasions.

Table 5 Overview of plant communities and terminal cluster (term. cl.), number of relevés, diagnostic species (diagn.), constant species (consts.), dominant species (diagn.), and sharpness of the woody plant communities.

No.	Term. cl.	Formation	Vegetation type	Plant community	relevés	diagn.	const.	dom.	sharpness
1.1	1	Miombo	Suffrutex grassland	*Cryptosepalum maraviense-Cryptosepalum exfoliatum ssp. suffruticans*	17	27	11	2	68.7
1.2	2	Miombo	Dense forest	*Cryptosepalum exfoliatum ssp. pseudotaxus-Copaifera baumiana*	9	31	16	5	46.6
1.3	3	Miombo	Dense woodland	*Diospyros batocana-Julbernardia paniculata*	5	15	18	1	32.7
1.4	4	Miombo	Forest	*Brachystegia spiciformis-Phyllocosmus lemaireanus*	9	30	16	4	43.6
1.5	5	Miombo	Woodland	*Uapaca kirkiana-Julbernardia paniculata*	12	31	10	4	55.7
2.1	6	*Baikiaea* woodlands	Wooded grassland	*Gymnosporia senegalensis – Burkea africana*	17	17	12	1	35.7
2.2	7	*Baikiaea* woodlands	Woodland	*Dichapetalum rhodesicum-Dialium englerianum*	26	14	18	2	34.1
2.3	8+9	*Baikiaea* woodlands	Woodland	*Combretum psidioides-Schinziophyton rautanenii*	31	22		3	38.2
3.1	10	Miombo	Suffrutex grassland	*Protea micans ssp. trichophylla-Syzygium guineense ssp. macrocarpum*	1	3	5	0	54.6
3.2	11	*Baikiaea* woodlands	Wooded grassland	*Piliostigma thonningii-Acacia sieberiana*	6	7	1	0	47.5

No.	Term. cl.	Formation	Vegetation type	Plant community	relevés	diagn.	const.	dom.	sharpness
3.3	12+13+14	*Baikiaea* woodlands	Thicket	*Combretum celastroides-Baikiaea plurijuga*	28	23		5	80.5
3.4	15+16	*Baikiaea* woodlands	Woodland	*Vitex angolensis-Terminalia sericea*	29	15		4	45.9

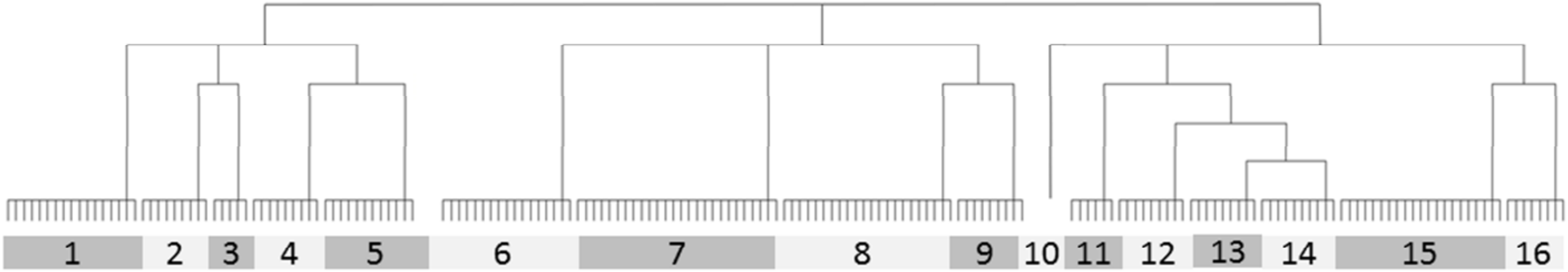

Figure 13 Dendrogram of the ISOPAM clustering of 190 relevés sized 1,000 m^2. Terminal clusters 1-5 comprise the Miombo group, terminal clusters 6-9 the wooded grasslands and *Baikiaea* woodlands on Kalahari sands (BW1) and terminal clusters 10-16 the *Baikiaea* woodlands on Arenosols with higher nutrient status (BW2).

Table 6 Combined synoptic table for the three major vegetation units derived from classification showing the cluster hierarchy level 1. The strength of the association of a species to the major vegetation unit was measured using the phi value standardizing for different group sizes. Only species with a phi value > 20 and a p-value <0.05 are shown. Frequent species occuring in more than half of the relevés of the community are marked with an asterisks following the phi value.

Group No. / Plant community	1	2	3	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3	3.1	3.2	3.3	3.4
Rank	Gr	Gr	Gr	VC	VC	VC	VC	VC	VC	VC	VC	VC	VC	VC	VC
ISOPAM terminal cluster(s)	1-5	6-9	10-16	1	2	3	4	5	6	7	8-9	10	11	12-14	15-16
No. of relevés	52	74	64	17	9	5	9	12	17	26	31	1	6	28	29
Cryptosepalum maraviense	51	---	---	96*	---	---	---	---	---	---	---	---	---	---	---
Pleiotaxis sp. 132909	50	---	---	85*	---	---	---	---	---	---	---	---	---	---	---
Cryptosepalum exfoliatum ssp. suffruticans	54	---	---	80*	---	---	---	---	---	---	---	---	---	---	---
Indigofera sutherlandoides	53	---	---	78*	---	---	---	---	---	---	---	---	---	---	---
Pleiotaxis cf. antunesii	39	---	---	70*	---	---	---	---	---	---	---	---	---	---	---
Monotes africanus	54	---	---	61*	---	---	---	---	---	---	---	---	---	---	---
Ochna sp. 134177	35	---	---	53	---	---	---	---	---	---	---	---	---	---	---
Protea angolensis var. divaricata	26	---	---	53	---	---	---	---	---	---	---	---	---	---	---
Syzygium guineense ssp. huillense	26	---	---	53	---	---	---	---	---	---	---	---	---	---	---
Asteraceae sp. 134155	26	---	---	53	---	---	---	---	---	---	---	---	---	---	---
Unknown 134262	23	---	---	47	---	---	---	---	---	---	---	---	---	---	---
Uapaca sp. 134199	28	---	---	44	---	---	---	---	---	---	---	---	---	---	---
Unknown dwarf shrub 134146	20	---	---	41	---	---	---	---	---	---	---	---	---	---	---
Indigofera 134314	31	---	---	40	---	---	---	---	---	---	---	---	---	---	---
Fabaceae sp. 134823	26	---	---	39	---	---	---	---	---	---	---	---	---	---	---
Combretum platypetalum	---	---	---	34	---	---	---	---	---	---	---	---	---	---	---
Faurea saligna	28	---	---	31	---	---	---	---	---	---	---	---	---	---	---
Leptactina prostrata	28	---	---	29	---	---	---	---	---	---	---	---	---	---	---
Ochna pygmaea	35	---	---	27	---	---	---	---	---	---	---	---	---	---	---

Group No. / Plant community	1	2	3	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3	3.1	3.2	3.3	3.4
Ochna arenaria	20	---	---	25	---	---	---	---	---	---	---	---	---	---	---
Eriosema sp. 134248	20	---	---	24	---	---	---	---	---	---	---	---	---	---	---
Strychnos spinosa	20	---	---	22	---	---	---	---	---	---	---	---	---	---	---
Oxygonum fructicosum	26	---	---	---	57	---	---	---	---	---	---	---	---	---	---
Warneckea sapinii	26	---	---	---	57	---	---	---	---	---	---	---	---	---	---
Tricalysia sp. 134221	23	---	---	---	47	---	---	---	---	---	---	---	---	---	---
Psorospermum tenuifolium	26	---	---	---	43	---	---	---	---	---	---	---	---	---	---
Protea baumii	20	---	---	---	40	---	---	---	---	---	---	---	---	---	---
Unknown 134128	---	---	---	---	40	---	---	---	---	---	---	---	---	---	---
Baphia bequaertii	20	---	---	---	36	---	---	---	---	---	---	---	---	---	---
Protea petiolaris ssp. petiolaris	28	---	---	---	26	---	---	---	---	---	---	---	---	---	---
Vitex doniana	28	---	---	---	22	---	---	---	---	---	---	---	---	---	---
Diospyros batocana	23	---	---	---	---	89*	---	---	---	---	---	---	---	---	---
Diospyros virgata	31	---	---	---	16	72*	---	---	---	---	---	---	---	---	---
Lannea discolor	---	---	---	---	---	39	---	---	---	---	---	---	---	---	---
Crotalaria sp. 134168	26	---	---	---	---	---	47	---	---	---	---	---	---	---	---
Phyllanthus welwitschianus	26	---	---	---	---	---	44	19	---	---	---	---	---	---	---
cf. Craterispermum schweinfurthii	20	---	---	---	---	---	38	---	---	---	---	---	---	---	---
Rhus cf. dumetorum	20	---	---	---	---	---	31	---	---	---	---	---	---	---	---
Memecylon flavovirens	26	---	---	---	---	---	27	19	---	---	---	---	---	---	---
Securidaca longepedunculata	---	---	---	---	---	---	24	---	---	10	---	---	---	---	---
Brachystegia floribunda	28	---	---	---	---	---	---	69*	---	---	---	---	---	---	---
Uapaca kirkiana	43	---	---	---	---	---	---	61*	---	---	---	---	---	---	---
Protea gaguedi	28	---	---	---	---	---	---	61*	---	---	---	---	---	---	---
Fabaceae sp. 134603	28	---	---	---	---	---	---	58	---	---	---	---	---	---	---

Group No. / Plant community	1	2	3	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3	3.1	3.2	3.3	3.4
Rothmannia engleriana	23	---	---	---	---	---	---	56	---	---	---	---	---	---	---
Fabaceae sp. 134592	30	---	---	---	---	---	---	54*	---	---	---	---	---	---	---
Faurea rochetiana	37	---	---	---	---	---	---	51*	---	---	---	---	---	---	---
Humularia welwitschii	---	---	---	---	---	---	---	43	---	---	---	---	---	---	---
Monotes adenophyllus ssp. homblei	39	---	---	19	---	---	---	40	---	---	---	---	---	---	---
Syzygium guineense ssp. macrocarpum	40	---	---	---	---	---	---	40*	---	---	---	---	---	---	---
Eriosema sp. 134547	23	---	---	---	---	---	---	39	---	---	---	---	---	---	---
Parinari curatellifolia	39	---	---	13	---	---	---	31*	13	---	---	---	---	---	---
Bridelia tenuifolia	23	---	---	---	---	---	---	23	---	---	---	---	---	---	---
Dombeya burgessiae	---	29	---	---	---	---	---	---	64	---	---	---	---	---	---
Amblygonocarpus andongensis	---	26	---	---	---	---	---	---	63	---	---	---	---	---	---
Gymnosporia senegalensis	---	41	---	---	---	---	---	---	56*	---	---	---	---	---	---
Unknown sp. 134372	---	20	---	---	---	---	---	---	46	---	---	---	---	---	---
Annona stenophylla	---	---	---	---	---	---	---	---	44*	---	---	---	---	---	---
Lannea edulis	---	---	---	---	---	---	---	---	41	---	---	---	---	---	---
Euclea crispa ssp. crispa	---	13	---	---	---	---	---	---	37*	---	---	---	---	---	---
Crossopteryx febrifuga	---	18	---	---	---	---	---	---	35	---	---	---	---	---	---
Parinari capensis	---	---	---	16	---	---	---	---	35*	---	---	---	---	---	---
Peltophorum africanum	---	22	---	---	---	---	---	---	31	---	13	---	---	---	---
Landolphia gossweileri	---	---	---	---	---	---	---	---	28	---	---	---	---	---	---
Dombeya quinqueseta	---	16	---	---	---	---	---	---	27	---	---	---	---	---	---
Bauhinia urbaniana	---	36	---	---	---	---*	---	---	---	57*	---	---	---	---	---
Dialium englerianum	---	37	---	---	---	---	---	---	---	43*	---	---	---	---	---
Cryptolepis oblongifolia	---	26	---	---	---	---	---	---	---	32	---	---	---	---	---
Dalbergia nitidula	---	---	---	---	---	---	---	---	---	24	---	---	---	---	---

Group No. / Plant community	1	2	3	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3	3.1	3.2	3.3	3.4
Indigofera sp. 136064	---	24	---	---	---	---	---	---	---	---	39	---	---	---	---
Clerodendrum dekindtii	---	19	---	---	---	---	---	---	---	---	31	---	---	---	---
Entada arenaria	---	22	---	---	---	---	---	---	---	---	24	---	---	---	---
Commiphora angolensis	---	---	---	---	---	---	---	---	---	---	24	---	---	---	---
Tricalysia cacondensis	---	20	---	---	---	---	---	---	---	19	21	---	---	---	---
cf. Hexalobus monopetalus	---	22	---	---	---	---	---	---	---	---	21	---	---	---	---
Protea micans ssp. trichophylla	---	---	---	3	---	---	---	---	---	---	---	94 *	---	---	---
Indigofera sp. 135325	---	---	---	---	---	---	---	---	---	---	---	91 *	---	---	---
Ochna sp. 134807	---	17	---	---	---	---	---	---	18	---	---	87 *	---	---	---
Acacia sieberiana	---	---	---	---	---	---	---	---	16	---	---	---	58*	---	---
Ximenia americana	---	---	---	---	---	---	---	---	---	---	---	---	51	---	---
Melhania acuminata	---	---	19	---	---	---	---	---	---	---	---	---	39	---	12
Ziziphus mucronata	---	---	---	---	---	---	---	---	---	---	---	---	32	---	---
Combretum celastroides	---	---	67*	---	---	---	---	---	---	---	---	---	---	89*	---
Combretum engleri	---	---	65*	---	---	---	---	---	---	---	---	---	---	79*	---
Rubiaceae sp. 136381	---	---	54	---	---	---	---	---	---	---	---	---	---	77*	---
cf. Feretia aeruginescens	---	---	44	---	---	---	---	---	---	---	---	---	---	77*	---
Steganotaenia araliacea	---	---	48	---	---	---	---	---	---	---	---	---	---	75*	---
Acacia ataxacantha	---	---	65*	---	---	---	---	---	---	---	---	---	---	70*	---
Dichrostachys cinerea	---	---	44	---	---	---	---	---	---	---	---	---	---	68*	---
Unknown sp. 136374	---	---	40	---	---	---	---	---	---	---	---	---	---	67*	---
Commiphora tenuipetiolata	---	---	51	---	---	---	---	---	---	---	---	---	---	62*	---
Lantana angolensis	---	---	43	---	---	---	---	---	---	---	---	---	---	57*	---
Fabaceae sp. 136415	---	---	31	---	---	---	---	---	---	---	---	---	---	55	---
Mundulea sericea	---	---	31	---	---	---	---	---	---	---	---	---	---	55	---

Group No. / Plant community	1	2	3	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3	3.1	3.2	3.3	3.4
Erythrococca menyharthii	---	---	30	---	---	---	---	---	---	---	---	---	---	52	---
Clerodendrum uncinatum	---	---	25	---	---	---	---	---	---	---	---	---	---	45	---
Solanum panduriforme	---	---	31	---	---	---	---	---	---	---	---	---	---	42	---
cf. Hymenodictyon floribundum	---	---	23	---	---	---	---	---	---	---	---	---	---	41	---
Vitex angolensis	---	---	44	---	---	---	---	---	---	---	---	---	---	---	65*
Dichapetalum cymosum	---	---	30	---	---	---	---	---	---	---	---	---	---	---	51
Commiphora africana	---	---	28	---	---	---	---	---	---	---	---	---	---	---	33
Ozoroa schinzii	---	---	---	---	---	---	---	---	---	---	---	---	---	---	31
Ximenia caffra	---	---	---	---	---	---	---	---	---	---	---	---	---	---	29
Gardenia volkensii	---	---	---	---	---	---	---	---	---	---	---	---	---	---	26
Mucuna sp. 132808	41	---	---	41	---	---	---	41	---	---	---	---	---	---	---
Sclerocroton oblongifolius	53	---	---	37*	---	---	---	35*	---	---	---	---	---	---	---
Chamaeclitandra henriquesiana	49	---	---	35*	---	---	---	33*	---	---	---	---	---	---	---
Ozoroa stenophylla	34	---	---	25	28	---	---	---	---	---	---	---	---	---	---
Englerophytum magalismontanum	39	---	---	---	67*	---	34	---	---	---	---	---	---	---	---
Landolphia camptoloba	51	---	---	---	64*	---	47*	---	---	---	---	---	---	---	---
Cryptosepalum exfoliatum ssp. pseudotaxus	59	---	---	---	60*	---	60*	16	---	---	---	---	---	---	---
Copaifera baumiana	37	---	---	---	56*	65*	---	---	---	---	---	---	---	---	---
Brachystegia bakeriana	43	---	---	---	55*	40*	---	---	---	---	---	---	---	---	---
Phyllocosmus lemaireanus	59	---	---	9	55*	---	46*	---	---	---	---	---	---	---	---
Acanthaceae sp. 134578	26	---	---	---	41	---	25	---	---	---	---	---	---	---	---
Uvaria angolensis var. angolensis	26	---	---	---	41	---	25	---	---	---	---	---	---	---	---
Guibourtia coleosperma	---	36	---	---	40*	---	---	---	---	36*	16	---	---	---	---
Chrysophyllum bangweolense	35	---	---	---	39	---	52*	---	---	---	---	---	---	---	---
Rytigynia orbicularis	39	---	---	---	36*	57*	---	---	---	---	---	---	---	---	---

Group No. / Plant community	1	2	3	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3	3.1	3.2	3.3	3.4
Ekebergia benguelensis	35	---	---	---	31	---	---	21	---	---	---	---	---	---	---
Rhus exelliana	33	---	---	---	30	---	---	30	---	---	---	---	---	---	---
Helichrysum krausii	35	---	---	---	30	---	42	---	---	---	---	---	---	---	---
Albizia gummifera	26	---	---	---	27	---	27	---	---	---	---	---	---	---	---
Terminalia brachystemma	30	---	---	---	24	---	---	29*	---	10	---	---	---	---	---
Xylopia odoratissima	30	---	---	---	24	31	---	---	---	---	---	---	---	---	---
Pseudolachnostylis maprouneifolia	---	29	---	---	22*	---*	---	---	16	27*	---	---	---	---	---
Tricalysia angolensis	31	---	---	---	21	---	35	---	---	---	---	---	---	---	---
Julbernardia paniculata	49	---	---	---	18	60*	---	35*	---	---	---	---	---	---	---
Ozoroa longipes	---	46	---	---	---	39*	---	---	---	---	34*	---	---	---	---
Bobgunnia madagascariensis	43*	---	---	14*	---	32*	23*	---*	14*	---	---	---	---	---	---
Ochna afzelii ssp. mechowiana	30	---	---	---	---	30*	18	41*	---	---	---	---	---	14	---
Brachystegia longifolia	59	---	---	---	19	---	60*	42*	---	---	---	---	---	---	---
Brachystegia spiciformis	56	---	---	---	---	---	58*	40*	---	---	---	---	---	---	---
Vitex madiensis	44	---	---	13	---	---	56*	23	---	---	---	---	---	---	---
Tricalysia coriacea ssp. nyassae	50	---	---	---	17	---	56*	31*	---	---	---	---	---	---	---
Anisophyllea boehmii	37	---	---	---	---	---	42	39	---	---	---	---	---	---	---
Myrsine africana	51	---	---	---	---	---	36*	61*	---	---	---	---	---	---	---
Albizia antunesiana	44	---	---	14	---	---	35	41*	---	---	---	---	---	---	---
Mucuna stans	35	---	---	---	---	---	31	51*	---	---	---	---	---	---	---
Isoberlinia angolensis	26	---	---	---	---	---	28	33	---	---	---	---	---	---	---
Combretum apiculatum	28	---	---	---	---	---	26	30	---	---	---	---	---	---	---
Uapaca nitida var. nitida	44	---	---	---	---	---	23	47*	---	---	---	---	---	---	---
Tephrosia sp. 134738	33	---	---	16	---	---	22	26	---	---	---	---	---	---	---
Diospyros chamaethamnus	---	51	---	---	---	---	---	---	43*	32	---	---	---	---	---

Group No. / Plant community	1	2	3	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3	3.1	3.2	3.3	3.4
Hymenocardia acida	---	29	---	---	---	---	---	19*	33*	27*	---	---	---	---	---
Piliostigma thonningii	---	---	---	---	---	---	---	---	29	---	---	---	63*	---	---
Strychnos cocculoides	---	39	---	---	---	---	---	---	26*	21	---	---	---	---	---
Dichapetalum rhodesicum	---	62	---	---	---	---	---	---	23	60*	---	---	---	---	---
Rhynchosia ambacensis	---	---	---	---	---	---	---	---	20	---	---	---	44	---	---
Strychnos pungens	---	46	---	---	---	---	---	---	---	46*	21	---	---	---	---
Gardenia brachythamnus	---	38	---	---	---	---	---	---	---	38*	36*	---	---	---	---
Schinziophyton rautanenii	---	47*	---	---	---	---	---	---	---	31*	36*	---	---	---	---
Ochna pulchra	---	44*	---	---	---	---*	---*	---	---	28*	28*	---	---	---	19*
Burkea africana	---	42*	---	---*	---	---*	---*	---*	17	24*	20*	---	---	---	---*
Lannea gossweileri ssp. gossweileri	---	45	---	---	---	---	---	---	---	21	34*	---	---	---	---*
Terminalia sericea	---	31*	29*	---	---	---	---	---	---	---*	48*	---	---	---	50*
Bauhinia petersiana	---	---	21	---	---	---	---	---	---	---	38*	---	---	---	29*
Clerodendrum glabrum	---	19	---	---	---	---	---	---	---	---	37	---	---	---	30
Grewia falcistipula	---	25	---	---	---	---	---	---	---	---	35*	---	---	---	35*
Clerodendrum ternatum	---	17	20	---	---	---	---	---	---	---	26	---	---	---	35*
Combretum zeyheri	---	---	---	---	---	---	---	---	---	---	26	---	---	---	29
Polygala schinziana	---	---	21	---	---	---	---	---	---	---	25	---	---	---	46*
Searsia tenuinervis	---	---	26	---	---	---	---	---	---	---	---	---	35	25	---
Philenoptera nelsii	---	---	68*	---	---	---	---	---	---	---	---	---	---	67*	26
Croton gratissimus	---	---	81*	---	---	---	---	---	---	---	---	---	---	62*	44*
Grewia retinervis	---	---	54	---	---	---	---	---	---	---	---	---	---	53*	32
Baphia massaiensis	---	---	68*	---	---	---	---	---	---	---	---*	---	---	48*	44*
Baikiaea plurijuga	---	---	59*	---	---	---	---	---	---	---	---	---	---	47*	47*
Grewia avellana	---	---	47	---	---	---	---	---	---	---	---	---	---	38*	39*

Group No. / Plant community	1	2	3	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3	3.1	3.2	3.3	3.4
Baissea wulfhorstii	---	---	53*	---	---	---	---	---	---	---	---	---	---	27*	47*
Grewia flavescens	---	---	32	---	---	---	---	---	---	---	---	---	---	24	22
Fadogia sp. 134167	62	---	---	39*	---	---	40*	34*	---	---	---	---	---	---	---
Monotes dasyanthus	46	---	---	30	33	---	22	---	---	---	---	---	---	---	---
Paropsia brazzaeana	38	---	---	---	44*	44*	37*	---	---	7	---	---	---	---	---
Xylopia tomentosa	48	---	---	---	37*	39*	45*	---	---	---	---	---	---	---	---
Combretum collinum	---	22*	---	---	33*	---	---	---	---	18*	26*	---	---	---	33*
Erythrophleum africanum	18*	34*	---	---	29*	---*	36*	---	---	31*	14	---	---	---	---
Combretum psidioides	---	62*	---	---	---	---	---	---	---	45*	43*	---	---	---	27*
Asparagus sp. 136019	---	21	18	---	---	---	---	---	---	29*	26*	---	---	---	47*
Pterocarpus angolensis	---	49*	---	---	---	35*	---	---	---*	31*	30*	---	---	---	23*
Diplorhynchus condylocarpon	---	64*	---	---	---*	33*	---	---	26*	33*	23*	---	---	---	---
Fadogia thamnus	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Fadogia fuchsioides	28	---	---	---	---	---	---	16	---	---	---	---	---	---	---
Combretum elaeagnoides	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Alvesia rosmarinifolia	20	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Asparagus cf. nelsii	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Erythrococca pauciflora	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---

Group two: wooded grasslands and *Baikiaea* woodland*s* on Kalahari sands (BW1)

This group is characterised by the tree species *Schinziophyton rautanenii*, *Pterocarpus angolensis* and *Guibourtia coleosperma*. The shrub layer is formed by species such as *Diplorhynchus condylcarpon*, *Combretum psidioides*, *Strychnos pungens*, *Ozoroa longipes* and *Ochna pulchra* and includes dwarf shrubs like *Dichapetalum rhodesicum*, *Diospyros chamaethamnus*, *Lannea gossweileri* and *Gardenia brachythamnus* (Table 6). The general appearance of the vegetation of this group is shaped by large individual trees forming a large crown. However, the canopy is never closed and hence there is ample light to support a rich shrub and grass layer, the latter usually dominated by tall growing Poaceae. The soils of group two are very sandy, acidic and nutrient poor. The climate is semi-arid with a mean annual precipitation of approximately 600 mm.

2.1 (terminal cluster 6): ***Gymnosporia senegalensis–Burkea africana***

Characterisation: grassland with scattered trees on the old floodplain of the middle reaches of the Cubango River with a range of exclusively diagnostic shrub species, i.e *Gymnosporia senegalensis*, *Dombeya burgessiae*, *D. quinqueseta* and *Crossopteryx febrifuga*. Dwarf shrubs are a common feature of this plant community and include the species *Diospyros chamaethamnus*, *Annona stenophylla*, *Lannea edulis* and *Parinari capensis*. Tall growing Poaceae, e.g. *Tristachya superba*, dominate the appearance of the plant community towards the end of the rainy season. There is a high fuel load of lightly flammable dry grass biomass and therefore fires are frequent and of high intensity during the dry season. The fire resistant tree *Burkea africana* is the only tree species frequently reaching heights of several meters.

The plant community is restricted to the *Baikiaea* region and occurs here primarily on the plains adjacent to the recent floodplain where, due to the proximity to the river, human influence is high. One of the relevés contains a giant termite mound with its specialised flora. Due to the similarity in the species composition of the dwarf shrubs, the vegetation unit also contains one relevé from the alluvial plains of the Miombo region. However, if all vascular plants would be considered the latter one would most likely form a plant community on its own.

Structure: Vegetation height and total cover are low. The unit is clearly dominated by Poaceae and dwarf shrubs, larger shrubs and small trees only have a scattered appearance.

Habitat: This community is influenced by anthropogenic activities centred along the river. Land use comprises cattle herding, extraction of natural resources and agriculture.

Presence of spiny species such as *Gymnosporia senegelensis* and *Strychnos* spp. are likely to be a result of human presence. The community shows the highest fire frequency with on average one fire almost every third year. Soils are predominately slightly acidic Arenosols.

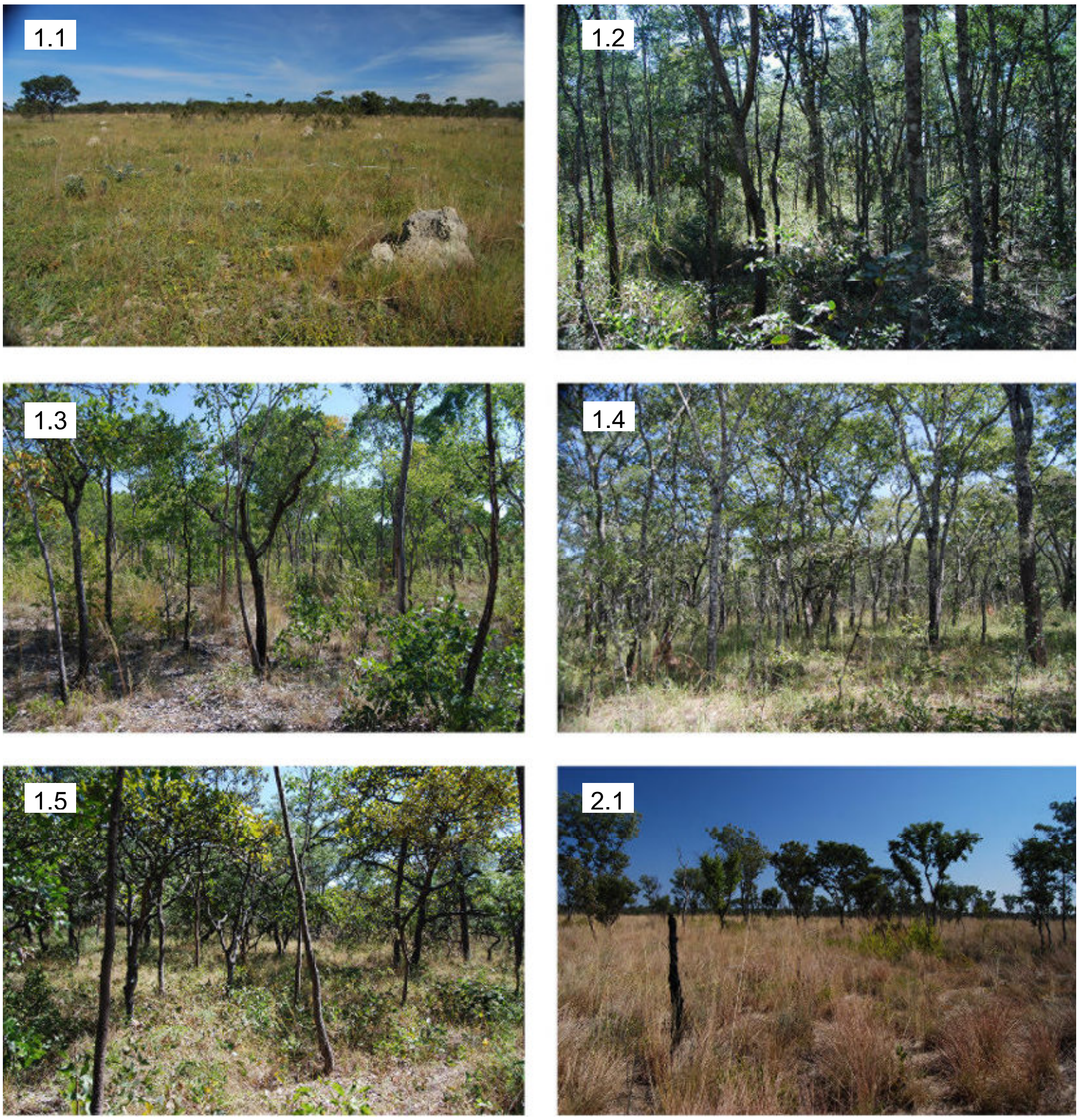

Figure 14 Representative photos of the derived woody vegetation communities a) 1.1: *Cryptosepalum maraviense*-*Cryptosepalum exfoliatum* ssp. *suffruticans*, b) 1.2: *Cryptosepalum exfoliatum* ssp. *pseudotaxus*-*Copaifera baumiana*, c) 1.3: *Diospyros batocana*-*Julbernardia paniculata*, d) 1.4 *Brachystegia spiciformis*-*Phyllocosmus lemaireanus*, e) 1.5 *Uapaca kirkiana*-*Julbernardia paniculata*, f) 2.1: *Gymnosporia senegalensis*-*Burkea africana*, Figure 14 continued on next page.

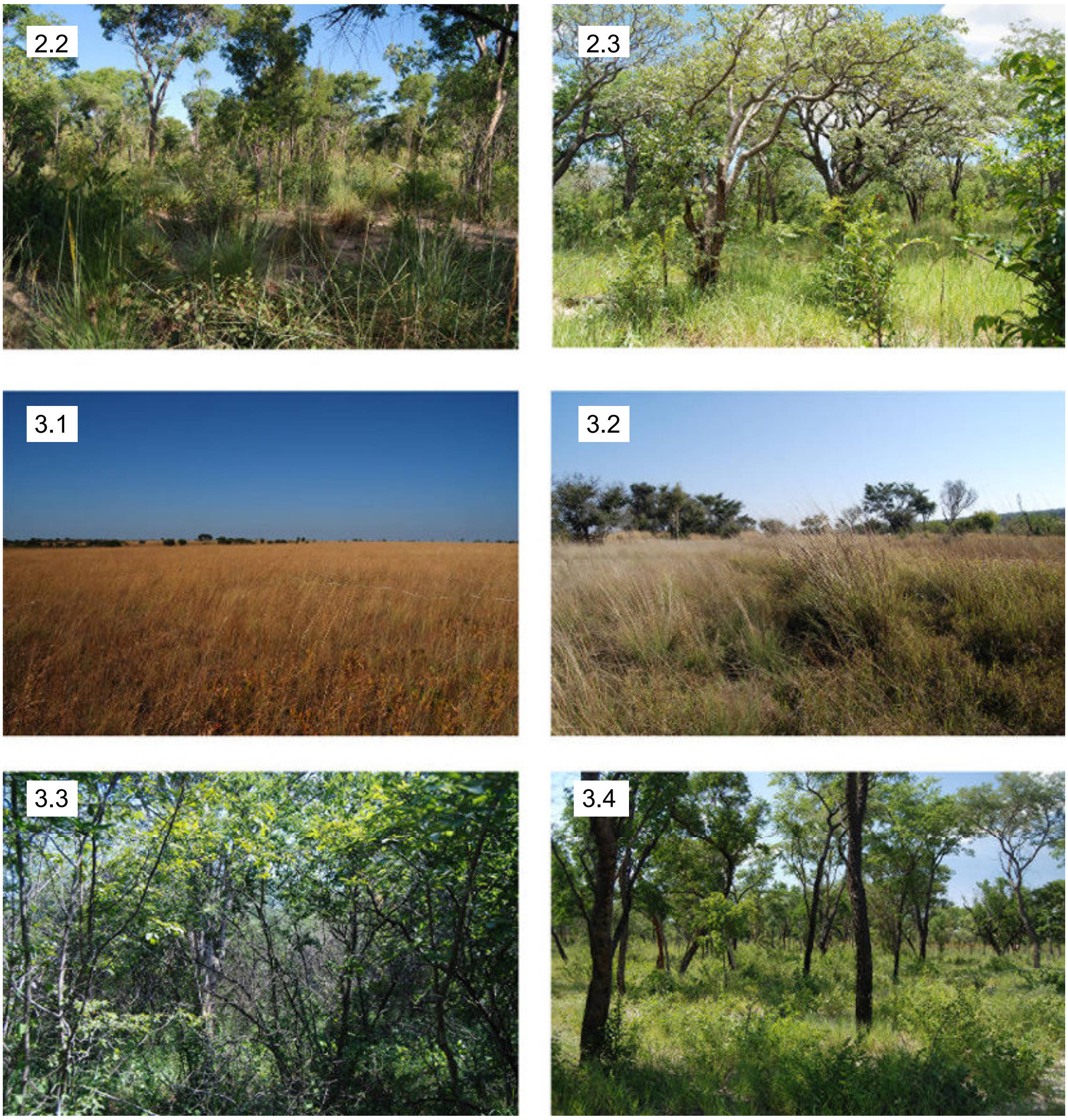

Figure 14 continued. g) 2.2: *Dichapetalum rhodesicum-Dialium englerianum*, h) 2.3: *Combretum psidioides-Schinziophyton rautanenii*, i) 3.1: *Protea micans* ssp. *trichophylla-Syzygium guineense* ssp. *macrocarpum*, j) 3.2: *Piliostigma thonningii-Acacia sieberiana*, k) 3.3: *Combretum celastroides-Baikiaea plurijuga*, l) 3.4: *Vitex angolensis-Terminalia sericea*

2.2 (terminal cluster 7): ***Dichapetalum rhodesicum-Dialium englerianum***

Characterisation: Woodland on Kalahari Sandveld with varying tree species composition. *Guibourtia coleosperma*, *Erythrophleum africanum*, *Pterocarpus angolensis*, *Schinziophyton rautanenii* and *Burkea africana* are diagnostic but show low constancy. In contrast, *Dialium englerianum* is exclusively diagnostic for this community and was therefore chosen as name giving species. In the lower tree layer *Combretum psidioides*, *Diplorhynchus condylocarpon*, *Hymenocardia acida*, *Pseudolachnostylis maprouneifolia* var. dekindtii and *Ochna pulchra* have good diagnostic value but at the same time are also diagnostic for other communities of the *Baikiaea* woodlands, e.g. 2.1 and 2.3. The shrub species *Bauhinia urbaniana* is exclusively diagnostic for this community.

Structure: Open woodland, large individual trees of *Schinziophyton rautanenii*, *B. plurijuga*, *E. africanum* and *G. coleosperma* forming large crowns, high ground coverage by Poaceae and some herbs.

Habitat: The community occurs on deep, acidic and nutrient poor Arenosols showing the lowest fraction of silt and clay within the studied site, fires occur regularly.

2.3 (terminal clusters 8 and 9): ***Combretum psidioides-Schinziophyton rautanenii***

Characterisation: Typical *Baikiaea* woodland*s* on Kalahari sands with large individual trees of *Schinziophyton rautanenii*, *Pterocarpus angolensis*, *Burkea africana* and *Baikiaea plurijuga*. *Terminalia sericea*, *Ozoroa longipes* and *Diplorhynchus condylocarpon* form the shrub layer. Exclusively diagnostic for the plant community are the shrubs *Clerodendrum dekindtii* and *Commiphora angolensis*.

Structure: Large individual trees over 10 m in height form large crowns, but the open canopy leaves enough light for of rich shrub layer and the growth of tall grasses.

Habitat: Deep Arenosols with low content of clay and silt and acidic pH-value.

Group three: *Baikiaea* woodlands on Arenosols with higher nutrient status (BW2)

This assemblage of woody vegetation communities is characterised by the presence of the tree species *Baikiaea plurijuga* and *Philenoptera nelsii*. Several shrub species were characteristic: *Croton gratissimus*, *Baphia massaiensis*, *Combretum celastroides* and *C. engleri* as well as three *Grewia* specices. Furthermore, the spiny shrub species *Acacia ataxacantha*, *Commiphora tenuipetiolata* and *Dichrostachys cinerea* had high phi values (Table 6). The vegetation structure varies strongly within this group ranging from wooded grasslands to dense woodlands with thicket like understorey. However, the group also contains one community (3.4) that is structurally very similar to group two. The typical soils of group three are Arenosols, too. However, they exhibit a higher content of silt and clay; have a slightly higher pH-value and higher electrical conductivity. Consequently, they offer better growing conditions (Figure S4). The mean annual precipitation is approximately 600 mm.

3.1 (terminal cluster 10): ***Protea micans ssp. trichophylla-Syzygium guineense ssp. macrocarpum***

Characterisation: Edaphic grassland with dwarf shrubs dominated by Poaceae and Cyperaceae. Only very few woody species occur, thus no detailed characterisation can be made based on woody species.

Structure: No trees present, only few individual shrubs and dwarf shrubs.

Habitat: Elevated plain on the Angolan Central Plateau with underlying hardpan in the soil leading to seasonally waterlogged conditions and peaty mineral topsoils.

3.2 (terminal cluster 11): ***Piliostigma thonningii-Acacia sieberiana***

Characterisation: grass and shrub land with scattered trees or giant termite mounds. The relevés of the plant community were all located in the southern half of the Cubango Basin and were situated on or close to the recent floodplain. In general, the plant community is dominated by tall growing grasses and only a limited number of woody species occurs; the lowest woody species richness was recorded here. Most of the diagnostic woody species of the community bear thorns or thorn like structures, i.e. *Acacia sieberiana*, *Ximenia americana*, *Ziziphus mucronata* and *Searsia tenuinervis*. *Acacia sieberiana* occurs on or in proximity of giant termite mounds while *Piliostigma thonningii* can be found scattered in the Poaceae dominated matrix. The small shrub *Rhynchosia ambacensis* frequently occurs in the grassy matrix and is characteristic for this plant community, but also diagnostic for plant community 2.1.

Structure: Total vegetation cover was high but coverage by shrubs and trees was low and the community is dominated by tall growing Poaceae. Woody species mainly occur on giant termite mounds forming wooded islands in the mainly grass dominated matrix.

Habitat: Soil properties are very different from the typical Arenosols dominating the region. Soils have a high content of silt and clay, are carbonate rich and show an alkaline pH-value. Sites are inundated during flood peaks.

3.3 (terminal clusters 12, 13 and 14): ***Combretum celastroides-Baikiaea plurijuga***

Characterisation: Dense *Baikiaea* woodland with thicket like understorey. The three terminal clusters 12, 13 and 14 were merged to one plant community as they all contain regenerating fallows, impoverished and mature stands. The plant community stands out in structure and species composition from the surrounding *Baikiaea* woodlands. Diagnostic species include several species carrying spines or thorn like structures, i.e. *Combretum celastroides*, *C. engleri*, *Acacia ataxacantha*, *Dichrostachys cinerea*, *Solanum panduiforme*, *Searsia tenuinervis*. *B. plurijuga* is the only emerging tree forming the upper canopy, only in some cases *Philenoptera nelsii* also reaches the upper canopy.

Geographically the community is restricted to a larger patch to the West of the Cubango River in the communal area of Savate and to some remaining patches on the opposite river bank to the Northeast. Furthermore, four relevés belonging to this community were recorded in the southern parts of the catchment area in regenerating woodlands.

Structure: Thicket like understorey, only few individual trees emerge and form an interrupted upper canopy. Hardly impenetrable by larger wildlife and humans, very high density of thin stems.

Habitat: The plant community exhibits a well-defined limit and sharp ecotone of only a few meters to the surrounding open *Baikiaea* woodlands. Soils have a higher content in fine material than found in the remaining *Baikiaea* woodlands. The exact underlying causes for this often sharp vegetation border of only a few meters is still debated (Wallenfang et al. 2015). In recent years, this type of woodland has been preferred by local communities for slash-and-burn agriculture due to the higher nutrient status and thus better yields.

3.4 (terminal cluster 15 and 16): ***Vitex angolensis*-*Terminalia sericea***

Characterisation: *Baikiaea* woodland*s* on the Kalahari Sand Veld of the southern part of the Basin. In order to achieve communities representative for a larger area the two terminal clusters 15 and 16 were merged to one. *Dichapetalum cymosoum*, *Asparagus* sp., the liana *Baissea wulfhorstii*, *Combretum collinum* and *Grewia* spp. are diagnostic as well as *Baphia massaiensis* that sometimes dominates the shrub layer. Frequent, associated species are *Burkea africana*, *Pterocarpus angolensis*, *Combretum psidioides* and *Bauhinia petersiana*. The community shares several diagnostic shrub species with community 2.3 and some with 2.2.

Structure: Tree cover is low with a mean of 15%. However, individual trees form large crowns. Ground cover by herbal layer is not dense but continuous.

Habitat: The community occurs on the Kalahari Sandveld of the hinterland of the river. The relief is usually flat and shows little variation. Thus, soils are mostly lightly coloured Arenosols. The community is subject to regular but not frequent fires and frost occurrence is highest among all studied communities.

Environmental characteristics

The large scale driver of vegetation composition was climate contributing 12% to the explained variance and 28% in combination with other environmental data (Figure 15). Evident from the CCA (Figure 16) were the opposing trend of higher mean annual temperature in the *Baikiaea* woodland*s* and higher mean annual precipitation in the Miombo woodlands. Occurrence of frost and fire had a low importance for explaining the overall pattern.

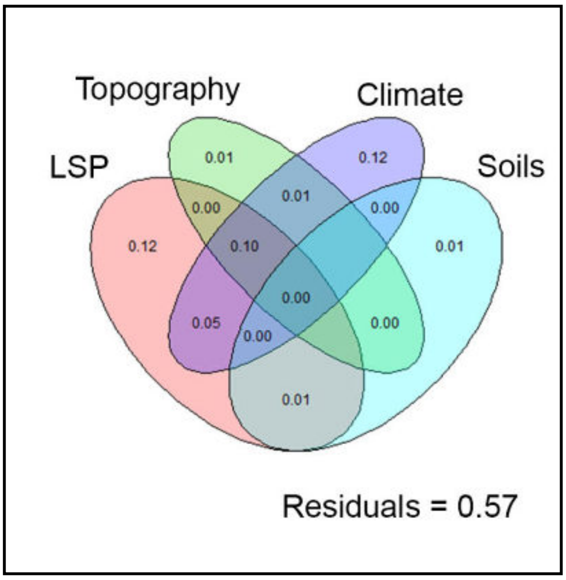

Figure 15 Variance explained by different environmental matrices: land surface phenology (LSP), topography, climate, and soil properties. For a description of all environmental variables see Table 4.

Land surface phenology had an equally high contribution to the explained variance as climate (Figure 15). The biomass related metric 'LargeIntegral' was significantly higher in the Miombo woodlands than in the *Baikiaea* woodlands. The *Combretum celastroides-Baikiaea plurijuga* community with its thicket like understorey took an intermediate position. The 'BaseValue' was also higher in the Miombo woodlands than in the more southerly *Baikiaea* woodlands. In contrast, no significant differences were detected for 'Amplitude' with the exception of the communities 3.3 and 1.1 which showed the highest and second highest amplitude respectively (Figure S3b).

The length of the growing season decreased significantly from the Miombo region to the *Baikiaea* woodlands. The longest growing season was observed in the geoxylic-grasslands community *Cryptosepalum maraviense-Cryptosepalum exfoliatum ssp. suffruticans* (1.1) with a mean of 286 days and the lowest mean of 224 days in the *Combretum celastroides-Baikiaea plurijuga* community (3.3, Figure S3b).

Soils did not show much variation throughout the study area and soil properties contributed only 1% to the explained variance (Figure 15). In general, soils can be characterised as acidic to slightly acidic with a mean pH-value ranging from 3.9 to 5.0. In

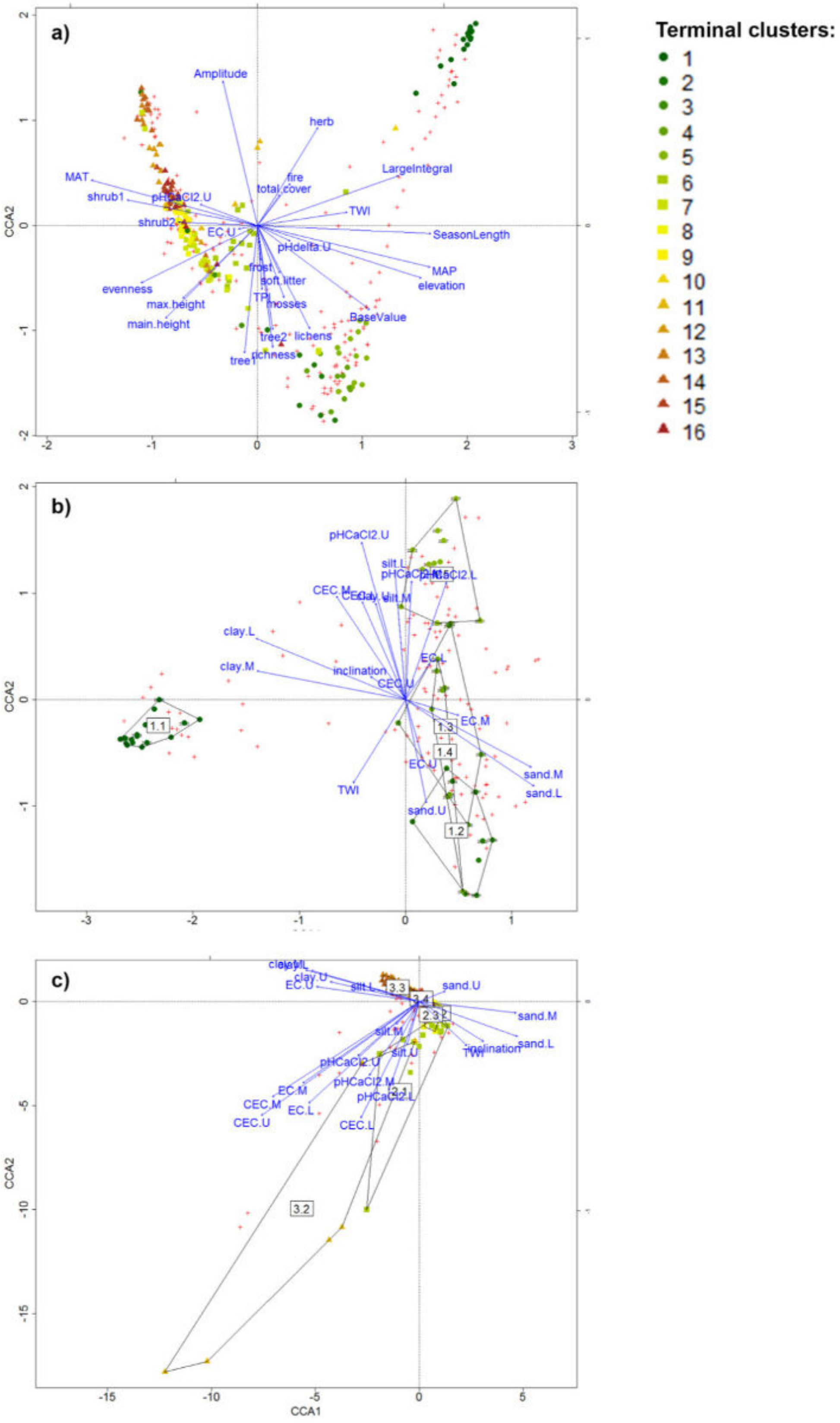

Figure 16 Canonical Correspondence Analysis of vegetation data (species shown as red cross), relevé data (according to terminal clusters, see colour coding in legend) and environmental data superimposed as vectors, for variable abbreviations see Table 3 and Table 4. a) all data, b) Miombo group c) *Baikiaea* groups.

the majority of the communities the substrate was very sandy and poor in clay and silt and the electrical conductivity and cation exchange capacity were low. However, soil properties of some communities deviate from the general pattern. As such, the sites situated in the recent floodplain and on giant termite mounds in community 3.2 had significantly higher pH-values and electrical conductivity as well as higher content of fine material than the other communities (Figure S3). In the soils of the *Baikiaea* woodlands no strong differences among upper, middle and lower soil horizons were detected. In contrast, in some communities of the Miombo woodlands significant differences between the soil surface and deeper horizons were detected. Another notable difference among Miombo and *Baikiaea* woodlands was a slightly lower pH-value in the upper horizon in the communities of the Miombo region.

Similarly, topography only explained 1% on its own (Figure 15) but was of importance locally. Generally, aspect and inclination had very low explanatory power to discern vegetation communities. However, elevation and the topographic attributes TPI and TWI were good predictors to differentiate among the Miombo vegetation types especially so for the delimitation the plant community *Cryptosepalum maraviense-Cryptosepalum exfoliatum ssp. suffruticans* (Figure 16).

Diversity of the woodlands of the Cubango Basin

In total 316 woody species were recorded in 191 plots. Thereof 126 species only occurred once or twice. According to the species accumulation models the size of the species pool of woody species within the Cubango Basin ranges from 437 to 545 species with a mean of 471 species. The Miombo group is the species richest with an estimated mean lower bound of 302 species compared to the combined mean value for both *Baikiaea* groups of 262 (Table 7).

The right hand side of the species accumulation curve for all plots showed still a slight increase and did not reach the asymptote, yet (Figure 17a). Constructing one species accumulation curve for each of the three major groups showed that for the *Baikiaea* woodland*s* (group two and three) the curve approached the asymptote. In contrast, the slope of the right hand side of the species accumulation curve of the Miombo woodlands was still much steeper (Figure 17b), thus indicating that with further sampling more new species are to be expected.

Table 7 Estimation of species pools of the Cubango Basin and of the three major vegetation units Miombo, wooded grasslands and *Baikiaea* woodlands on Kalahari sands (BW1) and *Baikiaea* woodlands on Arenosols with higher nutrient status (BW2) and the combined data set comprising both *Baikiaea* groups. The number of relevés per group, the observed number of species (S obs.), and four species richness estimators are given: the improved Chao2 estimator (iChao2), Incidence-based Coverage Estimator (ICE) and 1st and 2nd order jackknife. For each estimator the standard error is given.

	All	**Miombo**	**BW 1+2**	**BW1**	**BW2**
No. of relevés	190	52	138	74	64
S. obs.	314	215	168	120	111
iChao2	545±44	319±21	317±40	216±35	216±37
ICE	437±27	283±18	246±23	158±14	162±18
1st order jackknife	413±14	282±12	222±10	154±8	148±9
2nd order jackknife	487±24	323±20	263±18	180±14	178±15
mean	**471±29**	**302±11**	**262±20**	**177±14**	**176±14**

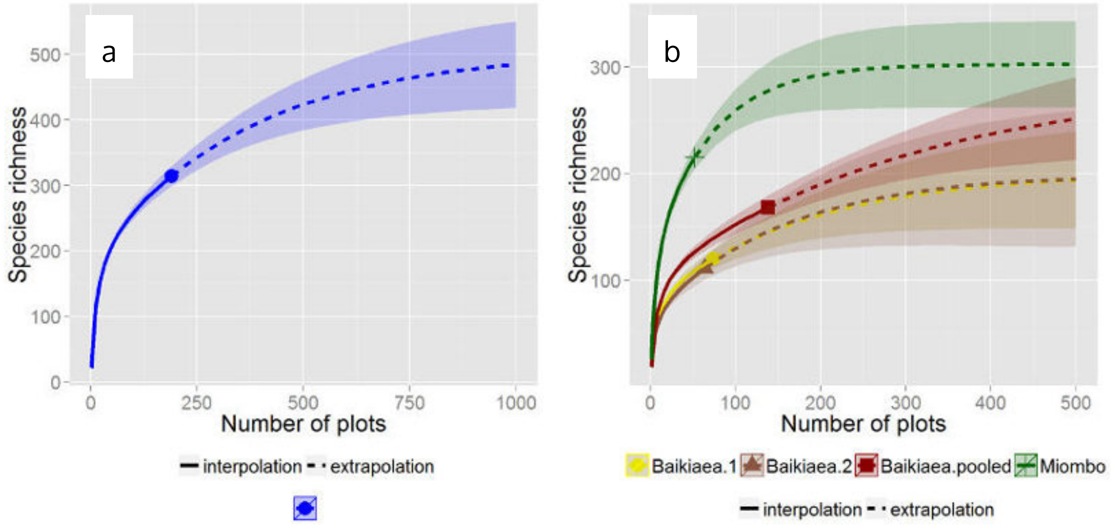

Figure 17 Sample based rarefaction and extrapolation curves for a) the entire data set, i.e. all relevés sampled in the Cubango Basin, and b) for the three major vegetation units derived by the classification: i) 'Miombo' (dark green), ii) 'open *Baikiaea*' (yellow), iii) 'closed *Baikiaea* woodlands' (brown), and iv) the combined data of both *Baikiaea* units (dark red). The lightly coloured area indicates standard deviation estimated from permutation.

The Miombo group showed the highest woody species richness followed by BW1 and BW2. However, for diversity indices giving more weight to evenness (higher values for the scale parameter alpha) *Baikiaea* woodlands showed higher values indicating that species have a more equal share (Figure 18). The absolute highest woody species richness was observed in the mature Miombo woodlands of the *Brachystegia spiciformis*-*Phyllocosmus lamerianus* community whereas the lowest was detected in the communities of the edaphic grassland and of the recent floodplain (*Protea micans* ssp.

trichophylla-Syzygium guineense ssp. *macrocarpum* and *Piliostigma thonningii-Acacia sieberiana*, Figure S3).

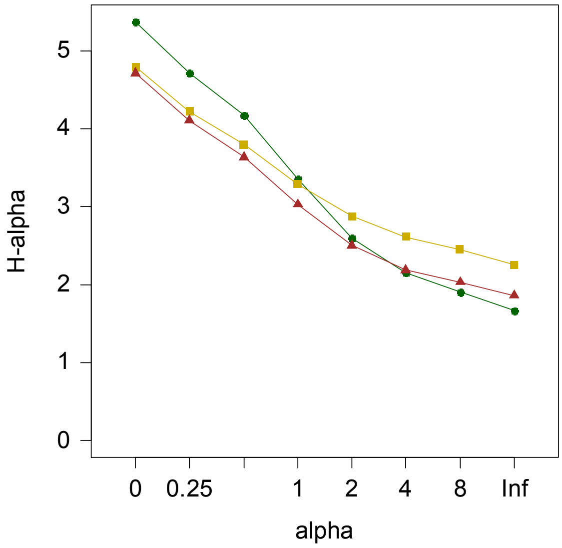

Figure 18 Reyni's diversity profile for cluster hierarchy level one: Miombo (dark green), open *Baikiaea* (dark yellow), closed *Baikiaea* (red brown). The scale parameter (α) gives the order of Renyi's diversity and can be mathematically converted to common diversity indices. Low α values represent diversity indices focusing on species richness, while with increasing α more weight is given to the aspect of evenness, e.g. α=0 is related to species richness, while α=1 corresponds to the Shannon diversity index, and α=2 to the logarithm of the reciprocal Simpson index, α=Inf refers to the proportion of the most abundant species.

Discussion

Characterisation of the woody vegetation communities of the Cubango Basin

Woody vegetation of the Cubango Basin was clearly dominated by plants of the Fabaceae family. In the Miombo zone the characteristic and dominant canopy species were *Brachystegia cf. longifolia*, *B. spiciformis*, *Cryptosepalum exfoliatum* ssp. *pseudotaxus* and *Julbernardia paniculata* (Table 6). The frequently cited typical Miombo species *Isoberlina angolensis* (Chidumayo 1987; Campbell 1996) was only found with very low frequencies and only had moderate diagnostic value for two vegetation communities (1.4 and 1.5). It was neither observed as frequent or even dominant species in the wider region surrounding the Cubango Basin.

Monteiro (1970) identified two associations within the Cubango Basin: 1) Association of *Brachystegia spiciformis-Copaifera baumiana* with two sub associations 1a) "typical" and 1b) *Chrysophyllum bangweolense*; 2) Association of *Brachystegia longifolia-Syzygium guineense* ssp. *afromontanum* with the sub associations 2a) *Xylopia tomentosa* and 2b) *Protea welwitschii* ssp. *welwitschii*. Based on the relevé data provided by Monteiro (1970) we checked the matching with the vegetation communities derived in this study. Although a similar species pool was recorded there was not a good match with the communities derived in this study. The communities 1.2, 1.3 and to some degree 1.4 shared some diagnostic species with the *B. spiciformis-C. baumiana* association of Monteiro but the *Brachystegia longifolia-Syzygium guineense* ssp. *afromontanum* did not match well with any of the vegetation communities.

The work of dos Santos (1982) on the vegetation of the Cuando Cubango Province did not provide full species tables. Instead, they based their vegetation map on the province on so called "floristic itinaries". The described and mapped vegetation boundaries can be roughly confirmed in this study. Interesting in this context is the fading out of Miombo species such as *Brachystegia bakeriana* and *Julbernardia paniculata* along an imaginary line connecting Baixo Longa and Mucundi. This transition zone is represented by plant community 1.3 *Diospyros batocana-Julbernardia paniculata*. The Climate in this zone with a mean annual precipitation of about 700 mm per year takes an intermediate position between the two major vegetation units (Figure S3b).

Some of the derived vegetation communities of this study deserve to be highlighted as they have rarely been described quantitatively but significantly contribute to the plant diversity of the Basin. As such, the *Combretum celastroides-Baikiaea plurijuga* community encountered in southern Cuando Cubango in Angola resembles a unique vegetation type that has first been described by Wallenfang et al. (2015). It is characterised by a distinct vegetation structure with an almost impenetrable shrubby understorey and only few emerging canopy trees and shows some similarity to the Itigi-Zumbu thicket of Zambia (White 1983). In this study, this community emerged as a subunit of the *Baikiaea* woodlands based on its compositionally similarity. However, it exhibited the highest sharpness (80.5%) indicating that a high proportion of species is confined to the community or only occurring rarely in others (Chytrý & Tichý 2003). Wallenfang et al. (2015) did not come to a final conclusion regarding the environmental constraints of this enigmatic plant community. Its distributional range was confined to the communal area of Savate in southern Cuando Cubango in Angola. In this study, it could be shown that four relevés from regenerating woodlands in the southernmost parts of the Cubango Basin also belonged to this plant community (Figure S2). The distributional range might therefore formerly have been larger from which in other parts only highly disturbed remnants are preserved.

A prominent phenomenon of the Zambezian phytoregion are geoxylic suffrutices (White 1976), dwarf shrubs with a high woody underground biomass. In this study, we identified one plant community dominated by geoxylic suffrutices, the *Cryptosepalum maraviense-Cryptosepalum exfoliatum ssp. suffruticans* community (1.1). Locally, this vegetation type is referred to as "Anharas de ongote" (Gossweiler & Mendonça 1939; Barbosa 1970). In the land cover classification of the Okavango Basin by Stellmes et al. (2013a) and in the accompanying description by Revermann and Finckh (2013c) the vegetation types are classified as *Cryptosepalum maraviense* grasslands on ferralitic soils. They cover 8.5% of the area of the Cubango Basin (Figure 11, Stellmes et al. 2013a) and hence have high ecological relevance. However, to our knowledge, this is the first vegetation classification approach analysing the species composition and the abiotic conditions of the "Anharas de ongote" in Angola.

A structurally closely related vegetation type occurs on better drained soils on deep alluvial sands, classified as *Parinari capensis* grasslands on humid sands in the land cover classification (Stellmes et al. 2013a) and are locally known as "Anharas de boracha" due to the presence of species of the genus *Landolphia* (Monteiro 1970). In the Cubango Basin it covers only 0.7% of the area but more extensive areas are located further east, e.g. in the neighbouring Cuito Basin. In this study, the community was only represented with one relevé. Due to some similarity in the species composition of the dwarf shrubs it was grouped with the *Gymnosporia senegalensis–Burkea africana* community (2.1) of the old floodplain of the southern reaches. However, it clearly represents a plant community on its own and more data needs to be collected.

Similarly, the *Protea micans ssp. trichophylla-Syzygium guineense ssp. macrocarpum* edaphic grasslands (3.1) were only covered by only one single relevé. However it represents a vegetation type common in the far north of the Basin where it occurs on plateaus with an underlying hardpan leading to temporarily waterlogged, peaty mineral soils.

Future work will have to focus on the development of a full phytosociological classification including the entire vascular flora. As such, vegetation classifications can provide a solid basis for conservation and natural resource management as pointed out by Luther-Mosebach et al. (2012). They provided the example of the Habitats Directive of the European Union, the most important environmental legislation in Europe that is primarily based on phytosociological units.

Vegetation environment relationships

Climate

The strong, opposing gradients of precipitation and temperature emerged as the main driver of species composition in the Cubango Basin (Figure 16). The occurrence of Miombo woodlands is delimited by mean annual precipitation and Miombo species gradually fade out with decreasing precipitation. The *Diospyros batocana-Julbernardia paniculata* community (1.3) receiving only approximately 700 mm of precipitation annually resembles the transition from Miombo to *Baikiaea* woodlands. Coupled with the shift in species composition is a change in vegetation structure. While the Miombo woodlands exhibit an open but more or less continuous tree canopy, the *Baikiaea* woodlands are characterised by individual trees of similar height with large crowns that usually do not reach the crown of the neighbouring tree. The lower amount of available water in the *Baikiaea* woodlands was also reflected in lower values for 'LargeIntegral', a proxy for total above ground biomass (Revermann et al. 2016a).

Topography

The topography of the southern part of the Basin is rather homogenous once leaving the floodplain surrounding the central river bed as shown by the geomorphological landscape units of Wehberg et al. (2013). Thus, the low contribution of topography to explaining vegetation patterns is not surprising. In the northern half of the Basin, however, topography played a role in differentiating the geoxylic grasslands of community 1.1 from the Miombo woodlands. For the vegetation of the lower Cubango Valley Strohbach (2013) nicely illustrated the importance of topography, height above river level in this case. Though, these herbaceous vegetation types were not the focus of this study.

Soil

Soil parameters are closely related to geomorphological landscape units and thus neither had high explanatory power (Figure 15). However, two communities had contrastingly different soil properties. One, the *Piliostigma thonningii-Acacia sieberiana* community (3.2) showed significantly higher proportion of silt and clay and occupied the only soil types with carbonate content detectable by field methods. This community primarily occurs on the floodplain, where recent fluviatile sediments provide much richer soils than the surrounding Kalahari Sandveld. Two, the *Cryptosepalum maraviense-Cryptosepalum exfoliatum ssp. suffruticans* geoxylic-grasslands (1.1) of the Angolan Central Plateau were set apart from the surrounding woodlands by shallow, ferralitic soils with higher contents of fine material. Again, the differing pedogenesis is coupled to their topographic position on the slopes. Furthermore, differing soil conditions prevailed at specific local sites such as giant termite mounds.

Although Arenosols were the predominant soil types throughout the Basin in all major vegetation units, there exist subtle differences among the soils of the Miombo and *Baikiaea* woodlands. The lower pH-value in the upper soil surface of Miombo soils can be explained by the higher precipitation causing the leaching of cations. The stronger differentiation of upper and lower soil horizons in Miombo woodlands, in particular a significantly higher content of clay in the lower horizons than commonly found in the *Baikiaea* woodlands, is caused by the underlying bedrock. In the southern and central part of the Cubango Basin, the bedrock is covered by thick layers of Kalahari sands. In contrast, in the northern part the bedrock is formed by granites and gneisses and was involved in the pedogenesis (Direcção Provincial dos Serviços de Geologia e Minas Angola 1969). Illuviation processes lead to the transport of clay to the lower horizons.

All in all, the measured parameters did not fully explain local changes in species composition and thus leaves the question what drives local changes in species composition. Soil parameters not investigated such as nitrogen and phosphorous levels and underlying impenetrable, hard crusts in the subsoil may be important factors. Such a crust formed by laterite was observed in one third of the relevés of *Uapaca kirkiana-Julbernardia paniculata* community (1.5) in less than one meter depth, but not in the remaining Miombo woodland communities. Similar crusts occurred in the communities 1.1 and 3.1 dominated by dwarf shrubs and grasses. Appropriate data for a systematic assessment of the influence of geological formations reaching deeper than standard soil sampling is unfortunately not available.

Fire and other drivers

Another important factor influencing local species composition is the disturbance history of the site. Chidumayo (1987) stated for Zambia that all Miombo woodlands were to some extent affected by human disturbance, mainly by shifting cultivation or charcoal production in the recent or more distant past; the situation in Angola is not different. Next to the direct influence of clearing woodland, indirect human influence is exerted through fire. It is used for various purposes and often escapes human control. Especially the southern half of the Basin exhibits a high fire return period of several fires per decade (Stellmes et al. 2013c). Our results showed that the open vegetation communities 1.1, 2.1, 3.1 and 3.2 have a higher fire return period although this effect was not always significant (Figure S3b). This evokes the question whether fire is the primary cause of the open vegetation communities or if their characteristics promote a high fire frequency, e.g. high amounts of highly inflammable dry grass biomass. For the wooded grasslands of the southern parts of the Basin (2.1 and 3.1) it is probable that tree saplings are captured in the so called 'fire trap' (Sankaran, Ratnam & Hanan 2004; Bond & Keeley 2005). Due to frequent fires, tree saplings are not able to outgrow the danger zone of ground fires. Thus, they do not reach their mature state when they develop fire resistant traits such as a thick, corky bark. In contrast, the vegetation communities of the upper Basin dominated by geoxylic suffrutices are more likely to have other environmental drivers restricting tree growth. For the *Cryptosepalum maraviense-Cryptosepalum exfoliatum ssp. suffruticans* community (1.1) microclimatic conditions fostering the occurrence of night frosts in the valleys during the dry season have been pointed out as a likely cause (Finckh, Revermann & Aidar 2016). In the edaphic grasslands of the extreme north (community 3.1) it is likely that temporarily water logged soils hinder the growth of trees.

LSP metrics

We used remotely sensed land surface phenology metrics (LSP) to infer information on the timing of the growing season as well as to obtain an approximation for differences in biomass among vegetation communities. LSPs can be regarded as a hybrid of properties inherent to the plant community on the one hand and on the other hand they are related to underlying environmental factors. In this study, LSPs provided a realistic picture of the length of the growing season that followed the climatic gradient and decreased southwards. Similarly, LSPs detected the highest above ground biomass in the Miombo woodlands indicated by higher values for the LSP metric 'LargeIntegral' (Revermann et al. 2016a). This is not surprising as the higher water availability and the longer growing season offer better growing conditions. Surprisingly, the highest values for 'LargeIntegral' was reached by the community with the lowest above ground biomass, the community 1.1 dominated by geoxylic suffrutices. This can be attributed to the fact that the highly dominant *Cryptosepalum* species form a very dense and green groundcover leading to high EVI values.

Interestingly, the 'BaseValue' was also significantly higher in the Miombo woodlands than in the *Baikiaea* woodlands. The 'BaseValue' refers to the amount of biomass remaining during the dry season and in this case can be explained by the higher share of evergreen species in Miombo woodlands. As such, the *Cryptosepalum exfoliatum* ssp. *pseudotaxus*-*Copaifera baumiana* community contains several dominant, evergreen species and also stood out with the overall highest 'BaseValue'. This illustrates how remote sensing data derived from dense time series can support the identification of ecological properties of vegetation communities. However, it needs to be highlighted that they have to be interpreted in light of the ecological background.

Woody species diversity

The highest woody species richness was encountered in the Miombo. Fanshaw (1971; cited in Chidumayo 1987) estimated the entire pool of woody species in the entire Miombo region of Zambia as 650. Compared to this number the 215 observed woody species and the estimated species pool of 288 woody species (Table 7) in the upper Cubango Basin is considerably high. Based on the small area covered in this study compared to the entire African Miombo belt it can be argued that current estimates of species numbers in Miombo ecoregion are likely to be an underestimation. The species accumulation models for the Cubango Basin (Figure 17) indicated that further sampling is necessary. In contrast, the *Baikiaea* woodlands were well covered.

Although the Miombo woodlands exhibited the highest richness the *Baikiaea* woodlands had a slightly higher evenness (Figure 18, but see Figure S3a), i.e. species contributed more equally to vegetation cover. This can be traced back to the higher diversity of canopy species in the latter. Studying the reasons for the sometimes close to monodominant stands in regard to the tree layer would be an interesting future research question, see also the current discussion on hyperdominance in Amazonia (ter Steege et al. 2013).

For the first time, we presented a comprehensive overview on the woody vegetation of the highly understudied Cubango Basin in south east Angola. The presented classification scheme provides solid foundations for future investigations of the vegetation of southeast Angola and will provide a robust basis for conservation planning and sustainable natural resource management.

Supplementary Materials available in the Appendix of the thesis

Figure S1 Plot design used in the vegetation survey. Figure S2 Geographic location of relevés of each plant community in the Cubango Basin. Figure S3 Comparison of the vegetation and environmental parameters of the derived vegetation communities. Differences among the vegetation communities are tested with an ANOVA and Tukey HSD post hoc test; group membership is indicated by letters. a) vegetation diversity and structure b) climate and land surface phenology c) soil 0-10 cm, d) soil 45-55 cm e) soil 70-90 cm. Figure S4 Canonical Correspondence Analysis (CCA) of vegetation data and soil properties for the communities of the *Baikiaea* woodlands without the community of the edaphic grassland 3.1 and the floodplain plant community 3.2.

Acknowledgements

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CHAPTER 4

Frost occurrence in tropical highlands as a driver of vegetation patterns

a) Microclimate – Cusseque

Rasmus Revermann and Manfred Finckh
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b) Climate refugees going underground – a response to Maurin et al. (2014)

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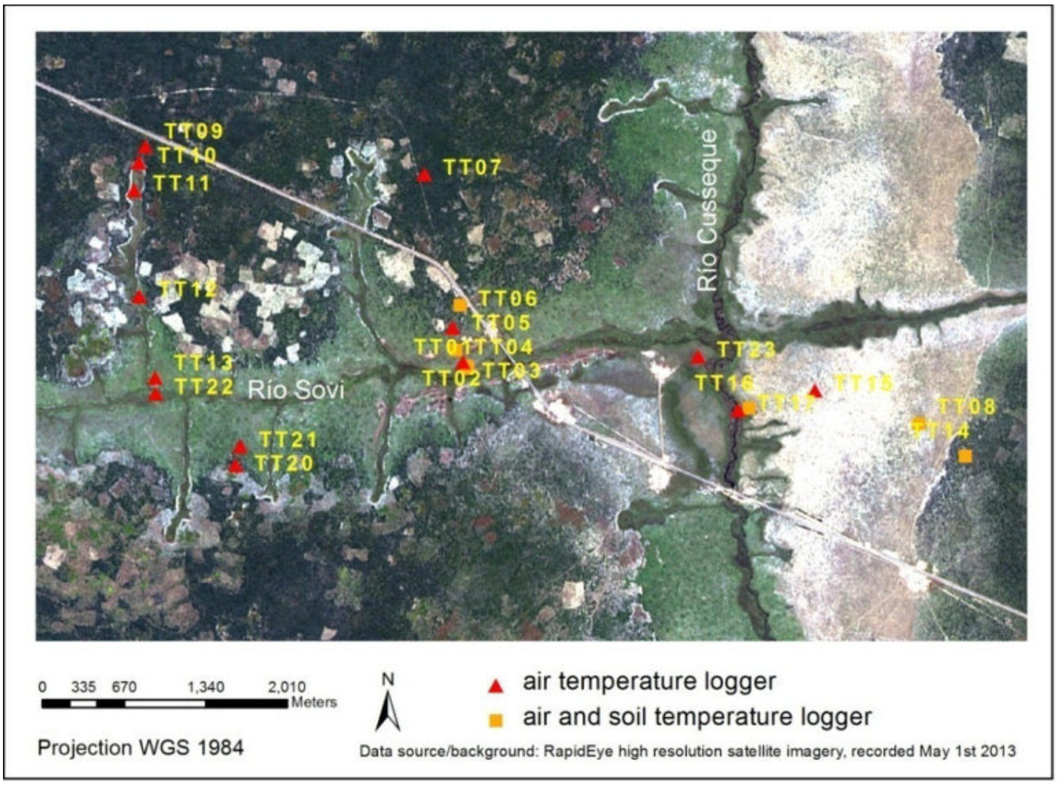
a) Microclimate – Cusseque

The Cusseque core site is embedded in a rolling landscape with a perpendicular stream network. While the hills are covered by Miombo forests and woodlands, the valley bottoms feature wetland vegetation. The striking features of this landscape, however, are the midand foot-slopes covered by open vegetation dominated by subterraneous shrubs and grasses. White (1976) describes the phenomenon of dwarf shrubs with an enormous woody underground biomass within the Zambezian Region and coins the term "geoxylic suffrutex" for this growth form. In order to investigate the extent to which micro-climatic conditions shape vegetation patterns and limit agricultural use, a network of 21 micro-climatic measuring stations was installed (Figure 19). The stations are distributed along three catenas extending from the woodlands on the hills through the dwarf shrub grasslands on the slopes down to the wetlands. Each station was equipped with a Gemini Tinytag® data logger measuring air temperature and air humidity at a height of 30 cm above the ground. At selected sites additional Gemini Tinytag® soil temperature loggers were installed at a soil depth of 10 cm. All stations provided a set of measurements at an



Data source/background: RapidEye high resolution satellite imagery, recorded May 1st 2013

Figure 19 Location of microclimate data loggers in the Cusseque core site interval of 15 minutes (Figure 20). In this paper data from three representative measuring stations in the Sovi Valley are presented: one from the wetlands (TT01, Figure 21) at the valley bottom, one from the mid slope (TT04, Figure 22) and one from woodlands on the hills (TT06, Figure 23). During the period 1st June 2012 to 31st May 2013, the lowest measured temperature was −6.3°C while the warmest temperature was 40.5°C. Daily minimum temperatures were constantly lower on the slopes than in the woodlands with only a few exceptions during the summer months. The same holds true for the comparison between the wetlands and woodlands. Comparing the wetlands with the slopes shows that temperatures are rather similar with the slopes being slightly warmer except for the coldest days of the year. Frost occurred on 21 days on the slopes, 19 days in the wetlands and on only two days in the woodlands. Frost conditions always ended shortly after sunrise (Figure 20). Soil temperatures display a less pronounced amplitude than air temperatures. Frost never occurs in the upper soil layers; in fact, soil temperatures never dropped below 10°C at any location. While soil temperatures display a strong diurnal pattern in the dwarf shrub grasslands and in the woodlands, the soil temperature in the wetlands exhibits a seasonal pattern. The high water content of the peat leads to a very balanced temperature regime with an average daily amplitude of only 1.7°C. In contrast, the average daily temperature amplitude is 6.0°C in the woodland and 10.6°C in the dwarf shrub grasslands (Figure 20). The data from these three measuring stations show that there is a nocturnal flow of cold air converging in the valleys during the dry season. Clear skies during night time in the months May to September facilitate outgoing longwave radiation, resulting in accumulation of cold air close to the soil surface and increasingly low air temperatures as the night progresses, reaching minima just before sunrise. Hence, frosts never lasted longer than 12 hours (Figure 25a). From personal observations, day-time skies are also usually clear during the dry season, leading to high temperatures during the day. Consequently, the temperature amplitude is much bigger in the dry season than during the wet season. In conclusion, it can be stated that there are distinct terrain and vegetation related microclimatic differences within the Cusseque core site. This has considerable implications for vegetation patterns as well as for agriculture, especially in the case of tropical, frost-sensitive crops such as cassava, sweet potatoes, corn or tropical fruits like bananas and mangos. Although there is no frost occurring in the soil, temperatures below 0 °C in the atmospheric layers close to the ground during the dry season clearly limit the potential of agricultural activities in the wetlands and demand cautious site selection for perennial tropical crops on the hills.

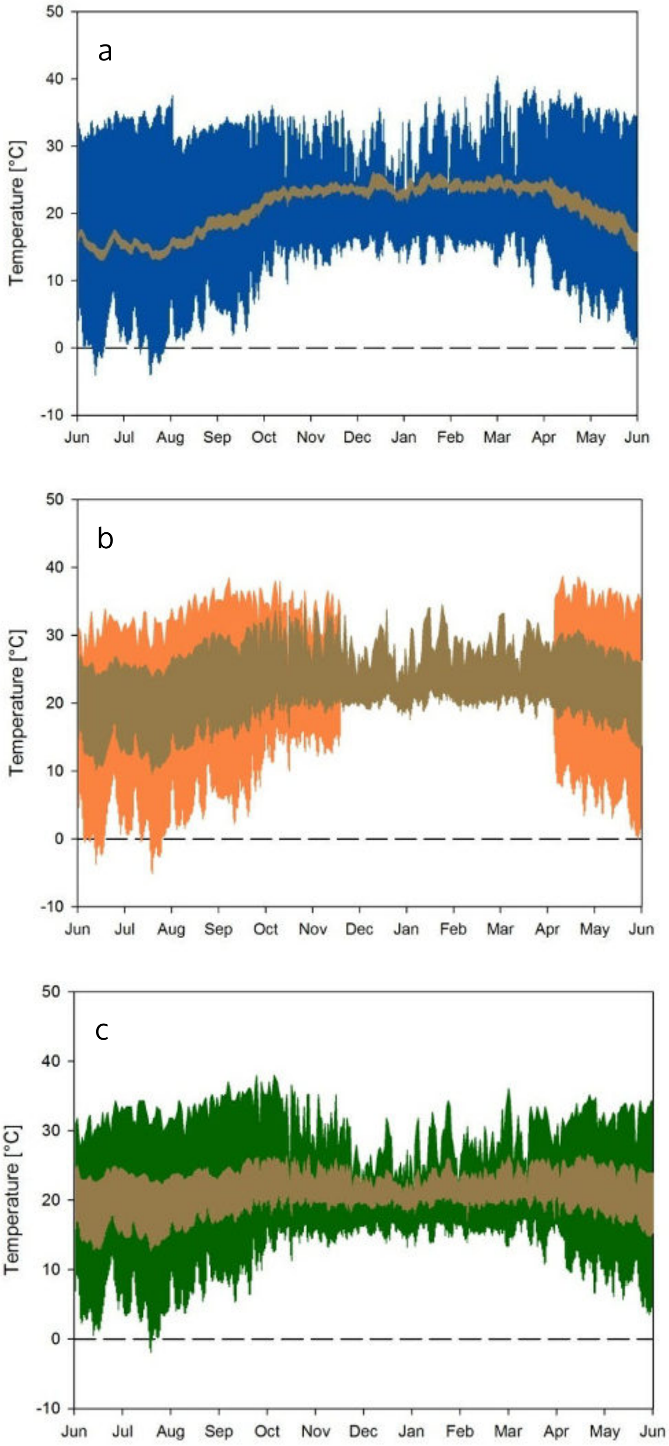


Figure 20 Bivariate difference plot depicting daily minimum and maximum air temperature at 30 cm above ground and soil temperature at 10 cm depth from 1st June 2012 to 31st May 2013;a) Peatland at TT01, blue denotes air temperature; brown refers to soil temperature; b) Dwarf shrub grassland at TT04; orange denotes air temperature; brown refers to soil temperature; c) Woodland at TT06; green denotes air temperature; brown refers soil temperature.

Figure 21 Microclimate measuring station in wetland in the Sovi valley (TT01).

Figure 22 Microclimate measuring station in dwarf shrub grassland in the Sovi valley (TT04).

Figure 23 Microclimate measuring station in Miombo woodlands in the Sovi valley (TT06).

b) Climate refugees going underground – a response to Maurin et al. (2014)

The paper of Maurin et al. (2014) has a lot of merit, bringing the fascinating and widely understudied subject of the 'underground forests of Africa' (White 1976) back onto the scientific agenda. Based on a large sample of geoxyles and their tree counterparts the paper places these species in a comprehensive dated phylogeny of the southern African flora. From there, the authors delineate very convincingly the phylogenetic relationship and evolutionary origin of the geoxylic life form, dating it back in most cases to the Pliocene. In their final analysis, however, the authors formulate the hypothesis that geoxyles have evolved in response to the interactive effects of high precipitation and frequent fires, and rather nonchalantly negate the possibilities of other environmental factors such as frost driving the evolution of suffrutices.

In our response we would like to challenge this interpretation and point out that the fire and precipitation hypothesis of Maurin et al. (2014) does not explain the coexistence of the geoxylic life form with closed forests in the immediate proximity. We base our argument on our own observations and measurements from the Angolan Plateau in the provinces of Bié and Moxico. This region is situated in the core of the Zambezian phytoregion as delineated by White (1983) and is rich in geoxyle diversity (White, 1976). The natural vegetation of the Bié Plateau is composed of closed Miombo forests, geoxyle-rich 'grasslands', and wetlands. Our field data on vegetation, soil temperature and microclimate show that night frosts occur frequently during the dry season, shaping the landscape boundaries between forests on topslopes and hills and geoxylic grasslands on midslopes and footslopes.

In the first part of our response, we will critically revisit the points in support of fire being an evolutionary driver in the Zambezian region. In the second part we will discuss the authors' points against frost playing an important role ecologically, and in the third part we will present arguments suggesting the contrary.

Fire as an evolutionary driver

Maurin et al. (2014) state that geoxyles in Africa are restricted to savanna habitats or upland grasslands and that they occur almost exclusively in higher rainfall savannas that are prone to fires. From our own data and observations we would like to question fire as the predominant evolutionary driver of geoxyle evolution using three arguments.

(1) Fire frequency

The savannas of southern Africa undergo frequent burning (Barbosa et al. 1999; Bond & Keeley 2005). Archibald et al. (2012) stated that in southern Africa most fires occur in the dry season when ignition by thunderstorms is largely absent. Similarly, for the region of the Angolan Plateau it has been shown that most grassland fires occur early in the dry season (Stellmes et al. 2013c). This indicates an anthropic rather than natural origin to fire. The available literature on paleofires makes no reference to fire frequency. However, it can be assumed that the fire return rates were much lower in the absence of human induced fires, which are the number one cause of wildfires today. According to Archibald et al. (2012) humans only learnt to ignite their own fires c. 200– 400 thousand yr ago. Moreover, the landscape of the Angolan Plateau has a forest cover (considered inflammable) beyond the threshold of 40% where fire cannot spread (Hennenberg et al. 2006; Archibald et al. 2009). However, only a short fire return rate of < 5 yr captures tree regeneration in the sapling stage. This process is commonly referred to as 'regeneration bottleneck' or 'fire trap' (Sankaran, Ratnam & Hanan 2004; Bond & Keeley 2005). Therefore, we question whether fire could have been the main evolutionary driver during the Pliocene, the evolutionary starting point of the geoxylic life form according to the study of Maurin et al. (2014).

(2) Vegetation patterns

The current vegetation of the southern slopes of the Angolan Plateau shows an inverse pattern as one would expect from a fire driven landscape pattern. By contrast, the natural landscape follows a very regular pattern. While the hill tracts are covered by forests, slopes are dominated by geoxylic grasslands and only narrow linear strips on the valley bottoms by wetlands (Figure 24; Figure S5). As wildfires normally run uphill due to chimney effects, a fire driven landscape pattern would be expected to show an inverse forest–open land distribution, with forest remnants in the valleys and creeks and grassland on the burned slopes. Vegetation inversion as found on the Bié Plateau is, however, a frequently cited phenomenon under topographic conditions which allow for the accumulation of cold air (see later).

(3) Resource allocation

Maurin et al. (2014) hypothesize that, notwithstanding the fire adaptation of many savanna trees (thick bark, fire-resistant shoots), geoxyles may have escaped fire by developing their woody component belowground, thus minimizing their resource input into annual vegetative growth to the benefit of flower and fruit production. The authors neither explain nor quantify how geoxyles optimize flower and fruit production with their dwarf stature and how this may lead to outcompete large trees. Thus, this argument only holds true if we assume short fire return periods of up to 5 yr (see comment earlier). Furthermore, the authors do not provide any evidence that the geoxyles optimize their resource allocation to the benefit of flower and fruit production as already pointed out by Pennington & Hughes (2014) in their commentary on Maurin et al. (2014).

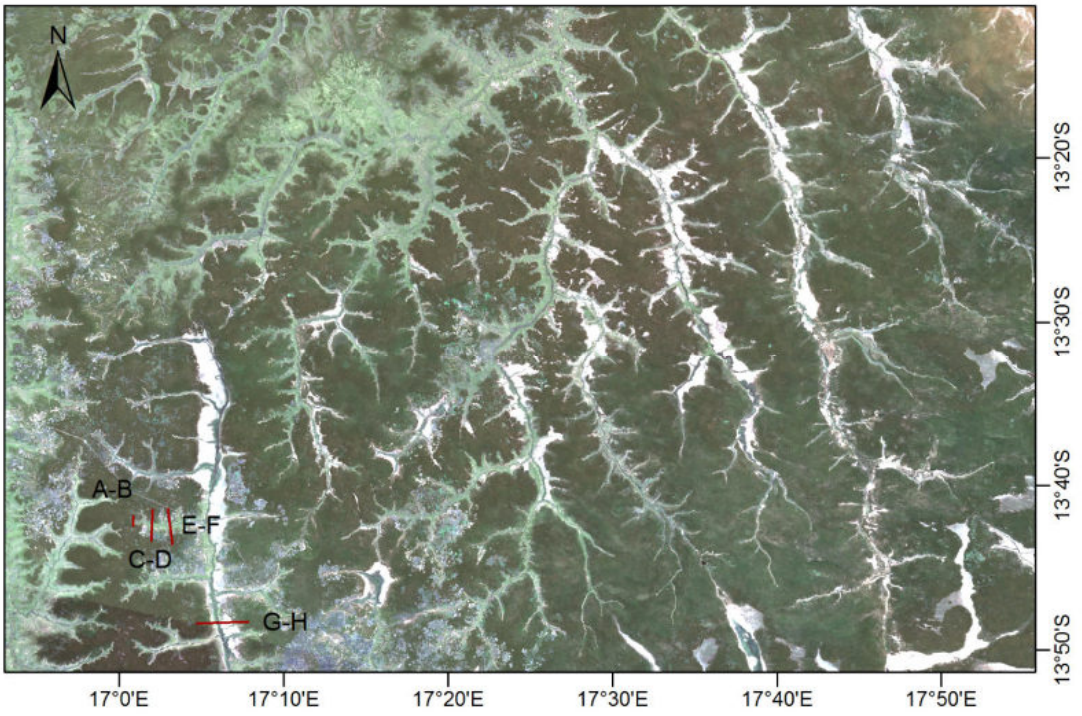


Figure 24 Typical forest-open land distribution of the Angolan Plateau. Forests on hills are visible as dark green, and geoxylic grasslands in the valleys as light green on ferralitic soils and creamy-white on sandy deposits. The valley cross-sections of Figure S5 are indicated as red lines. Data source: detail of Landsat 8 scene, RGB composite with band combination 3-2-1, 23 May 2014, Path 179 Row 69.

A valid point emphasized by Pennington & Hughes (2014) is the synchronicity of the evolution of geoxyles in South America and southern Africa, which calls for a global explanation. Their argument for a 'complex set of shared climate–fire–vegetation feedback mechanisms' is partly flawed by the fact that in climatically comparable regions, for example the Sudanian centre of endemism, only a very small number of geoxylic species occurs, as already pointed out in White's ground-breaking paper (White 1976).

Figure 25 Frost occurrence on the Angolan Plateau. (a) Morning fog lifting from the Cusseque Valley, Bié Province, Angola, during the early morning in the dry season, indicating the accumulation of cold air in the valleys of the Plateau (taken on 30 May 2011); (b) Parinari curatellifolia sapling showing frost burn, in the ecotone of geoxylic grassland and forest, taken on 11 June 2013 in the Cusseque Valley, Bi_e Province, Angola; (c) geoxylic suffrutex Syzygium guineense subsp. huillense with frost burn taken on 7 June 2013 in the Cusseque valley, Bié Province, Angola.

Mean annual temperature as indicator of frost occurrence

Maurin et al. (2014) admit that, in the South African context, cold temperatures may well have been a contributing factor in the evolution of underground trees. However, they claim that the region of greatest geoxyle diversity, the northern areas of the Zambezian Domain (White 1983), receives little or no frost. Maurin et al. (2014) further state that they did not find a general relationship between the geoxylic life form and mean annual temperature or elevation.

Here we would like to contradict Maurin et al. (2014) based on our own measurements. Data from our network of 21 microclimatic temperature loggers installed in the upper Cubango catchment, Angola, show that frost nights occur recurrently in valleys and depressions of the Zambezian Domain (Note S1, Figure 19). The predominant weather conditions for frost occurrence in the Zambezian region are cloudless nights in the dry season with thermal radiation and subsequent accumulation of cold air in the valleys (Figure 25a). Between the end of May and mid-September 2012 to 2014 we measured up to 44 frost nights yr^{-1}, reaching an absolute minimum of −7.5°C. However, we recorded frost mainly on the grasslands and peatlands on slopes and in valley bottoms, with only a few light frost events in the forest-covered hill tracts (Figure 26, Table S1). These measurements support the bioclimatic assessment by Le Houerou (2009) who shows that the Angolan Plateau is under risk of frost hazard for as much as 30 to 60 d yr^{-1}. The gridded climate data set CRU TS v3.22 for the period 1971-2000 (Harris et al. 2014) also shows recurrent frost events in the Zambezian region. At the half degree grid resolution of the data set mean annual frost occurrence in our study area is about four frost nights (Figure 27); however, our data depict nicely that local topography can strongly accentuate frost occurrences.

The use by Maurin et al. (2014) of mean elevation of the distributional range of a species as an explanatory variable has little value in this regard as topographic position of the site is more important. In our case study on the Angolan Plateau we found that in many cases the tree partner of geoxyles occurs on the hills while the suffrutices grow in close proximity on the footslopes.

Furthermore, the authors make use of mean annual temperature (MAT) derived from the Worldclim database (Hijmans et al. 2005) for their analysis. MAT does not reflect frost occurrence in subtropical and tropical regions with a diurnal instead of a seasonal temperature regime and hence has hardly any explanatory power at all. By contrast, frost events are related to cloudless days in the dry season (May to September) with high temperatures during daytime. The registered frost events are always coupled to sunny days with temperature amplitudes reaching > 35°C within 8 h (Figure 28).

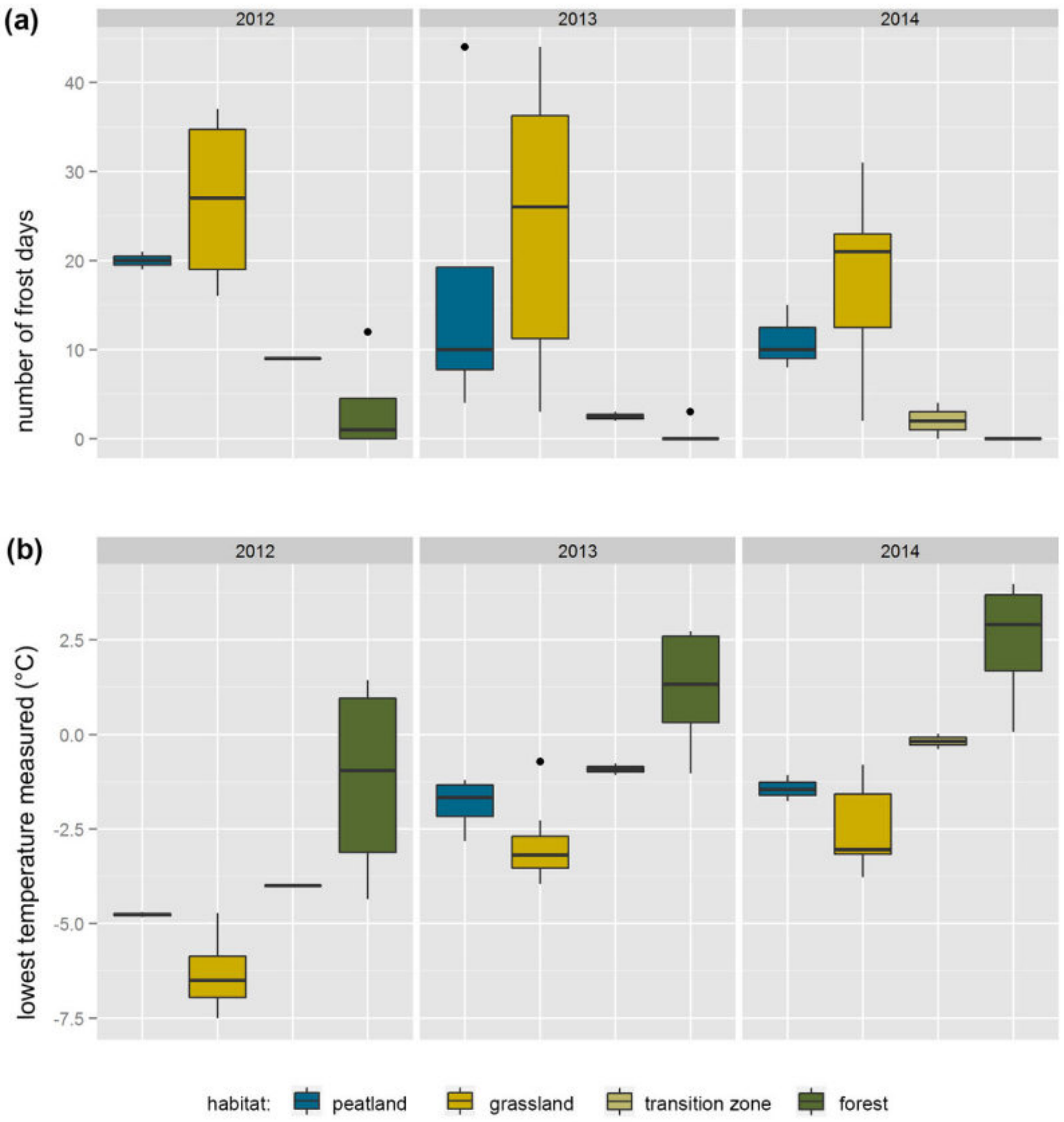


Figure 26 Box and whisker plots showing the logger measurement in different habitat types (forest, forest–grassland–ecotone, geoxylic grassland, and peatland); (a) the annual number of frost days per logger and (b) the absolute minimum temperature per logger (°C). Due to losses by fire and vandalism, the numberof logger stations differed from year to year (2012, n = 11; 2013, n = 21; 2014, n = 16); for more details refer to Supporting Information Table S1).

Frost as a major ecological driver

Impact of frost on southern African savanna ecosystems has been documented by several authors (Holdo 2007; Chafota & Owen-Smith 2009; Whitecross, Archibald & Witkowski 2012). Whitecross et al. (2012) in their case study on the impact of frost on

Colophospermum mopane in South Africa proved that frost resembles a disturbance regime maintaining saplings in a 'freeze trap' similar to the often cited 'fire trap' and 'browse trap'. Furthermore, they found evidence that topographic position in the landscape has an influence on the severity of frost damage.

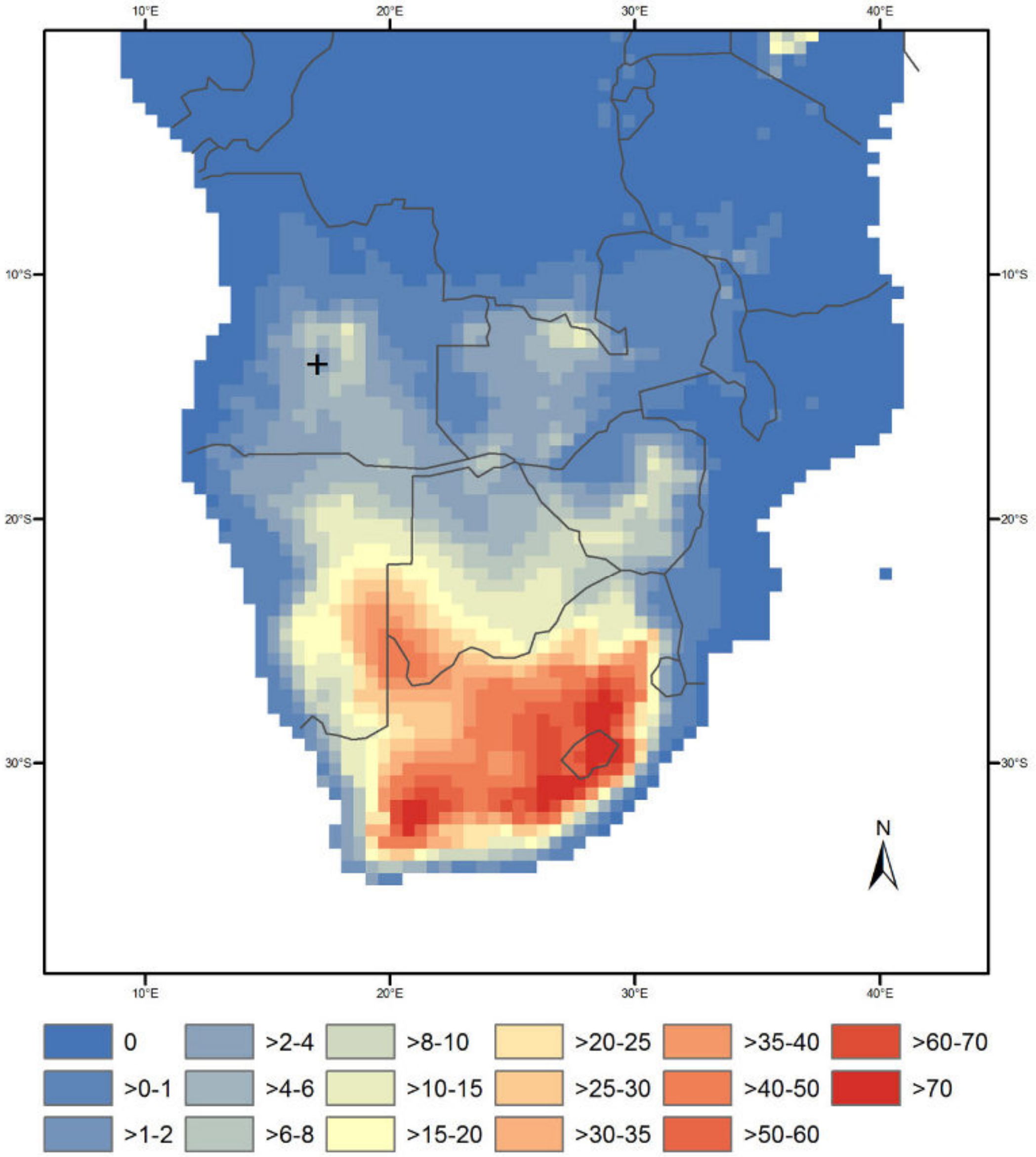


Figure 27 Mean annual frost days with a resolution of 0.5° for south-central Africa based on the CRU TS v3.22 data set for the time period 1971–2000 (Harris et al., 2014). The black cross indicates the location of the microclimatic measurements.

Similarly, Brando & Durigan (2004) studied changes in the Brazilian Cerrado vegetation after disturbance by frost. Of 57 species studied, 15% were unaffected, 19% had only their leaves damaged, 25% had some of their leaves and branches damaged, and 41% had all their aerial parts killed. They conclude that the frequency and intensity of frosts can maintain open forms of Cerrado vegetation even in sites where both water and nutrient availability could support denser vegetation. Several other studies report frost events in the Cerrado core area (Hamilton & Tarifa 1978), and that Cerrado plants are subject to the 'freeze trap' phenomenon killing saplings and seedlings, but not the adult trees (de Vuono et al. 1982; Delitti 1984; Filgueiras & Peña 1989).

In our study area, we frequently found frost burns on tree species in the ecotones between forests and grasslands (Figure 25b). Most suffrutices in the low-lying grassland die back due to frost burns at the beginning of the dry season (Figure 25c) and start resprouting from their buried and frost protected buds at the end of the frost season. In general, buds of suffrutices are placed in the upper 10 cm of the soils. As nocturnal frost episodes are always of short duration, this soil depth is sufficient to prevent any frost damage. On frost prone sites soil temperature at 10 cm depth never drops below 9°C (Figure 29, Revermann & Finckh 2013c).

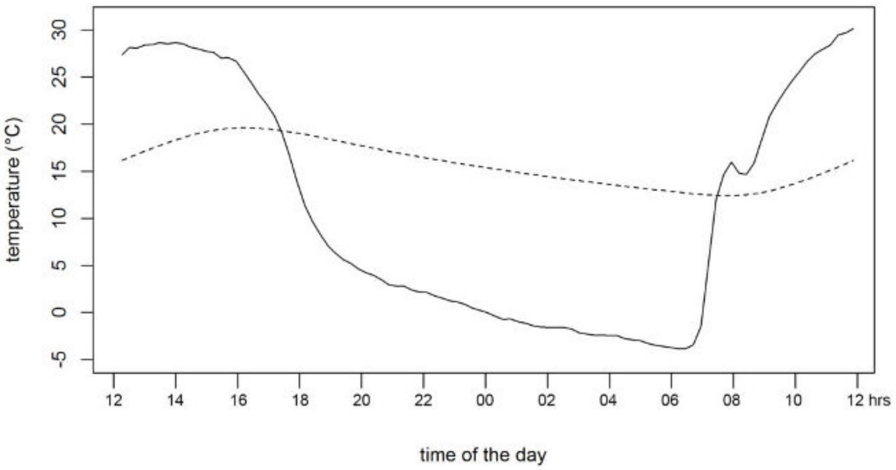


Figure 28 Air temperature at 0.3m above the ground (solid line) and soil temperature at a depth of 0.1m (dashed line) in the course of a day, noon 14 July to noon 15 July 2013, logger number TT02.

In spite of their short duration, these frost events have a high impact on the flora of the Zambezian phytoregion. Sakai & Larcher (1987) indicate that most tropical plants are sensitive to freezing and killed by temperatures of −1 to −4°C, and some of them are even severely damaged by low temperatures above freezing level. Most geoxyle species listed by Maurin et al. (2014) belong to woody tropical and subtropical families such as Apocynaceae, Moraceae, Myrtaceae, or Rubiaceae, being notorious for lacking ecophysiological adaptations to frost (Griffin & Antikienen 1996). Werneck (2011) and Giehl & Jarenkow (2012) consider intolerance to low temperatures to be one of the major factors preventing the tropical flora of South America from occurring in subtropical regions, including the Cerrado.

Maurin et al. (2014) argue that a shift in general climatic conditions has favored the expansion of savannas. We concur with the fact that the climate has changed, and triggered evolutionary development of the geoxylic life form. However, we see the main significance of such change being the increasing seasonality of the climate starting in the late Miocene with a marked dry season and corresponding enhanced risk of frost nights via thermal radiation (Keeley & Rundel 2005). Frost as an evolutionary driver would therefore explain the evolutionary onset of the geoxylic life form long before men started burning. The geoxylic life form – evolved to escape thermic stress – is, however, a perfect preadaptation to man-made fires as frost burns and fire burns have similar effects on plants and necessitate immediate resprouting. The strong increase in fire frequency and burnt area since people learned to use fire as a tool (Archibald, Staver & Levin 2012) probably has allowed geoxyles to leave their localized frost-prone niche and expand into secondary grasslands maintained by frequent fires.

In conclusion, there are good reasons to regard the evolution of the geoxylic life form as an adaptation to low temperatures by frost avoidance rather than purely as a response to fire. We therefore could look at the Zambezian geoxyles as climate refugees gone underground. In general, the role of frost should be reconsidered as an evolutionary driver for the vegetation of south-central Africa and tropical biomes beyond.

Supplementary Materials available in the Appendix of the thesis

Note S1 Technical note on the climate logger network in the Cusseque Valley, Bié Province, Angola. Table S1 Annual minimum air temperatures at 0.3 m above ground, number of frost days and length of frost period (date of first and last frost in the course of the year) during the years 2012–2014. The logger network occasionally suffered from fire and vandalism, therefore data is not available (n/a) for all stations in all years. For locations of measuring stations please refer to Figure 19. Figure S5 Cross section of the Sovi Valley (A–B, C–D, E–F) and the Cusseque Valley (G–H) indicating forest (green), geoxylic grassland (yellow), peat and wetlands (blue). The dashed lines show the lower tree line and reflects the increasing volume of cold air masses accumulating valley downwards. The *y*-axis indicates the elevation in meters above sea level (meters above sea level).

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CHAPTER 5

Linking land surface phenology and vegetation-plot databases to model terrestrial plant α-diversity of the Okavango Basin.

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Remote Sensing (2016) **8**: 370

Abstract

In many parts of Africa, spatially-explicit information on plant α-diversity, i.e. the number of species in a given area, is missing as baseline information for spatial planning. We present an approach on how to combine vegetation-plot databases and remotely-sensed land surface phenology (LSP) metrics to predict plant α-diversity on a regional scale. We gathered data on plant α-diversity, measured as species density, from 999 vegetation plots sized 20 m × 50 m covering all major vegetation units of the Okavango Basin in the countries of Angola, Namibia and Botswana. As predictor variables, we used MODIS LSP metrics averaged over 12 years (250-m spatial resolution) and three topographic attributes calculated from the SRTM digital elevation model. Furthermore, we tested whether additional climatic data could improve predictions. We tested three predictor subsets: (1) remote sensing variables; (2) climatic variables; and (3) all variables combined. We used two statistical modelling approaches, random forests and boosted regression trees, to predict vascular plant α-diversity. The resulting maps showed that the Miombo woodlands of the Angolan Central Plateau featured the highest diversity, and the lowest values were predicted for the thornbush savanna in the Okavango Delta area. Models built on the entire dataset exhibited the best performance followed by climate-only models and remote sensing-only models. However, models including climate data showed artifacts. In spite of lower model performance, models based only on LSP metrics produced the most realistic maps. Furthermore, they revealed local differences in plant diversity of the landscape mosaic that were blurred by homogenous belts as predicted by climate-based models. This study pinpoints the high potential of LSP metrics used in conjunction with biodiversity data derived from vegetation-plot databases to produce spatial information on a regional scale that is urgently needed for basic natural resource management applications.

Keywords: Angola; Botswana; dry tropical forests; EVI; Miombo; MODIS; Namibia; phenological metrics; predictive modelling; species density

Introduction

Globally, biodiversity is declining at a high rate (Butchart et al. 2010), and international treaties, such as the Convention on Biological Diversity, pledged to halt biodiversity loss. Paramount for safeguarding biodiversity is a better understanding of biodiversity patterns and spatially-explicit information. The recent discussion on 'essential biodiversity variables' has shown that remote sensing applications are indispensable in the process and are needed to monitor changes in biodiversity over large areas with a consistent methodology (Pereira, Ferrier & Walters 2013; Pettorelli & Skidmore 2015). In this context, field-based ecological data also play a prominent role as baseline data for biodiversity models and as ground truth information for remote sensing applications. In a recent effort, the initiative on a global index of vegetation-plot databases (GIVD) created a meta-database containing over 200 existing vegetation-plot databases worldwide with over three million vegetation plots (Dengler et al. 2011; Jansen et al. 2012). These databases harbor an enormous potential as ground truth information for future remote sensing studies and spatial modelling approaches from local to global scales; yet, so far this potential remains unexploited. However, there are a few studies combining MODIS data with vegetation databases, e.g. to predict tree species richness in the USA (Nightingale et al. 2008) or to analyze vegetation responses to drought in Dutch dune ecosystems (2015). The main reasons for the missing integration of remote sensing, spatial modelling and ecological research are not only the differing traditions of the disciplines, but are rooted in the mismatch of the spatial scales of satellite imagery and the size of ecological field sites. However, in recent years remote sensing products have diversified, and even more importantly, many have become readily available at no cost with appropriate spatial and temporal resolution; for a review from the remote sensing perspective, see Wang et al. (Wang et al. 2010). Likewise, the availability of field-based data has increased and has become more accessible through the formation of global (meta-) databases.

Vegetation plots are samples of a specific area of the landscape and vary in size depending on vegetation type and the purpose of the study: the size of vegetation plots in woodlands and forests commonly ranges from 400 m^2 to 25,000 m^2 (Sutherland 1997). Typically, they hold information of the co-occurring plant species, their cover or abundance, vegetation structure and are often connected to abiotic parameters, such as soil properties. Generally, vegetation plots are stored in a vegetation database compiling information of several vegetation plots within a region. From these databases, one can extract information on plant diversity. Diversity has many dimensions, and its measurement strongly depends on the observed spatial scale (Magurran 2004). Commonly, diversity is treated in three different components: (1) α-diversity defined as the diversity of a vegetation plot; (2) α-diversity is the difference in species composition between vegetation plots; and (3) α-diversity reflects the diversity at the landscape level, i.e. the species pool of all sampled vegetation plots (Magurran 2004). The α-diversity measure "species density" is often regarded as the "common currency" in diversity research (Gaston & Spicer 2004) and is defined as the number of species present in a given area, e.g. in a vegetation plot.

Turner et al. (2003) list two main approaches to assess biodiversity using remote sensing: (i) direct measurements where species are recognized based on their spectral properties; or (ii) indirect ones where no direct link is established, but instead, relies on the spatially-explicit localization of distinct vegetation units. Closely linked to these vegetation units are properties, such as α-diversity, i.e. the average species number of a defined site or habitat, that we seek to extrapolate using statistical models (Gillespie et al. 2008). In ecology, the establishment of species distribution models (SDMs) as a standard tool to make predictions for unsurveyed areas based on field surveys has boosted the integration of robust statistical methods for predictive modelling (Elith & Leathwick 2009). In predictive modelling, statistical algorithms are used to relate the attributes in question, i.e. the response variable, to a set of environmental predictor variables, such as climate data or remotely-sensed information.

Spectral properties of vegetation change throughout the seasons due to changes of biophysical and biochemical properties, i.e. pigment, sugar and water content of leaves in the canopy, above ground biomass or vegetation structure. As such, land surface phenology (LSP) metrics can be derived from dense spectral observations reflected in remotely-sensed vegetation indices across large areas (Justice et al. 1985; Jönsson & Eklundh 2002). Software, such as TIMESAT (Jönsson & Eklundh 2004), is frequently used to derive various LSP metrics, i.e. (1) temporal metrics defining phenological stages of the vegetation (e.g. start and end of the green season); (2) biomass-related metrics (e.g. integrals or amplitudes); and (3) seasonality-related metrics (e.g. the green-up rate).

As every vegetation unit has a more or less unique combination of phenological metrics, LSPs are highly suited to distinguish different vegetation types, as demonstrated by Fan et al. (2015), who used LSP to identify rubber plantations in fragmented tropical forests. Moreover, LSP metrics served for mapping above-ground woody biomass (Karlson et al.

2015) and have been successfully applied in species distribution modelling (Tuanmu et al. 2010; Cord et al. 2014), change detection (Stellmes et al. 2013d; Fensholt et al. 2015) and for vegetation mapping (Hüttich et al. 2009; Senf et al. 2013). So far, no study tested the suitability of LSP metrics for modelling plant α-diversity. However, especially biomass-related LSP metrics, i.e. integrals or base values, could be promising predictors for plant α-diversity due to strong empirical linkages of above ground biomass and species richness (Fraser et al. 2015; Laanisto & Hutchings 2015).

Generally, climate is regarded as the main driver of biogeographic patterns at large spatial scales (Pearson, Dawson & Liu 2004). However, with increasing spatial resolution, factors, such as topography, soil properties or disturbance patterns, gain importance. It has been shown that climatic predictors serve as large-scale determinants, while land cover data increase the predictive power of species distribution models on finer resolutions of 1 km to 20 km (Pearson, Dawson & Liu 2004; Luoto, Virkkala & Heikkinen 2007). Most studies on plant α-diversity using remote sensing data focus either on global or continental scales with very coarse resolution (100 km, Barthlott et al. 2005) or have a small extent, but operate on fine grain sizes (1 m to 30 m, Feilhauer & Schmidtlein 2009; Hernández-Stefanoni et al. 2012; Viedma et al. 2012). The study of Saatchi et al. (2008) is an exception in this regard and covers the entire Amazon Basin at 1- to 5-km spatial resolution.

The aim of this study was to test the suitability of MODIS EVI land surface phenology metrics at 250-m spatial resolution to predict vascular plant α-diversity derived from the vegetation-plot database of the Okavango Basin. We used two statistical model algorithms, boosted regression trees (BRT) and random forests (RF), and compared the performances of the models on three predictor subsets: (1) only LSP metrics and topography; (2) only climate data; and (3) the entire set of predictor variables including both LSP metrics and climate data. Finally, we analyzed the α-diversity maps generated for the Okavango Basin using the different models and datasets. In doing this, we aimed to provide recommendations for generating spatially-explicit maps on plant α-diversity on a regional level with comparatively high spatial resolution to support natural resource management and conservation applications.

Data and Methods

Study Site

The Okavango Basin is situated in southern Africa and is shared by the countries of Angola, Namibia and Botswana (Figure 29). The Okavango River and its tributaries originate on the Angolan Central Plateau, where the large majority of the runoff is generated (Steudel et al. 2013a). The middle reaches of the river form the border between Angola and Namibia before entering Botswana, where it terminates in the Okavango Delta, one of the largest inland deltas of the world. The course of the river follows a strong environmental gradient from its source on the Angolan Central Plateau at altitudes of 1850 m a.s.l. to the Okavango Delta in Botswana at around 940 m a.s.l. Mean annual temperature increases from northwest to southeast from 18 °C to 24 °C. Precipitation shows an inverse trend: the Angolan Central Plateau features a sub-humid climate with mean annual precipitation of over 1400 mm, and the delta receives less than 500 mm per year (Weber 2013a). Accordingly, vegetation changes along the course of the river. Miombo forests are the dominant vegetation type of the Angolan Central Plateau with its gently rolling landscape. However, topography has a strong impact on local vegetation patterns;

mid- and bottom slopes of the valleys feature geoxylic grasslands, and the valley bottoms of many tributaries harbour wetlands (Revermann et al. 2013). As climate becomes drier, the closed Miombo woodlands give way to the more open *Baikiaea-Burkea* woodlands of the middle reaches. The area surrounding the delta to the east is dominated by *Colophospermum mopane* woodlands, while the driest areas to the west and south of the delta are covered by thornbush savannas formed by various *Acacia* communities (Revermann & Finckh 2013a).

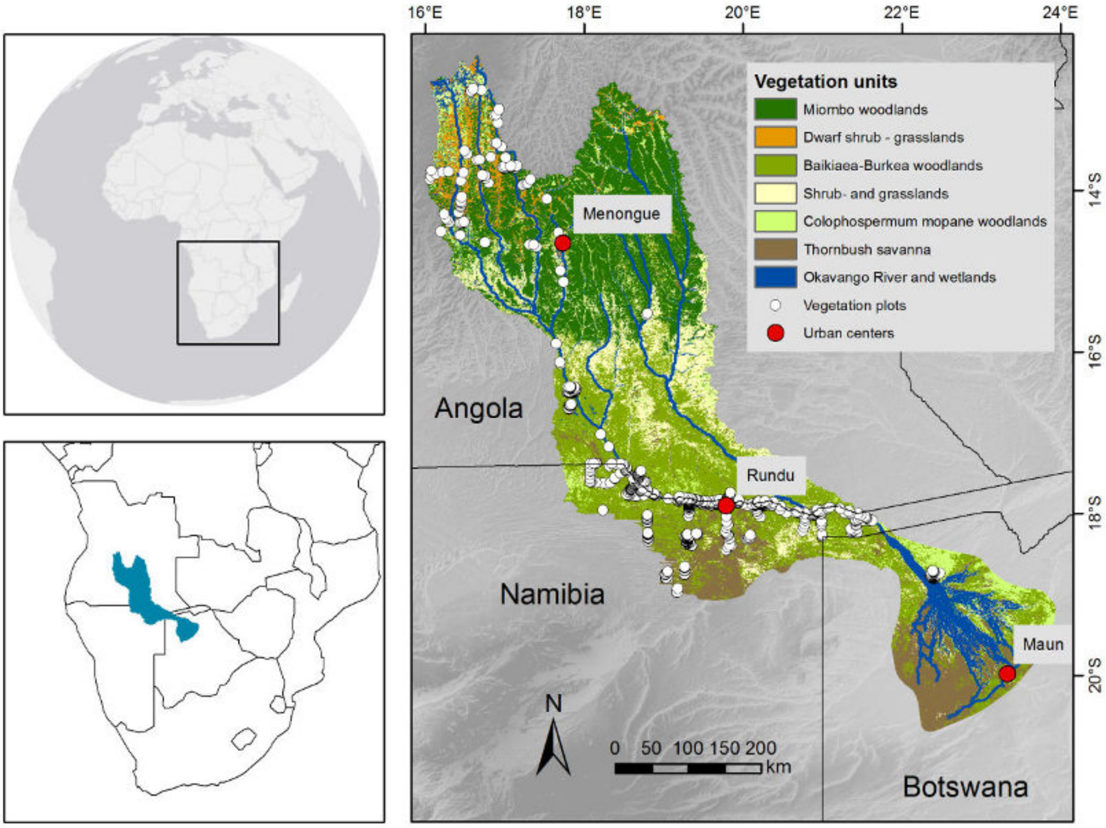


Figure 29 Location of the Okavango Basin in southern Africa. The map of the Okavango Basin shows major vegetation units modified after Stellmes et al. (2013b) and the location of vegetation plots used in this study. The three major urban centres of the Basin, Menongue, Rundu and Maun, are indicated by a red dot. The map datum is WGS84, and the background shows the SRTM digital elevation model. The extent of the study area, the Okavango Basin, follows the definition of The Future Okavango (TFO) project (Wehberg & Weinzierl 2013). For a map on observed species density, see Figure S6.

Data

Vegetation Data

Quantitative information on the vegetation, especially on the large Angolan share of the Okavango Basin, is scarce and limited to descriptive studies from the pre-independence era, i.e. before 1975 (Gossweiler & Mendonça 1939; Barbosa 1970; Monteiro 1970; dos Santos 1982). During The Future Okavango (TFO) project, we initiated an extensive plot-based vegetation survey based on a random stratified sampling design to ensure coverage of all major vegetation types of the Basin (GIVD database ID: AF-00-009, Revermann & Finckh 2013a; b; Revermann et al. 2013, 2016b; Wallenfang et al. 2015). However, the remoteness, limited access and the danger of land mines posed restrictions on the sampling. On vegetation plots sized 20 m × 50 m, all vascular plant species were recorded. Vegetation surveys were carried out during the growing seasons (November to

May) of the years 2011 to 2014. Additionally, data from the National Phytosociological Database of Namibia were used (GIVD database ID: AF-NA-001, Strohbach & Kangombe 2012). For the present study, we only considered plots from terrestrial vegetation, i.e. forests, woodlands and grasslands, as plots from semi-terrestrial and aquatic vegetation units were too small to properly relate to MODIS data. To avoid mixed pixel problems, we only selected plots that were not located at the edge of vegetation units and had a minimum distance of 500 m between plots, i.e. there was only one vegetation plot within one MODIS pixel. In total, 999 vegetation plots were selected for modelling. This dataset comprises the best available data for the region. However, some vegetation units were underrepresented, such as the thornbush savanna in the southwest of the Okavango Delta and the transition zone between Miombo woodlands and *Baikiaea-Burkea* woodlands. As a plant α-diversity measure, we derived species density per 10^3 m^2, i.e. the number of vascular plant species per vegetation plot (Magurran 2004).

MODIS

We compiled a MODIS-enhanced vegetation index (EVI) time series with a spatial resolution of 250 m × 250 m (MOD13Q1 product). The main requisition of an appropriate vegetation index is its capability of differentiating biomass at a certain point in time, as well as tracing phenological changes reliably (Sonnenschein et al. 2011). We used the standard MODIS vegetation 16-day EVI product, because this vegetation index overcomes some limitations of the NDVI that are of relevance in our study area. Thus, the EVI is less sensitive to the background signal, such as soil brightness, and it does not saturate as fast with high biomass values. Moreover, still, inherent atmospheric effects should be lessened (Huete et al. 2002; Waring et al. 2006). Using TIMESAT (Jönsson & Eklundh 2004), we derived eleven land surface phenology (LSP) metrics based on the 16-day EVI composite time series ranging from July 2000 to June 2012 (Table 8). As a consequence of the Southern Hemisphere, the start of the year was set to the middle of the year, 1st July, when most deciduous species have shed their leaves and annual plants have died back. In order to reduce the effect of the inter-annual variability of LSP, we used the long-term mean of the annual metrics. Additionally, we used the mean and the minimum of the near infrared (NIR) channel of the surface reflectance product (MOD13Q1) to differentiate between vegetation-scarce surfaces with different brightness, such as water and soil.

Topography

We selected three predictor variables describing topography (Table 8), as it has been shown that the local topography of the Angolan Central Plateau creates micro-climatic conditions strongly influencing vegetation patterns (Revermann & Finckh 2013c; Finckh, Revermann & Aidar 2016). Moreover, water availability plays a primary role in the semi-arid parts of the Okavango Basin. Based on the global digital elevation model SRTM (Shuttle Radar Topography Mission) with a horizontal resolution of 90 m × 90 m, we calculated the topographic position index (TPI, Wilson & Gallant 2000), the topographic wetness index (TWI, Beven & Kirkby 1979) and the topographic ruggedness index (TRI, Riley, DeGloria & Elliot 1999) in the open source GIS SAGA (Conrad et al. 2015). Subsequently, the topographic attributes were resampled using bilinear interpolation to match the MODIS resolution.

Climate

Weinzierl et al. (2013) provided a regionalization of climate data from 1950 to 2000 for the Okavango Basin based on orographic parameters and a geographically-weighted regression algorithm with a resolution of 1 km × 1 km. The original climate data stem from the regional climate model REMO for the domain of south central Africa forced with the global circulation model ECHAM (Jacob 2001). We resampled the regionalized data using bilinear interpolation to match the resolution of the MODIS data. Based on monthly values of minimum temperature, maximum temperature and monthly precipitation, we derived 15 bioclimatic predictors using the "dismo" package in R (Hijmans et al. 2015).

To test whether the quality of predictions depended on climate, we additionally tested a second climate dataset compiled from two sources: (1) precipitation data were obtained from the gridded African Rainfall Climatologies Version 2 with a spatial resolution of 0.1° (ARC2, Novella & Thiaw 2013); input data of the ARC2 data are 3-hourly satellite-based infrared measurements and daily gauge measurements; (2) temperature data were derived from the Climate Research Unit (CRU) TS3.10 dataset (Harris et al. 2014). CRU is based on meteorological stations across the global land area and has a spatial resolution of 0.5°. These climate data were subject to the same treatment as the REMO climate data, and the same bioclimatic predictor variables were calculated. For results based on the modelling using the second climate dataset, refer to the Supplementary Material.

Table 8 Description of predictor variables and data sources. All variables excluded from modelling after screening for collinearity among predictor variables are denoted with an asterisk. SRTM: digital elevation model of shuttle radar topography mission; REMO: regional climate model for the domain of south central Africa forced with the global circulation model ECHAM. RS TOPO: remote sensing and topography data set.

Dataset	Variable	Variable Description	Dataset
RS TOPO	Amplitude	maximum of EVI–minimum of EVI	MODIS EVI time series
	BaseValue	base value of EVI in the course of year	MODIS EVI time series
	LargeIntegral	total integral of EVI in the course of year	MODIS EVI time series
	SmallIntegral *	integral of EVI above BaseValue	MODIS EVI time series
	NIR	near infrared band	MODIS EVI time series
	NIR_min *	minimum of the near infrared band	MODIS EVI time series
	MaxFit *	maximum fitted value of EVI	MODIS EVI time series
	RateDecrease *	rate of senescence (slope of the line connecting the annual peak and the point at the end of greenness)	MODIS EVI time series
	RateIncrease *	rate of green up (slope of the line connecting the point of the onset of greenness and the annual peak)	MODIS EVI time series
	SeasonEnd	day of year, end of greening	MODIS EVI time series
	SeasonLength	number of days, duration of greening	MODIS EVI time series
	SeasonMid	day of year, peak of greening	MODIS EVI time series
	SeasonStart	day of year, start of the greening	MODIS EVI time series
	TPI	topographic position index	SRTM 90 m
	TRI	topographic ruggedness index	SRTM 90 m
	TWI	topographic wetness index	SRTM 90 m
CLIMATE	bio1	annual mean temperature (°C)	REMO
	bio2 *	mean diurnal range (°C) (mean of monthly (max temp–min temp))	REMO
	bio3	isothermality ((BIO2/BIO7) × 100)	REMO
	bio4	temperature seasonality (standard deviation ×100)	REMO
	bio5 *	max temp. of warmest month (°C)	REMO
	bio6 *	min temp. of coldest month (°C)	REMO
	bio7	temp. annual range (BIO5 to BIO6) (°C)	REMO
	bio8 *	mean temp. of wettest quarter (°C)	REMO
	bio9 *	mean temp. of driest quarter (°C)	REMO
	bio10 *	mean temp. of warmest quarter (°C)	REMO
	bio11 *	mean temp. of coldest quarter (°C)	REMO
	bio12	annual precipitation (mm)	REMO
	bio15	precipitation seasonality (coefficient of variation)	REMO

Statistical Modelling

To test whether remote sensing data or climate data are better suited to predict plant α-diversity, we tested three subsets of the predictor variables: (1) remote sensing data and topographic data denoted as remote sensing and topography "RS TOPO"; (2) only climatic data "CLIMATE"; (3) all predictor variables "ALL" (Table 8).

Collinearity among predictor variables can lead to erroneous estimation of the parameters of a statistical model and, hence, cause misleading interpretations (Dormann et al. 2013). Therefore, all predictors were screened prior to modelling and tested for collinearity using a Spearman rank-correlation test (r_S). For visualizing the strength of the correlation, we used the R package "corrplot" (Wei 2013). For all pairs of variables with $|r_S| > 0.7$, the variable better reflecting ecological processes determining vegetation patterns was selected (Dormann et al. 2013).

The choice of the statistical model type is a common source of the algorithmic prediction error (Pearson et al. 2006). Thus, we tested and compared two modelling techniques that have been used in various areas of ecological modelling and have been demonstrated to have a high predictive power (Elith et al. 2006): boosted regression trees (BRT, Friedman 2002) and random forests (RF, Breiman 2001; Prasad, Iverson & Liaw 2006). BRT combines the strength of traditional regression trees and boosting, the adaptive, stage-wise combination of a multitude of individual models. High predictive performance is enabled through accommodating non-linear relationships and fitting interactions among predictor variables. We used the R packages "gbm" (Ridgeway 2015) and 'caret' (Kuhn et al. 2015) to compute BRT assuming a Poisson distribution of the response variable. There are three important parameters that need to be set by the user: interaction depth, number of trees and the learning rate. We systematically varied the three parameters using a 10-fold cross-validation to find the optimal settings for each data subset (Elith, Leathwick & Hastie 2008).

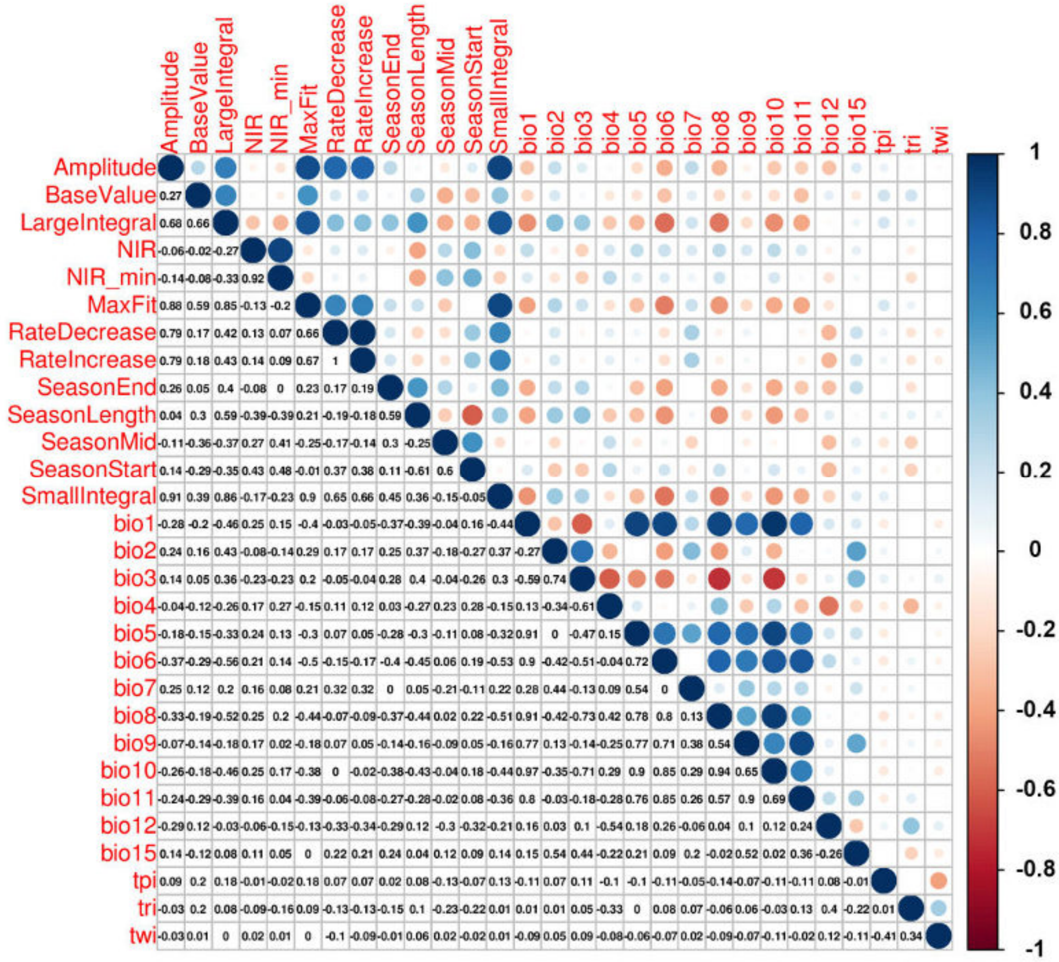
RF builds multiple regression trees based on bootstrap samples with each tree being grown on a randomized subsample of the predictor variables. A large number of trees is grown without pruning, and final results are averaged. In RF, the specification of model parameters has less influence on model output. We operated RF with default settings for the number of variables used at each split (number of candidate variables divided by 3); the number of trees to grow was set to 1000. RF was calculated using the R package 'randomForest' (Liaw & Wiener 2002).

BRT and RF offer slightly different measures of variable importance, and the measures cannot be compared directly among model types. In BRT, variable importance is measured as the relative influence of each variable averaged over all trees. For RF, we display the increase in the mean square error of the prediction (Liaw & Wiener 2002).
For validation, the dataset was split into training and test data samples with a ratio of 80:20 using random stratified sampling. The following criteria of model performance were calculated: explained variance, the Pearson's coefficient of correlation (r_p) between the predicted and observed values of species density, the coefficient of determination R^2, the root mean square error (RMSE), and the relative root mean square error (rRMSE in percent) (Kuhn et al. 2015). The models were calibrated on training data and then used to predict plant α-diversity of the entire Okavango Basin at 250-m spatial resolution. All analyses were carried out in R (R Development Core Team 2015).

Results

Model Building and Validation

After screening for collinearity, seven LSP metrics, three topography predictors and six climate variables were selected for modelling out of the 29 potential predictor variables (Figure 30, Table 8). Models on all subsets ("RS TOPO", "CLIMATE" and "ALL") showed a clear correlation of predicted and observed values of plant α-diversity, and values of the Pearson correlation (r_p) ranged from 0.69 to 0.80 on test data. In order to compare r_p values based on confidence intervals, we computed the z-scores based on the Fisher transformation. Comparisons revealed no significant differences in the correlation for "ALL" and "CLIMATE" models. However, "RS TOPO" models showed consistently significantly lower correlation in comparison to "ALL" (BRT: *z*-value −2.475, *p*-value 0.007; RF: *z*-value −1.758, *p*-value 0.039) and "CLIMATE" (BRT: *z*-value −2.475, *p*-value 0.007; RF: *z*-value −1.758, *p*-value 0.039). The RMSE was moderately high with values of 9.3 to 11.0 species per 10^3 m^2, and the relative RMSE ranged from 26.8% to 31.4%. The R^2 indicated a moderate goodness-of-fit ranging from 0.48 to 0.64.



	Amplitude	BaseValue	LargeIntegral	NIR	NIR_min	MaxFit	RateDecrease	RateIncrease	SeasonEnd	SeasonLength	SeasonMid	SeasonStart	SmallIntegral	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio15	tpi	tri	twi
Amplitude																													
BaseValue	0.27																												
LargeIntegral	0.68	0.66																											
NIR	-0.06	-0.02	-0.27																										
NIR_min	-0.14	-0.08	-0.33	0.92																									
MaxFit	0.88	0.59	0.85	-0.13	-0.2																								
RateDecrease	0.79	0.17	0.42	0.13	0.07	0.66																							
RateIncrease	0.79	0.18	0.43	0.14	0.09	0.67	1																						
SeasonEnd	0.26	0.05	0.4	-0.08	0	0.23	0.17	0.19																					
SeasonLength	0.04	0.3	0.59	-0.39	-0.39	0.21	-0.19	-0.18	0.59																				
SeasonMid	-0.11	-0.36	-0.37	0.27	0.41	-0.25	-0.17	-0.14	0.3	-0.25																			
SeasonStart	0.14	-0.29	-0.35	0.43	0.48	-0.01	0.37	0.38	0.11	-0.61	0.6																		
SmallIntegral	0.91	0.39	0.86	-0.17	-0.23	0.9	0.65	0.66	0.45	0.36	-0.15	-0.05																	
bio1	-0.28	-0.2	-0.46	0.25	0.15	-0.4	-0.03	-0.05	-0.37	-0.39	-0.04	0.16	-0.44																
bio2	0.24	0.16	0.43	-0.08	-0.14	0.29	0.17	0.17	0.25	0.37	-0.18	-0.27	0.37	-0.27															
bio3	0.14	0.05	0.36	-0.23	-0.23	0.2	-0.05	-0.04	0.28	0.4	-0.04	-0.26	0.3	-0.59	0.74														
bio4	-0.04	-0.12	-0.26	0.17	0.27	-0.15	0.11	0.12	0.03	-0.27	0.23	0.28	-0.15	0.13	-0.34	-0.61													
bio5	-0.18	-0.15	-0.33	0.24	0.13	-0.3	0.07	0.05	-0.28	-0.3	-0.11	0.08	-0.32	0.91	0	-0.47	0.15												
bio6	-0.37	-0.29	-0.56	0.21	0.14	-0.5	-0.15	-0.17	-0.4	-0.45	0.06	0.19	-0.53	0.9	-0.42	-0.51	-0.04	0.72											
bio7	0.25	0.12	0.2	0.16	0.08	0.21	0.32	0.32	0	0.05	-0.21	-0.11	0.22	0.28	0.44	-0.13	0.09	0.54	0										
bio8	-0.33	-0.19	-0.52	0.25	0.2	-0.44	-0.07	-0.09	-0.37	-0.44	0.02	0.22	-0.51	0.91	-0.42	-0.73	0.42	0.78	0.8	0.13									
bio9	-0.07	-0.14	-0.18	0.17	0.02	-0.18	0.07	0.05	-0.14	-0.16	-0.09	0.05	-0.16	0.77	0.13	-0.14	-0.25	0.77	0.71	0.38	0.54								
bio10	-0.26	-0.18	-0.46	0.25	0.17	-0.38	0	-0.02	-0.38	-0.43	-0.04	0.18	-0.44	0.97	-0.35	-0.71	0.29	0.9	0.85	0.29	0.94	0.65							
bio11	-0.24	-0.29	-0.39	0.16	0.04	-0.39	-0.06	-0.08	-0.27	-0.28	-0.02	0.08	-0.36	0.8	-0.03	-0.18	-0.28	0.76	0.85	0.26	0.57	0.9	0.69						
bio12	-0.29	0.12	-0.03	-0.06	-0.15	-0.13	-0.33	-0.34	-0.29	0.12	-0.3	-0.32	-0.21	0.16	0.03	0.1	-0.54	0.18	0.26	-0.06	0.04	0.1	0.12	0.24					
bio15	0.14	-0.12	0.08	0.11	0.05	0	0.22	0.21	0.24	0.04	0.12	0.09	0.14	0.15	0.54	0.44	-0.22	0.21	0.09	0.2	-0.02	0.52	0.02	0.36	-0.26				
tpi	0.09	0.2	0.18	-0.01	-0.02	0.18	0.07	0.07	0.02	0.08	-0.13	-0.07	0.13	-0.11	0.07	0.11	-0.1	-0.1	-0.11	-0.05	-0.14	-0.07	-0.11	-0.11	0.08	-0.01			
tri	-0.03	0.2	0.08	-0.09	-0.16	0.09	-0.13	-0.13	-0.15	0.1	-0.23	-0.22	0.01	0.01	0.01	0.05	-0.33	0	0.08	0.07	-0.06	0.06	-0.03	0.13	0.4	-0.22	0.01		
twi	-0.03	0.01	0	0.02	0.01	0	-0.1	-0.09	-0.01	0.06	0.02	-0.02	0.01	-0.09	0.05	0.09	-0.08	-0.06	-0.07	0.02	-0.09	-0.07	-0.11	-0.02	0.12	-0.11	-0.41	0.34	

Figure 30 Correlation matrix of predictor variables measured by Spearman's rank-correlation coefficient (r_S) ranging from –1 to 1. The lower half of the diagonal gives the numeric value of r_S; the upper diagonal visualizes the correlation coefficient: the size of the circles corresponds to the strength of the correlation; red denotes negative and blue positive correlation coefficients. For details on predictor variables, see Table 1.

Table 9 Validation results for the two model types boosted regression trees (BRT) and random forests (RF) on the three subsets of the predictor variables: remote sensing and topography ("RS TOPO"), only climate data ("CLIMATE") and all data ("ALL"). The following performance measures were calculated: explained variance (expl. var. (%), Pearson's correlation coefficient (r_P) between observed and predicted values, the coefficient of determination (R^2), the root mean square error (RMSE, in species per 10^3 m^2), and the relative root mean square error (rRMSE in percent). The results for training and test data are displayed (training 80% of the data and testing 20%).

Model	Dataset	Expl. var.	Correlation (r_P)		R^2		RMSE		rRMSE	
		Train (%)	Train	Test	Train	Test	Train	Test	Train	Test
BRT	RS TOPO	54	0.80	0.69	0.60	0.48	10.1	11	28.8	31.8
	CLIMATE	61	0.82	0.80	0.68	0.63	9.1	9.3	25.8	26.8
	ALL	67	0.86	0.80	0.74	0.64	8.3	9.3	23.5	26.8
RF	RS TOPO	43	0.94	0.70	0.89	0.49	5.9	10.9	16.7	31.4
	CLIMATE	50	0.94	0.78	0.87	0.61	5.8	9.6	16.6	27.6
	ALL	54	0.95	0.79	0.90	0.63	5.3	9.4	15.2	27.0

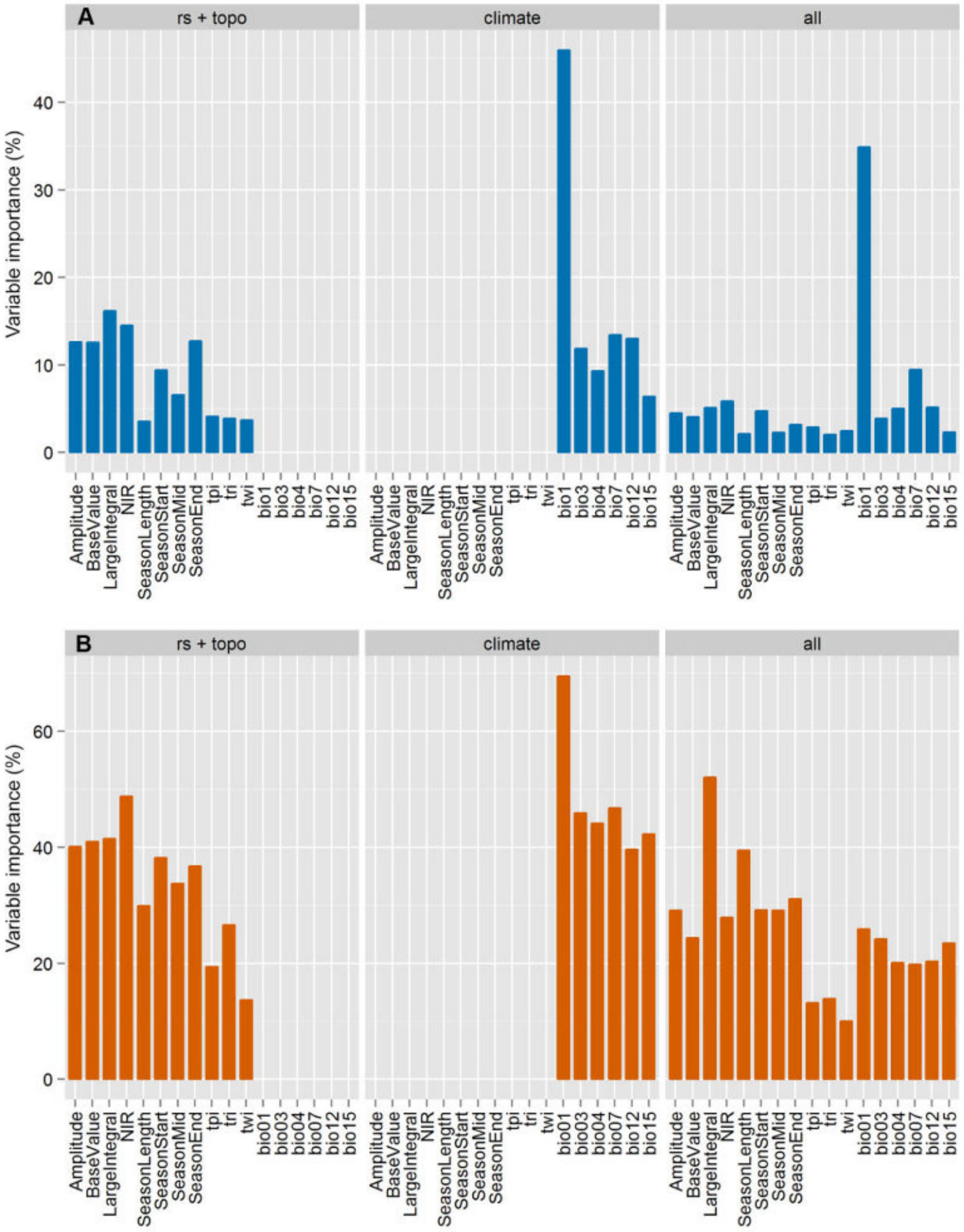


Figure 31 Variable importance for the two model types: (a) BRT, calculated as the relative influence (%); (b) RF, calculated as the increase in MSE (%). As the calculation of variable importance differs among BRT and RF, only the ranking of the variables can be compared, but not the absolute values.

The explained variance ranged from 43% to 67% (Table 9). The two statistical model algorithms BRT and RF performed almost equally well regarding all performance criteria. Only the explained deviance was consistently higher in BRT for all datasets than in RF. The difference of the performance criteria between training and test data was much higher in RF than in BRT. Regarding the different input data, the "ALL" models performed best, closely followed by "CLIMATE", while "RS TOPO" models exhibited the poorest performance.

Variable Importance

Variable importance varied among the three subsets of predictor variables and between the model types. However, a few general trends were evident (Figure 31). The topographic variables had only limited influence in all model runs. In the "RS TOPO" dataset, the "NIR" and "LargeIntegral" were the two most important variables. Most of the biomass-related metrics were superior to the temporal metrics, i.e. length, start or end of the season. Among the climatic variables, annual mean temperature ('bio1') was the most important predictor throughout all model runs. Precipitation-related variables did not have much predictive power. In BRT, in the dataset "ALL", climatic predictors had the highest importance, while the opposite was observed in RF, where LSP metrics yielded higher predictive power than climatic predictors (Figure 31).

Patterns of Plant α-Diversity

The predicted plant α-diversity in the Basin ranged from 15 to 65 species per 10^3 m^2. All derived maps showed that the Miombo woodlands of the upper reaches of the Okavango River featured the highest plant α-diversity, reaching values of over 60 species per 10^3 m^2 (Figure 32). Generally, plant α-diversity followed a decreasing trend southwards. The *Baikiaea-Burkea* woodlands of the middle reaches took an intermediate position, while the area around the Okavango Delta in Botswana showed the lowest values of 20 to 25 species per 10^3 m^2. Furthermore, the surroundings of the larger urban centres Rundu and Menongue depicted the absolute lowest plant α-diversity.

The predictions of BRT and RF were similar for "RS TOPO", but showed regional differences for the models built on the datasets "CLIMATE" and "ALL" (Figure 32c,f,i). On these datasets, BRT predicted higher plant α-diversity for the Miombo woodlands of the far northeast of the Basin and for the *Baikiaea-Burkea* woodlands of the middle reaches of the Okavango River. In contrast, RF predicted higher values than BRT in the thornbush savanna of the delta region. The maps based on the models on "CLIMATE" and "ALL" datasets showed belts of undifferentiated plant α-diversity (Figure 32d,e,g,h). In contrast, "RS TOPO" showed fine-scale patterns of the landscape of the Miombo region (Figure 32 a,b, Figure 33).

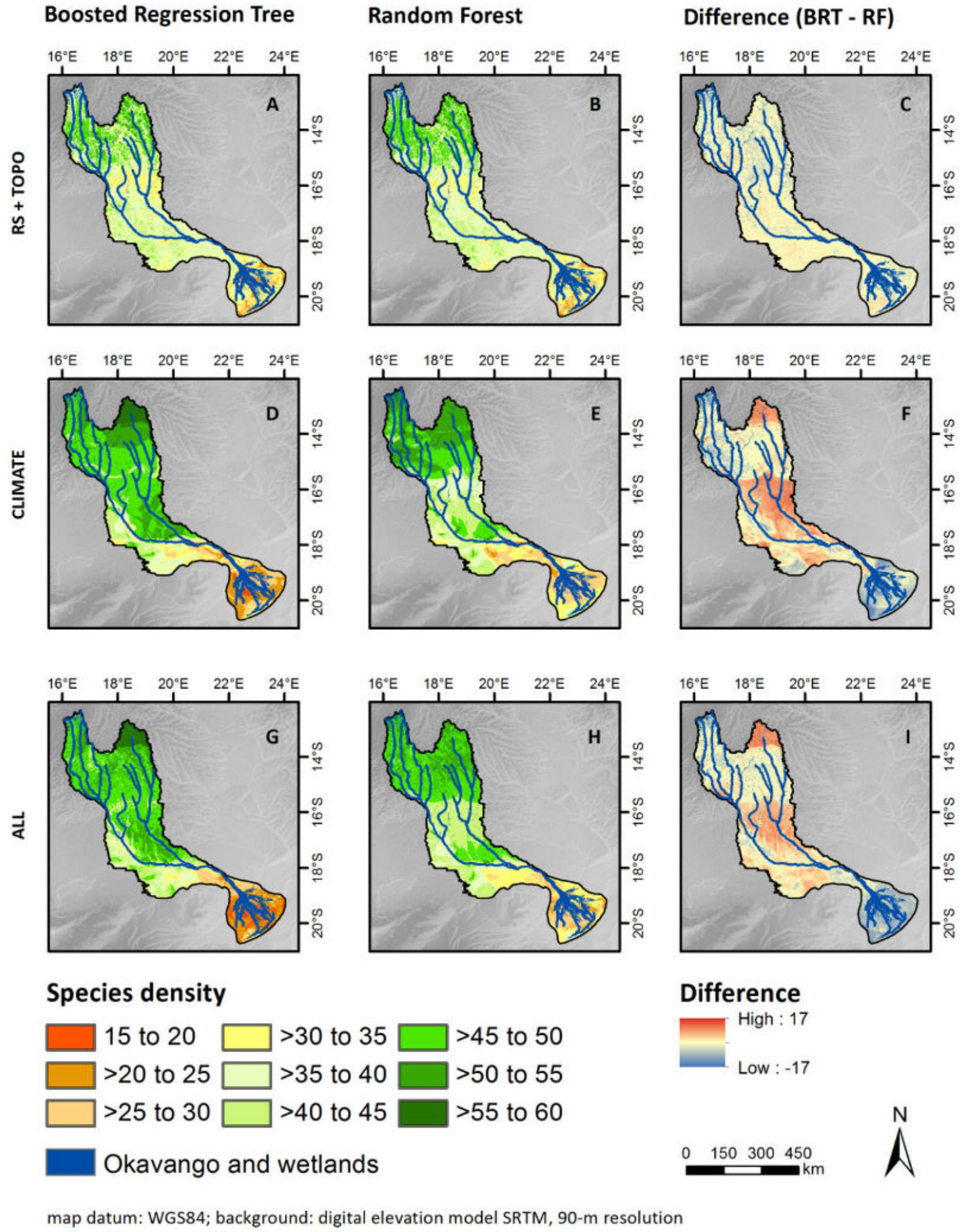


Figure 32 Plant α-diversity (species density per 10^3 m^2) in the Okavango Basin predicted by boosted regression trees (BRT) and random forests (RF) and the difference between the two model algorithms displayed for the three datasets 'RS TOPO' (a,b,c), 'CLIMATE' (d,e,f), and 'ALL' (g,h,i). BRT (a,d,g), RF (b,e,h), difference (c,f,i). For a map on observed species density, see Figure S6.

Discussion

Model Evaluation and Quality of Predictions

Pearson et al. (2006) divided the prediction error of species distribution models in two components: (1) the algorithmic prediction error emanating from the choice of the statistical model and other parameters set during the modelling exercise; and (2) quality of the input data. In our study, the performance of BRT and RF models was very similar for all tested performance criteria showing good to moderate performance (Table 9). While there was little difference between the plant α-diversity maps of BRT and RF on the "RS TOPO" dataset (Figure 4a,b), the maps based on models including climate data showed discrepancies between the two model algorithms (Figure 4c-f; for a detailed discussion, see the discussion on climate data below). Thus, depending on the dataset, the algorithmic prediction error varies in magnitude, although BRT and RF are both machine learning techniques based on regression trees and exhibited comparable model performance.

Data Quality

The response variable in this study was derived from two vegetation-plot databases. As shown by García Márquez et al. (2012), spatial bias is an inherent problem of many vegetation-plot databases and can lead to the wrong model predictions. In Angola, very limited accessibility and the danger of land mines put strong restrictions on a purely random stratified sampling design. Consequently, some areas of the Basin and some vegetation units are under-sampled, e.g. the vegetation belt in the transition from the Miombo woodlands to the *Baikiaea-Burkea* woodlands at the base of the Angolan Central Plateau. Furthermore, the data of the thornbush savanna surrounding the Okavango Delta are scarce. The spatial bias of the response variable may also explain considerably high RMSE values. Beyond that, regions with lower sampling intensity showed the highest discrepancies between the two model algorithms on the datasets "CLIMATE" and "ALL". However, generally, the vegetation database contains a sufficient number of plots and represents the best available vegetation dataset for the region.

The relatively coarse resolution of MODIS data might also be a potential error source, where especially small vegetation units are acquired in mixed pixels and, thus, are negatively affecting the proper linkage to the smaller vegetation plots. Hence, substituting MODIS imagery with spatially appropriate remote sensing data could improve predictions. However, at the current state, deriving LSP based on Landsat for tropical Africa remains problematic, as one image at least every 16 days is required (Archibald & Scholes 2007). This is not the case in tropical Africa due to the reduced data availability for this region in the Landsat archive (Kovalskyy & Roy 2013) and missing clear sky images from the wet season. Nevertheless, the increasing revisit frequency of the medium-resolution satellite-platforms Landsat and Sentinel-2 might account for this problem, alleviating the direct derivation of LSP at the required spatial scale.

Patterns of Plant Alpha Diversity

In general, the derived maps based on MODIS LSP ("RS TOPO") showed a realistic pattern of plant α-diversity when compared to the vegetation map of the region (Stellmes et al. 2013b). The highest plant α-diversity was predicted for the more mesic regions of the upper reaches of the Okavango Basin and steadily decreased southwards. Hence, plant α-diversity followed the environmental gradient of decreasing precipitation and increasing temperatures in a north-south direction. This pattern is in line with the globally-observed phenomenon of a latitudinal gradient of species richness (Willig, Kaufman & Stevens 2003). However, the gradient is a rough abstraction with many exceptions, and the underlying process are still debated (Gaston 2000). Apart from global or continental maps, there are no previous studies depicting plant α-diversity of the Okavango Basin. The global map on vascular plant diversity of Barthlott et al. (2005) operates on a spatial scale of 10,000 km^2 and features only three diversity zones for the Okavango Basin. According to this map, plant α-diversity ranges from 500 to 2000 species per 10,000 km^2. Naturally, the number of species increases with increasing plot size or reference area of a map. However, the increase in species number with increasing area is system dependent and, thus, results in species area curves that vary according to vegetation type (Dengler 2009a). Therefore, given this scale dependency of plant α-diversity, our results cannot be easily scaled up to the larger map units of Barthlott et al. (2005) to directly compare the data. Nevertheless, it becomes evident that due to the high spatial resolution, our maps reveal diversity patterns with unprecedented detail showing more than a purely latitudinal gradient. On the Angolan Central Plateau in the north of the Okavango Basin, two major vegetation units occur in close proximity following the pattern of the gently rolling topography of the landscape: Miombo woodlands dominate on elevated areas, while geoxylic grasslands inhabit the slopes (Revermann et al. 2013). The measured plant α-

diversity of the Miombo woodlands was significantly higher than plant α-diversity of the geoxylic grasslands (Figure 33a). The models on the 'RS TOPO' dataset were capable of capturing this difference, but not the 'CLIMATE' models (Figure 33). The major urban centres of the Basin showed low plant α-diversity, which can be explained by their spectral similarity to open vegetation types or shrub-dominated thornbush savanna also featuring low diversity.

Incorporating climate data into modelling species densities did improve model performance when compared to remote sensing-only models "RS TOPO" (Table 9). However, a visual evaluation of the resulting maps revealed artefacts in the presented patterns, i.e. the predicted patterns of plant α-diversity did not match existing patterns in the vegetation of the Okavango Basin (Figure 29). Maps produced by BRT and RF on the full set of predictor variables (including climate, but also remote sensing information, dataset "ALL") showed less obvious artifacts. Nevertheless, the maps exhibited sharp borders with abruptly changing values of plant α-diversity (Figure 32). Only in some cases did these changes coincide with climatic borders resulting in actual alteration of land cover, i.e. at the southern foothills of the Angolan Central Plateau. Moreover, the differences between the predictions of plant α-diversity by BRT and RF were much larger when climate data were included in the modelling. The differences did not follow a systematic pattern, but showed a spatial pattern (Figure 32c,f,i). Thus, the error can be related to the fact that the model algorithms give different weight to the climatic predictor variables (Figure 31).

Models including climate ("CLIMATE" and "ALL") reproduced large-scale climatic gradients resulting in belts of undifferentiated plant α-diversity. In contrast, models based on LSP metrics and topography ("RS TOPO") produced by far better maps as judged by experts. The maps depict local differences in plant α-diversity reflecting the mosaic of the landscape that is blurred in the climate models, as evident from the Miombo region (Figure 33). Climatic predictors are known to be large-scale determinants, while land cover predictors gain importance on smaller spatial scales (Waring et al. 2006; Luoto, Virkkala & Heikkinen 2007). Therefore, extra- and azonal vegetation types pose challenges in predictive modelling if climatic predictors are included and make careful checks or even post-processing required (Jürgens et al. 2013).

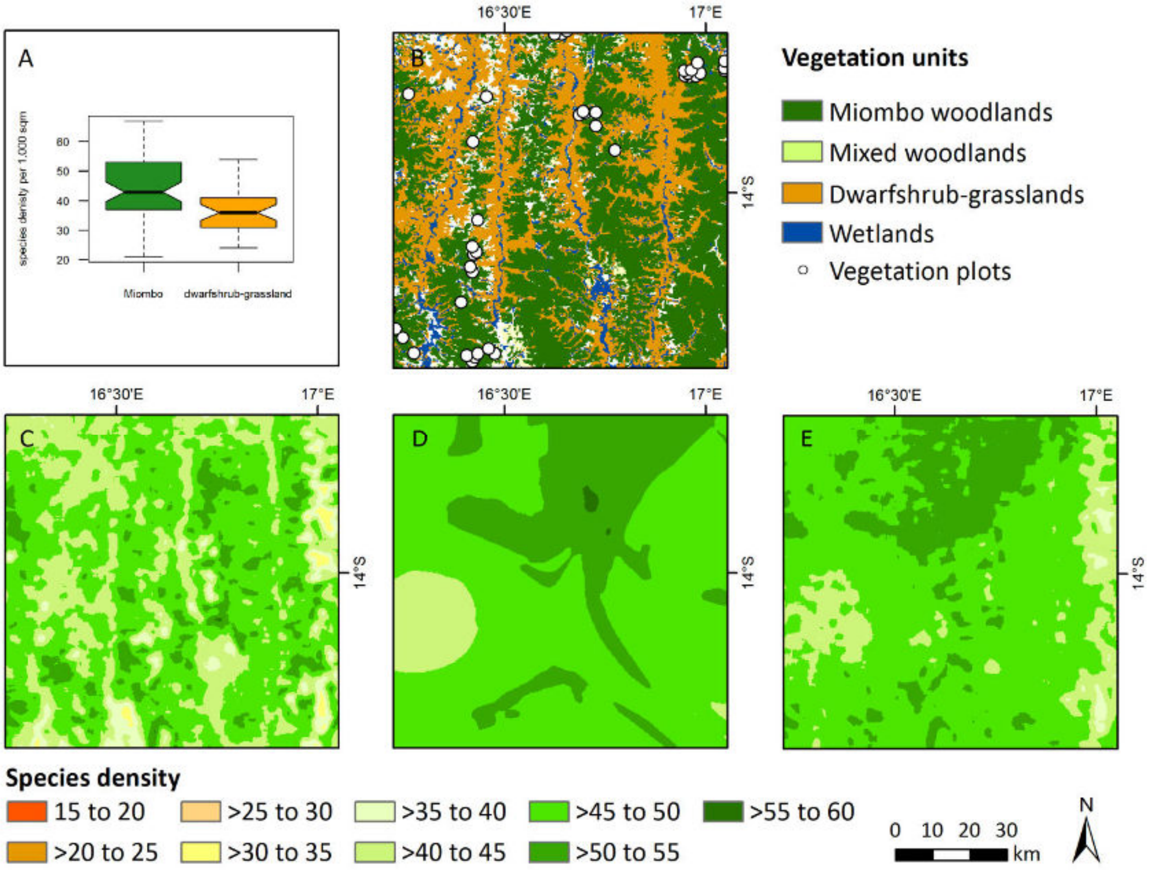


Figure 33 Plant α-diversity (species density per 10^3 m^2) in the Miombo region. (a) Observed species density of the vegetation units "Miombo woodlands" and "dwarf shrub/grassland" in the upper reaches of the Okavango Basin derived from vegetation-plot database. "Miombo woodlands" (mean = 44.0, SD = 10.8) exhibit significantly higher species density than "dwarf shrub-grasslands" (mean = 35.9, SD = 7.3) according to a two-group *t*-test ($p < 0.001$); (b) Major vegetation units of the area according to Stellmes et al. (2013b) and location of vegetation plots; (c) Species density as predicted by BRT on the "RS TOPO" dataset; (d) Species density predicted by BRT on the "CLIMATE" dataset; (e) Species density predicted by BRT on the "ALL" dataset.

Biophysical Meaning of LSP Metrics

The productivity-diversity hypothesis (Grime 1973) links the variation in species diversity to productivity measured as plant biomass and proposes a hump-backed relationship. However, four decades after it was first hypothesized, the exact form of the relationship between plant α-diversity and biomass, as well as its generality across biomes is still hotly debated (Fraser et al. 2015, and citations therein; Laanisto & Hutchings 2015). While empirical studies usually measure biomass in kg·ha^{-1}, we had to rely on LSP metrics derived from EVI time series as a proxy. The "LargeIntegral" can be considered an indicator for total biomass (DeFries, Hansen & Townshend 1995; Helman et al. 2015), the "Amplitude" for the build-up of life biomass during the vegetation period (DeFries, Hansen & Townshend 1995) and 'BaseValue' as the share of biomass that remains after senescence of the vegetation during the dry season (Helman et al. 2015).

In this study, we showed that biomass-related LSP metrics (e.g. "LargeIntegral", "Amplitude" and "BaseValue") are good predictors for plant α-diversity (Figure 31). The models for the Okavango Basin showed that areas with low productivity, such as the dry thornbush savanna, featured low species numbers, while the mesic Miombo woodlands exhibited the highest productivity and also the highest number of species. However, we did not find the originally-proposed unimodal relationship, but diverse response functions of plant α-diversity to above ground biomass-related LSP metrics in all BRT and RF models (sigmoidal, linear and bimodal relationships; Figure S11).

Although vegetation indices, such as the EVI, are well-known proxies for above ground biomass, they tend to saturate at high biomass values (Huete, Liu & Leeuwen 1997). Consequently, the forecasted effect of low plant α-diversity at sites with high biomass (Grime 1973; Fraser et al. 2015) could be blurred and, hence, might restrict our observed response to an apparently linear relationship. Furthermore, the generality of the productivity-diversity relationship is still debated and could be biome or even formation specific. Sampling across multiple biomes and plant formations ranging from grasslands, savannas to forests as in the case of this study could lead to superimposition of multiple relationships, resulting in an overall weak linear response. Nonetheless, the productivity-diversity relationship could provide an important theoretical background for spatially-modelled α-diversity based on remotely-sensed LSP metrics.

Do Additional Climate Data Improve Models and Maps?

In spite of higher model performance of the models incorporating climate data, the resulting diversity maps are unrealistic and not meaningful when compared to actual observations (Figure 32 and Figure 33). The low quality of the spatial representation of plant α-diversity of the climate models could be related to the coarse spatial resolution of the climate data. The study region of the Okavango Basin encompasses an area with very limited historic climate data available to calibrate regional climate models. One reason could therefore be that the regionalized climatologies of the regional climate model REMO do not capture the climatic patterns in the Okavango Basin well enough. We thus tested a second climate dataset from independent sources: for temperature, we used data from the Climate Research Unit (CRU, Harris et al. 2014); for precipitation, we used the remotely-sensed information from the African Rainfall Climatologies (ARC2, Novella

& Thiaw 2013). The resulting models had comparable model performance and contained different, but similar artefacts (Table 9, Figure S11). In conclusion, artefacts in modelled diversity maps were not related to the source of climate data, but the problem is inherent to using climate data as predictors for modelling plant α-diversity of the ecosystems of southern Africa on a medium spatial resolution. Modelling tree diversity of the Amazon Basin, Saatchi et al. (2008) came to a similar conclusion that gridded climate data cannot fully capture landscape-scale variation in plant α-diversity, as the patterns are, apart from climate, controlled by local phenomena, such as soil properties, geology, nutrient availability and past history of the area. Land cover, in turn, is a result of large-scale (climatic) gradients, but also mirrors site conditions and the history of disturbance events. For the Okavango Basin, predicted patterns of plant α-diversity are similar to patterns of the land cover classification of Stellmes et al. (2013b, Figure 34b,c), hence supporting the assumption of Turner et al. (Turner et al. 2003) that land cover is a good proxy for estimating diversity.

The fact that the chosen performance criteria did not identify the models delivering the most realistic maps as the best ones is highly problematic and poses fundamental questions on how to judge the validity of models. At the same time, it highlights the importance of cross-checking model results with experts and revising the resulting maps within an ecological context. Not to treat statistical significance synonymously with ecological relevance is paramount if communicating scientific results to stakeholders and policy makers (Martínez-Abraín 2008).

One explanation may lie in the ecology of the studied ecosystems. To a large extent, savanna ecosystems are disturbance driven; especially fire has played a major role in their evolution and maintenance (Sankaran, Ratnam & Hanan 2004; Bond & Keeley 2005). Midgley and Bond (2015) therefore argued that climatic predictors are not an ideal choice to model these ecosystems. Therefore, remote sensing predictors depicting the current land cover irrespective of the potential natural vegetation serve as better predictors. Nevertheless, this is not reflected by the higher model performance of the "RS TOPO" models. However, in RF, the LSP predictor variables had higher predictive power than climatic predictors, while in BRT, the opposite was the case. This also explains the different patterns of the resulting maps. Including further remote sensing-based predictors depicting fire will be promising. In savanna ecosystems, the fire frequency and the timing of fire in the vegetation period are of paramount importance (Stellmes et al. 2013c). On the one hand, short fire return periods may impede tree generation, capturing trees permanently in the sapling stage, the so-called "demographic-bottleneck" (Sankaran, Ratnam & Hanan 2004). On the other hand, fires early in the dry season mainly affect the herbaceous layer, while hot, late dry season fires are more likely to also impact canopy species. The corresponding parameter can be derived from the MODIS active fire product (MOD14A1 and MYD14A1) and MODIS burned area (MCD45, 500-m resolution, Stellmes et al. 2013c) and included in the modelling.

Another important ecological feature shaping the spatial pattern of the dwarf shrub-grasslands of the Angolan Central Plateau is the frequent occurrence of nocturnal frost in the low-lying valleys during the dry season (Revermann & Finckh 2013c; Finckh, Revermann & Aidar 2016). Generally, adaptations to frost are limited in the flora of tropical Africa. Therefore, the regular frost events reduce the species pool of the dwarf shrub-grasslands to a large extent to frost avoidance specialists protecting their buds underground, e.g. dwarf shrubs or so-called "geoxyles" (White 1976), or under dry leaf matter, e.g. many tufted C4 grasses. To develop topographically-corrected climate datasets showing spatial and temporal extents of cold air during night frost events will thus be a promising way forward to improve vegetation modelling in tropical highlands.

Conclusions

Vegetation-plot databases harbor a great potential to provide response variables for modelling ecosystem properties using remote sensing data. In this study, we showed that plant α-diversity derived from such databases can be used for predicting plant -diversity of unsurveyed areas using land surface phenology derived from MODIS EVI time series. The models for the Okavango Basin showed that the Miombo woodlands of the Angolan Central Plateau feature the highest plant α-diversity and that plant α-diversity decreases southwards, reaching the lowest values in the thornbush savanna surrounding the Okavango Delta. In spite of higher model performance, models incorporating resampled climate data did not produce realistic maps on plant α-diversity. The suitability of climate predictors for modelling plant α-diversity on a medium spatial resolution has therefore to be questioned. Using MODIS LSP metrics as predictor variables has several advantages for modelling plant diversity. First, the global coverage ensures transferability of modelling frameworks to other regions. Second, the medium spatial resolution is fine enough to display local patterns of the landscape mosaic. Third, using land cover-related predictor variables instead of climatic predictors improves the representation of extraand azonal vegetation types. The presented modelling approach combines plot-based ecological field data with continuous remote sensing data and, hence, enables predictions of ecosystem properties for vast, unsurveyed areas as they exist in many parts of the world. In this way, the approach may contribute to systematic conservation planning, as it provides the much needed spatial information for, e.g. identifying biodiversity hot spots or the delimitation of protected areas.

Supplementary Materials available in the Appendix of the thesis

Table S2 Validation results for the two model types boosted regression trees (BRT) and random forest (RF) on the three subsets of the predictor variables (a) remote sensing and topography 'RS TOPO' (b) only climate data derived from CRU and ARC2 'CLIMATE CRU/ARC2', (c) all data 'ALL2' ('RS TOPO and 'CLIMATE CRU/ARC2'). The following performance measures were calculated: explained variance (expl. var. [%]), Pearson's correlation coefficient (r_p) between observed and predicted values, coefficient of determination (R^2), the root mean square error (RMSE, in species per 10^3 m^2) and the RMSE normalized by the mean, the relative root mean square error (rRMSE in per cent). The results for training and testing data are displayed (training 80% of the data and testing 20%); Figure S6: Observed values of alpha diversity plotted against predicted values on training data for (a) BRT on data set 'RS TOPO'; (b) RF on data set 'RS TOPO'; (c) BRT on data set 'CLIMATE'; (d) RF on data set 'CLIMATE'; (e) BRT on data set 'ALL'; (f) RF on data set 'ALL'; Figure S7: Observed plant alpha diversity (species density per 10^3 m^2). Data is based on 999 vegetation plots sized 20 × 50 m; Figure S8: Model residual for the two model types: boosted regression trees (a,c,e) and random forest (b,d,e) on the three datasets: 'RS TOPO' (a,b); 'CLIMATE' (c, d); 'ALL'; (g, h). Furthermore, we calculated variograms to check for spatial autocorrelation but no sever spatial auto correlation was detected; Figure S9: Plant alpha diversity (species density per 10^3 m^2) predicted by the two model types: BRT (a,c,e) and random forest (b,d,f) on the three data (sub-)sets: 'RS TOPO' (a,b); 'CLIMATE' (d,e); 'ALL' (e,f); Figure S10 Partial dependence plots of the LSP metrics 'Amplitude' (a,d), 'BaseValue' (b,e) 'LargeIntegral' (c,f) for the two model types BRT (a–c) and RF (d–f); Figure S11 Plant alpha diversity (species density per 10^3 m^2) predicted by the two model types: BRT (a,d) and random forest (b,d) on the second climate data set CRU/ARC2 (a,b); and on the entire data set comprising the second climate data set CRU/ARC2 and remote sensing data (d,e) and the difference between the two model algorithms (c,f).

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Author Contributions

All authors contributed to the final version of the manuscript. R.R. designed the study, compiled environmental data, carried out statistical modelling and wrote the first draft of the manuscript. J.O. continuously contributed to the modelling part and study design. B.S., M.F. and R.R. carried out field work. M.S. and D.F. processed satellite data and produced the LSP metrics.

CHAPTER 6

Species richness and evenness respond to diverging land-use patterns – a cross-border study of dry tropical woodlands in southern Africa

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Abstract

Cross-border studies offer unique situations to study the impact of different land-use regimes on ecosystems. Along the Angolan and Namibian border formed by the Okavango River the environmental conditions and traditional land-use practises are the same on either side of the river. However, decades of civil war in Angola led to a stagnant development while political stability in Namibia fostered a recent socio-economic transformation. We investigated the impact of spatially diffuse land use on plant diversity of the dry tropical woodlands covering the vast, sandy hinterlands of the river. As accessibility is the major factor governing land use, we used distance to road as a proxy for land-use intensity.

Based on 58 vegetation plots sized 20 m x 50 m we showed that species richness increased with distance to road in Angola while in Namibia it remained constant on a lower level. Evenness showed an inverse pattern to species richness and Shannon diversity index showed no response. Analysing diversity patterns according to life forms revealed that these patterns are primarily driven by woody species. The study showed that spatially diffuse land use has a measurable effect on plant diversity and illustrates that roads act as vectors of change.

Keywords: Angola; cross-border contrast; diffuse land use; Namibia; Okavango; plant diversity

Introduction

The aim of ecological research is to understand processes and anticipate changes in ecosystems. However, in most cases the necessary long term data to carry out such analyses is lacking. Therefore, space-for-time substitutions (Pickett 1989; Blois et al. 2013) or studies of so-called fence-line contrasts (Todd & Hoffman 2009) offer an alternative approach to investigate impacts of land management or effects of changing environmental conditions on ecosystem properties. Ecological boundaries are usually defined by changing environmental conditions. Boundaries of vegetation units for example are governed by topography, microclimate or soil properties on local scales and climatic gradients on large spatial scales (Belnap, Hawkes & Firestone 2003; Strayer et al. 2003). In contrast, political boundaries are artificially drawn for administrative purposes. They may follow topographic features but often cut straight through homogenous environments. Political borders frequently reflect different economic and regulative frameworks for land management and hence offer the possibility to study impacts of land use on ecosystems. Cross-border studies have been successfully carried out analysing impacts on diversity of reptiles (Shanas et al. 2006) and of arthropods (Shanas et al. 2011). A similar approach has been used to investigate the impact of grazing on plant diversity using fence line contrasts in southern Africa (Todd & Hoffman 2009; Hanke et al. 2014).

Biodiversity has been attributed to foster ecosystem stability and resilience (Cardinale et al. 2012; Mace, Norris & Fitter 2012; Oliver et al. 2015). However, the exact role of biodiversity in sustaining continuous delivery of ecosystem services is still strongly debated (Isbell et al. 2011; Kleijn et al. 2015). In the discussion on biodiversity loss, tropical rain forests have been in the focus ever since the start of the debate. In contrast, the role of dry tropical woodlands and forests has featured a much less prominent role on the scientific agenda although they resemble one of the largest terrestrial biomes (Olson et al. 2001; Miles et al. 2006). Recently, Hansen et al. (2013) highlighted the dramatic losses of dry tropical forests at the global scale, and Angola was among one of the hotspots of deforestation. The dry tropical woodlands and forests of southern Africa supply a large array of provisioning ecosystem services especially to local, rural populations. Globally they have high relevance for the water and carbon cycles (Chidumayo & Gumbo 2010).

The Okavango region in southern Africa can serve as an example region to study impacts of land use on dry tropical woodlands. It is a hot spot of accelerating land-use change and intensification coupled with changing socio-economic factors (Röder et al. 2015). Two socio-ecological systems with different land-use intensities are encountered along the middle reaches of the Okavango River forming the political border between Angola in the north and Namibia in the south. In the pre independence era, socio-economic settings were similar in the two countries on either side of the river. However, since its independence in 1992 Namibia has enjoyed political stability and continuous economic growth leading to a socio-economic transformation coupled with population growth. Traditional life style and agricultural practices are still of importance but at the same time modern consumerism and market orientation have started to dominate the society of the Kavango regions of Namibia (Pröpper et al. 2013; Pröpper 2015). In contrast in Angola, several decades of civil war lasting from the 1960s to 2002 have led to a stagnant development. Although today Angola is recovering at a high pace, income generation of the majority of the population is still based on traditional subsistence agriculture.

The cross-border contrast between the two countries along the shared river section is evident in the landscape and clearly visible from the sky. Based on time series of satellite images Röder et al. (2015) unravelled the temporal and spatial dynamics of woodland clearing for agriculture. What satellite images do not show are the patterns created by spatially diffuse land use on unfenced communal land, i.e. local extraction of fire wood and construction material or the usage as pasture and browse for livestock. These types of land use play an important socio-economic role in the region (Pröpper et al. 2013). However, it is difficult to measure their intensity and extent as diffuse land-use patterns do not manifest in an easily spatially detectable manner as for example agricultural fields. Furthermore, diffuse land use exhibits high seasonal and interannual variability with regard to intensity and spatial allocation. In the following, we use the term 'diffuse land use' to refer to all kinds of anthropogenic activities that extract natural resources not bound to a specific location and often not carried out in a systematic way. Typically, the intensity of diffuse land use will increase in the proximity of settlements or infrastructure and therefore, distance measurements can be used as a proxy for intensity of diffuse land use.

Due to the commonality of both, the environmental conditions as well as the traditional land use practices in combination with the discrepancy in recent socio-economic development the cross-border region along the Okavango River between Angola and Namibia offers a unique situation to study the impacts of diffuse land use on biodiversity in a dry tropical woodland ecosystem. The purpose of this study is to investigate whether diverging land use in the cross-border region of Angola and Namibia has caused detectable differences in plant diversity patterns along the Okavango River over the last decades. As diversity has various different components we base our investigations on three indices a) species richness b) Shannon index and c) Shannon evenness. Furthermore, we analyse if different life forms, i.e. woody species, herb and forb species, and grass and sedge species respond in the same way.

Methods

Study site

The study was carried out along the middle reaches of the Okavango River stretching over 100 km from the towns of Cuangar/Nkurenkuru in the West to Calai/Rundu in the East (Figure 34). The central landscape element is the Okavango River traversing the region in a west-east direction. The river cuts through the aeolian sand deposits of the Kalahari system and soils are therefore predominately sandy and nutrient poor with the exception of the floodplain (Gröngröft et al. 2013a). The climate is semi-arid with a pronounced dry season lasting from April to October and is categorized as BSh climate according to the classification of Köppen-Geiger (Peel, Finlayson & Mcmahon 2007). Mean annual precipitation is approximately 570 mm and mean annual temperature ranges from 22 to 23°C (Weber 2013a; Harris et al. 2014). The vegetation of the floodplain and the river banks vary over short distances and is primarily determined by topographic position above river level (Strohbach 2013). In contrast, the vegetation of the vast sandy plains of the hinterland, the Kalahari Sandveld, is relatively homogeneous and is dominated by dry deciduous tropical *Baikiaea-Burkea* woodlands (De Cauwer 2013; Revermann & Finckh 2013a).

The northern Angolan side and the southern Namibian side of the river are inhabited by the same ethnic groups with close family links across the river sharing traditional land-use practices (Röder et al. 2015). Income is mainly generated by smallholder agriculture based on semi-permanent shifting cultivation as well as livestock husbandry and the use of various provisioning ecosystem services such as wild fruits or construction materials. Traditionally, at both sides human settlements concentrate along the river as water availability is a prerequisite for any human activity in this semi-arid region. The 2011 census for the Kavango region in Namibia resulted in an average population density of 4.6 persons per km^2 (Namibia Statistics Agency 2013) and in 2014 the census in Angola showed on average 6.2 persons per km^2 in the municipalities of Cuangar and Calai (Instituo Nacional de Estatística 2014). However, Mendelsohn et al. (2010) showed that in a narrow strip of five kilometres along the southern bank of the river in Namibia population densities are much higher ranging between 51 and 100 persons per km^2. Furthermore, overexploitation of the river terrace and installation of boreholes have led to the establishment of settlements in remote areas; consequently land use intensity has increased and economic activities have been extended substantially into the Namibian hinterland (Pröpper et al. 2010).

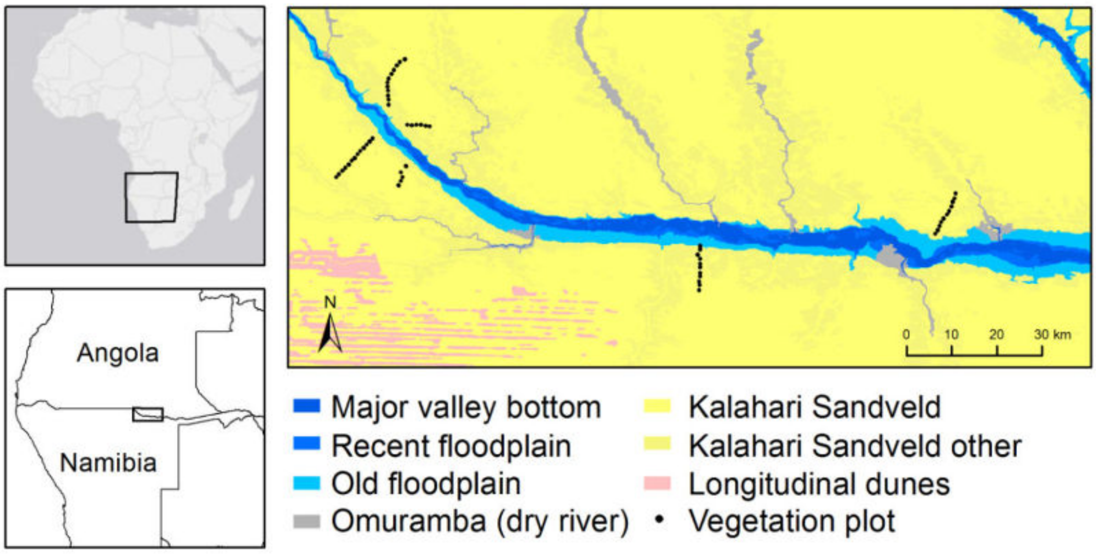

Figure 34 Location of study site in southern Africa, location of vegetation plots and geomorphological landscape units. Geomorphological landscape units were derived from the global digital elevation model SRTM (Shuttle Radar Topography Mission, USGS 2004) following an automated classification based on the topographic position index (Iwahashi & Pike 2007; Wehberg et al. 2013); 90-m spatial resolution; Map datum WGS84 UTM zone 34S.

Vegetation sampling

Plant species composition was sampled using vegetation plots sized 20 m x 50 m (Strohbach 2001; Revermann et al. 2016b). In each plot all vascular plant species including their visually estimated, projected cover were recorded in per cent. Water and access are the key factors governing anthropogenic activities in the middle reaches of the Okavango River (Mendelsohn et al. 2010). Therefore, the proximity to access routes and water supply can serve as a proxy for the intensity of land use. In the setting of our study the distance to road was regarded as equivalent to distance to river as the main road always follows the course of the Okavango River. Therefore, vegetation plots were placed in a systematic manner at intervals of 1 km along sandy tracks perpendicular to the Okavango

River into the hinterland in both countries. In order to avoid confounding effects arising from sampling different vegetation units, sampling was restricted to the Kalahari Sandveld where environmental conditions are relatively homogenous. The delineation of the Kalahari Sandveld was based on the geomorphological landscape units identified by Wehberg et al. (2013) and confirmed by visual validation with high resolution satellite imagery in Google Earth. In total 60 vegetation plots were sampled, 30 on the Namibian and 30 on the Angolan side of the river. Two plots were excluded as they were situated at the border to the adjacent landscape unit 'old floodplain' (Figure 34). Vegetation sampling was carried out in the growing season in the month February to April in the year 2013.

Statistical analysis

Species turnover was analysed by calculating the length of the first axis of a detrended correspondence analysis (DCA). The DCA axis is scaled in units of the average standard deviation (SD) and a value greater than SD = 4 indicates a complete species turn over (McCune, Grace & Urban 2002). To compare plant diversity of the vegetation plots of the two sides of the river we calculated diversity profiles. Diversity profiles have the advantage that they visualize various aspects of diversity. The scale parameter α can be mathematically converted to common diversity indices: Low α values represent diversity indices focusing on species richness, while with increasing α more weight is given to the aspect of evenness. If the profiles of two data sets do not intersect the diversity of the respective data set can be considered as truly higher or lower (Tóthmérész 1995; Kindt, Van Damme & Simons 2006). Diversity profiles were calculated in R (R Development Core Team 2015) using the package 'BiodiversityR' (Kindt & Coe 2005).

We calculated the distance to the main road for each vegetation plot using the 'proximity toolset' in ArcGIS 10.0. The effect of distance to the main road on plant diversity was tested using a generalized linear model (GLM, McCullagh & Nelder 1989). As response variable we used species richness (S), Shannon index of diversity (H', equation 1) and Shannon evenness (J', equation 2).

Equation (1) $H' = -\Sigma(p_i \times \ln(p_i))$

with p_i = abundance of species i / total abundance

Equation (2) $J' = H/\ln(S)$

with H' = Shannon index and S = species richness

The explanatory variables of the GLM were distance to the main road in kilometres with the country (Angola/Namibia) as interaction term. As fire is an important driver of vegetation patterns in southern Africa (Bond & Keeley 2005) we also tested a GLM that included the number of fires as additional explanatory variable. We used remotely sensed information on fire history provided by Stellmes et al. (2013c). Based on the MODIS MCD45 burnt area product with a 500 m-resolution Stellmes at al. recorded the number of fires per year for the years 2001-2012. The formula of the GLMs is presented in equation (3).

Equation (3) glm (y ~ fire + distance to road * country, family = gaussian)

with y = one of the three diversity indices (S, H′, J′); fire = number of fires in the years 2001-2012; distance to main road in km; country as two level factor (Angola, Namibia)

In order to detect if life forms show different trends all GLMs were run for four data (sub) sets a) for all species, b) woody species, c) herbs and forbs, and d) grasses and sedges. In order to visualize the differences among the countries and the impact of distance to road we plotted the GLMs excluding fire as predictor. All statistical analyses were carried out using R (R Development Core Team 2015) and the packages vegan (Oksanen et al. 2015), and visreg (Breheny & Burchett 2015).

Results

In total, 240 species were recorded, thereof 72 woody species, 127 herb and forb species, and 41 grass and sedge species. This totals to 2,775 species occurrences thereof 42% woody species, 43% herbs and forbs, and 15% grasses and sedges. The DCA with a length of the first axis of SD = 3.182 showed no complete species turnover and hence vegetation of both sides of the river share a common species pool.

Renyi's diversity profiles indicated that plant diversity was similar on the Angolan and Namibian side. The lines of the diversity profiles intersected and hence neither side can be regarded as more diverse. Nevertheless, the pooled plots on the Namibian side exhibited slightly higher evenness than the Angolan ones as indicated by the higher alpha values of the diversity profile (Figure 35).

Table 10 Results of the GLMs for the effect of distance to main road and the interaction of distance to road and country (Angola vs. Namibia) on three diversity indices: species richness (S), Shannon index (H′), and Shannon evenness (J′). Results are shown for four data sets: a) all species pooled, b) tree and shrub species, c) forb and herb species, d) grasses and sedges. For the formula of the GLM see eq. (3). The intercepts and the slopes of the regression for the variable distance to road are given for each country separately. P-values <0.05 are marked with an asterisk "*" and p-values <0.01 with a dot "•".

		all species		trees and shrubs		forbs and herbs		grasses and sedges	
		estimate	p-value	estimate	p-value	estimate	p-value	estimate	p-value
S	Intercept Angola	40.669	*<0.001	16.108	*<0.001	17.997	*<0.001	6.564	*<0.001
	Slope Angola	1.426	* 0.020	0.592	* 0.031	0.744	• 0.080	0.090	0.609
	Intercept Namibia	44.903	0.439	20.380	• 0.086	18.664	0.861	5.859	0.659
	Slope Namibia	0.026	• 0.076	-0.184	* 0.030	0.036	0.197	0.173	0.712
H′	Intercept Angola	2.459	*<0.001	2.039	*<0.001	1.090	*<0.001	1.065	*<0.001
	Slope Angola	0.020	0.286	0.012	0.578	0.009	0.825	0.008	0.751
	Intercept Namibia	2.179	0.101	1.795	0.229	1.928	* 0.029	0.877	0.429
	Slope Namibia	0.039	0.428	0.025	0.669	-0.004	0.803	0.031	0.498
J′	Intercept Angola	0.663	*<0.001	0.732	*<0.001	0.378	*<0.001	0.592	*<0.001
	Slope Angola	<0.001	0.962	-0.003	0.606	-0.001	0.920	0.001	0.937
	Intercept Namibia	0.574	* 0.033	0.591	* 0.017	0.684	* 0.008	0.509	0.468
	Slope Namibia	0.011	• 0.082	0.012	• 0.073	-0.005	0.829	0.010	0.575

Species richness increased with distance to road from an average of 43 species to 60 per 1,000 m^2 in Angola considering all species disregarding their growth form. In contrast, species richness in Namibia showed no trend and remained at the same level of about 45 species per 1,000 m^2. At a distance of about 7 km away from the road species richness in Angola reached significantly higher values than the Namibian side (Figure 36). The Shannon index exhibited no trend at all on both sides of the river. But the evenness indicated an almost inverse trend to species richness. While the Angolan side showed constant evenness of approximately 0.66 regardless of distance to road, evenness increased with distance to the road in Namibia. In proximity to the road evenness was lower on the Namibian side compared to the Angolan side but reached similar values in more distant areas (Table 10, Figure 36).

The three life form groups showed different patterns. The woody species exhibited the same pattern in the GLMs as all pooled species for all three diversity indices studied. For the herb and forb species this holds true only for species richness and no trend was observed for Shannon index and evenness. Although there was no trend with regards to distance to road, both Shannon index and evenness exhibited constantly higher values on the Namibian side for herb and forb species than for the Angolan side. We did not detect any pattern for the subsets containing only grass and sedge species. Overall, the explained deviance of the twelve models without fire as a predictor variable ranged from 2.3% to 41.4% with an average of 15.1%.

In general, fire frequency had low explanatory power. This variable only showed a negative effect on species richness and Shannon index for the subset including grasses and sedges (Table S3).

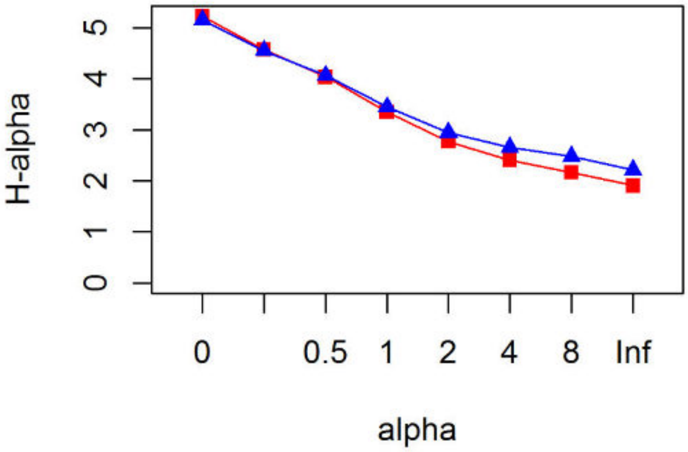

Figure 35 Diversity profiles for the Angolan side denoted in red squares and for the Namibian side in blue triangles showing Renyi's diversity Hα. The scale parameter (α) gives the order of Renyi's diversity and can be mathematically converted to common diversity indices. Low α values represent diversity indices focusing on species richness, while with increasing α more weight is given to the aspect of evenness, e.g. α=0 is related to species richness, while α=1 corresponds to the Shannon diversity index, and α=2 to the logarithm of the reciprocal Simpson index, α=Inf refers to the proportion of the most abundant species.

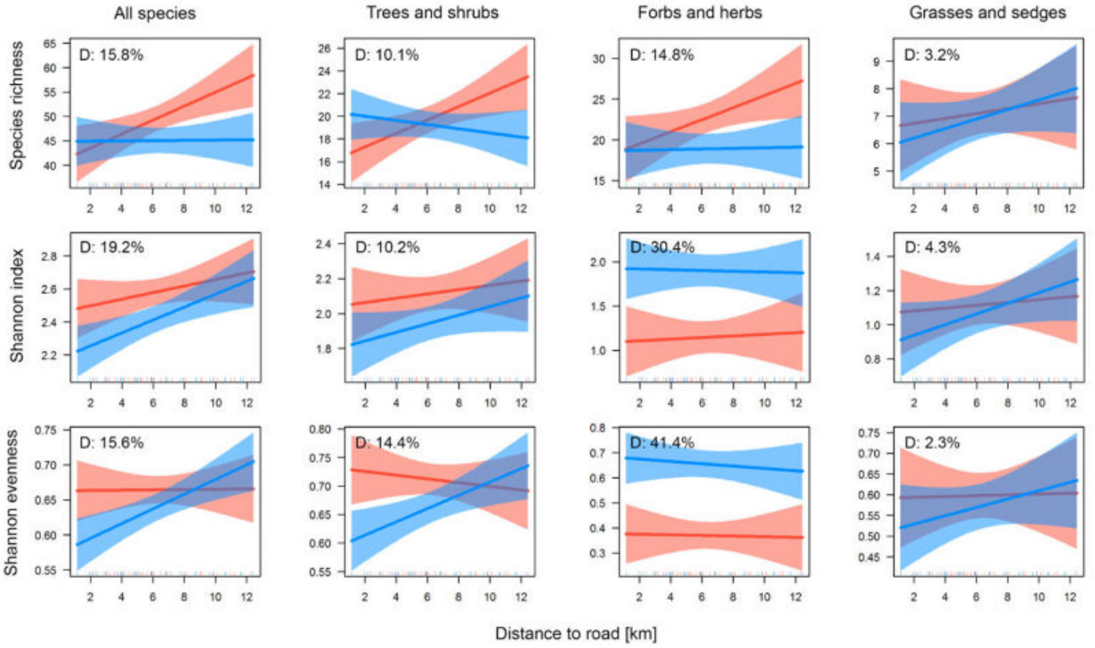

Figure 36 GLMs of distance to main road versus species richness, Shannon Index (H') and Shannon evenness (J') according to 'all species', and three subsets according to life form: 'trees and shrubs', 'herbs and forbs', 'grasses and sedges'; red denotes Angola, blue Namibia; the coloured area around the graph represents a confidence band with alpha = 0.1; the explained deviance in per cent (D) is given for each model in the upper left corner of the graph.

Discussion

Our study showed that plant diversity patterns in the dry tropical woodlands of the Okavango Region were influenced by the intensity of spatially diffuse land use. Distance to road as a proxy for land-use intensity explained some of the variation of species richness and evenness from the river to the hinterland. As shown by the DCA, all 58 vegetation plots from both sides of the river were located in the same vegetation unit and over all featured similar plant diversity as illustrated by the diversity profiles (Figure 35).

While species richness in Angola increased with distance to the road, no trend was detected on the Namibian side where species richness remained constant. In Angola land use is still restricted to areas that are easily accessible on foot from the settlements that concentrate along the main road as shown for agricultural fields (Röder et al. 2015). In contrast in Namibia, settlements and agricultural fields extend further into the hinterland and consequently the intensity of diffuse land uses increases, too. Although there might be other factors impacting species richness, our results suggest that diffuse land use has a negative impact on species richness of the *Baikiaea-Burkea* woodlands of the middle reaches of the Okavango River.

Species richness is often regarded as the common currency of diversity but in fact biological diversity has many more facets (Gaston & Spicer 2004). In this study, the index for evenness showed an inverse pattern to species richness. Shannon index, mathematically combining information on richness and evenness, on the other hand, showed no pattern at all as the opposing trends of richness and evenness are superimposed. The increase in evenness with distance to the road in Namibia means that the abundance of woody species is more equally distributed in areas further away from the road or, in other words, vegetation is less dominated by single species.

The analyses of the diversity measures according to growth form reveals that the trend described above for species richness and evenness found for all species pooled together was mainly based on the signal of the woody species and in case of species richness was also supported by the herb and forb species. The grass and sedge species did not show any response to distance to road which can in part be explained by their low contribution of 15% to total observations. This could imply that woody plants are most affected by diffuse land use, e. g. by selective logging of preferred timber species in close proximity to the main road. Frequent, illegal logging of valuable hard wooded tree species with commercial value has been reported from the Namibian Kavango region (Pröpper & Vollan 2013). Especially Kiaat, *Pterocarpus angolensis* DC, is sought after and commercial harvesting becomes interesting from a breast height diameter of 35-45 cm in the case of *Pterocarpus angolensis* DC (De Cauwer et al. 2014). However, timber is also extracted in smaller size classes and used for domestic fire wood and as construction material for huts etc. Hence, the extraction of timber might explain the lower evenness in proximity to the main road on the Namibian side compared to the Angolan side (Figure 36).

In woodland ecosystems such as the Okavango region livestock is another important source of disturbance as browse makes up a significant part of the diet of domestic herbivores in these ecosystems (Bergström 1992). Hence, cattle and other livestock densities can be expected to have a significant impact on the vegetation. Modelled livestock densities show higher densities in Namibia than in Angola (Robinson et al. 2014).

At the locations of the vegetation plots predicted cattle densities on the Namibian side range from three to eight cattle per km^2; in contrast in Angola, cattle densities are always lower than 1.2 cattle per km^2. It has been shown for South African rangelands and savannas that livestock have a strong impact on species richness patterns. However, the response of species richness can vary from slightly positive to strongly negative depending on the vegetation type and the grazing intensity (Rutherford & Powrie 2013). Out of the four vegetation types investigated in the study of Rutherford and Powrie (2013) the *Colophospermum mopane* savanna can be considered as the most comparable to the Okavango woodlands. Here, Rutherford et al. (2012) did not find an effect of high grazing pressure on species richness nor on Shannon diversity. But they found that evenness decreased with higher grazing utilization, as it is also the case in the areas in proximity to the road in Namibia where impact of cattle is highest in the study area (Figure 36).

Surprisingly, fire showed limited explanatory power. Only species richness and Shannon index for the subset of grasses and sedges showed a negative impact of fire (Table S3) suggesting that most species of these dry woodland ecosystems are well adapted to fires. However, it needs to be noted that two other important factors influencing the impact of fire on vegetation were not included in the analysis: timing of the fire (early or late in dry season) and fuel load.

Throughout the world there are numerous studies showing the manifold impacts of roads on surrounding ecosystems (Geist & Lambin 2006; Morton et al. 2006). Roads lead to improved accessibility and in this way foster conversion of natural ecosystems to agricultural land or for other uses as shown for the Angolan Miombo woodlands by Schneibel et al. (2013c) and Schneibel et al. (2016). Globally, the transformation of habitats through land-use change is one of the main causes of biodiversity loss (Millennium Ecosystem Assessment 2005; Butchart et al. 2010). This study demonstrates that roads apart from evident destruction of natural habitat also lead to inconspicuous changes in plant diversity patterns through spatially diffuse forms of land use.

Supplementary Materials available in the Appendix of the thesis

Table 10 Results of the GLMs for the effect of distance to main road and the interaction of distance to road and country (Angola vs. Namibia) on three diversity indices: species richness (S), Shannon index (H'), and Shannon evenness (J'). Results are shown for four data sets: a) all species pooled, b) tree and shrub species, c) forb and herb species, d) grasses and sedges. For the formula of the GLM see eq. (3). The intercepts and the slopes of the regression for the variable distance to road are given for each country separately. P-values <0.05 are marked with an asterisk "*" and p-values <0.01 with a dot "•".

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CHAPTER 7

Impact of shifting cultivation on dense tropical woodlands in southeast Angola

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Abstract

Dry tropical woodlands are the characteristic natural vegetation type of southeast Angola, where precipitation is seasonal and nutrient content of soils is very low. Subsistence farmers overcome the poor abiotic conditions by using shifting cultivation based on specific site selection. We describe the vegetation composition of a previously unstudied dense woodland tract, which is preferred for agriculture, comparing it to nearby open woodland. We placed 25 vegetation plots randomly in the two types of natural woodland vegetation (open and dense) as well as in fallows with three different durations of land use. In each plot the cover of all vascular plant species was recorded. Variables describing vegetation structure, including basal area and leaf area index, were recorded. We analyzed soil samples for texture, pH, conductivity and nutrients, and investigated the impact of land-use duration on woodland regeneration. We found that species composition and vegetation structure of the dense woodland differed greatly from the surrounding open woodland. The dense woodland is preferable for agriculture because of its higher soil content of silt, clay and potassium, higher woody biomass, and more abundant soft litter. A longer duration of land use affects species composition and diversity of the regenerating vegetation as well as nutrient content in the soil. In the near future, the increasing demand for agricultural land is likely to change the structure and composition of the dense woodland.

Keywords: dry forests; fire; Kalahari; Okavango; slash and burn agriculture; succession

Introduction

Shifting cultivation involves the clearing of vegetation, usually by slashing and burning, and a few years of cropping, followed by a fallow period in which farmers shift to surrounding areas (Ruthenberg et al. 1980). In the past, the majority of studies focused on the ecological impact of slash and burn agriculture in the tropical rain forest and more studies from dry tropical forests are needed (Kennard 2002). Dry tropical forests cover more than 60 % of sub-Saharan Africa and are home to a disproportionate number of people below the poverty line, many of whom depend on the woodlands for their livelihoods (Chidumayo & Gumbo 2010). The area required for agriculture in this region is increasing due to population growth. At the same time, the Miombo woodlands of southern Africa have been identified as a tipping point for the Earth system. Reaching such a tipping point would lead to significant changes in biodiversity and provision of ecosystem services (Secretariat of the Convention on Biological Diversity 2010). Therefore, investigations of the impact and sustainability of shifting cultivation by a growing population are increasingly important.

Southeast Angola is part of the larger Zambezian dry deciduous forests identified by White (1983). However, descriptions of the vegetation of the area are restricted to broad vegetation units (Barbosa 1970; dos Santos 1982). A first classification of the woodlands along the Cubango River by Revermann and Finckh (2013a) identified dense *Baikiaea-Burkea* woodlands, the preferred locations for shifting cultivation. These woodlands are distinguished from the otherwise dominant open woodlands of the surrounding area by their closed canopy, thicket-like understorey, and unique species composition.

Conditions in southeast Angola are unfavorable for agriculture, with highly variable rainfall (Weber 2013e) and predominantly sandy soils that have low water and nutrient retention capacity (Wisch et al. 2010; Gröngröft et al. 2013d). The subsistence farmers in southeast Angola, with limited knowledge of modern soil conservation techniques and little or no access to chemical fertilizers, overcome the low productivity of the ecosystem by using shifting cultivation. New fields are created by cutting the shrubs and trees down and burning the vegetation afterwards. The burning process has a fertilizing effect on the soil through the ash, but also causes a substantial loss of nutrients through volatilization (Giardina et al. 2000). An adequate choice of the most suitable sites for cropping is paramount (Ruthenberg et al. 1980).

The ecosystem's potential to regenerate is of great importance in areas where there is long-term use of shifting cultivation. When a field is abandoned, plant regeneration and succession start. In dry tropical forests, the deforestation may initially lead to increasing grass production (Strang 1974). In general, fast-growing pioneer species with high light demand establish first and are replaced in time by increasingly shade-tolerant species (Bazzaz & Carlson 1982). This succession process is strongly influenced by soil conditions (Uhl 1987; Tambara et al. 2013) and the intensity and duration of former land use (Donfack, Floret & Pontanier 1995). Longer land use can reduce biomass (Steininger 2000; Gehring et al. 2005), the seed bank (Pickett, Collins & Armesto 1987) and biodiversity (Uhl 1987). Biodiversity is essential to the resilience of the ecosystem as a whole (Folke et al. 2004) and so is important to conserve. Therefore, it is instructive to compare the species composition and diversity patterns in the natural vegetation to those of the fallows.

In our study area the regeneration of the vegetation is particularly important to the sustainable use and stability of the ecosystem, as shifting cultivation is concentrated in the spatially limited dense woodland. The preferred cropping sites have high agricultural productivity and are often re-used after a certain fallow period. The agricultural usage of the dense woodland patch under study has increased greatly within the last decade, and is evident from satellite data (Hansen et al. 2013). This means that the existence of this unique vegetation type might soon be threatened by expanding agricultural use. As pristine areas decrease, fallows might be reused earlier and fields might be cultivated for longer periods of time. Hence, a crucial question is whether longer usage of fields has a negative impact on regeneration processes of the vegetation and soils.

The major goals of this study are to:

(i) describe the species composition, diversity, and structure of the dense woodland and compare it to the surrounding open woodland matrix;
(ii) determine whether abiotic conditions in the dense woodland differ from the open woodland, and why the dense woodland is preferred for agriculture;
(iii) determine whether the duration of agricultural use has a negative impact on the regeneration, species composition, vegetation structure, and soil properties of the fallows.

Methods

Study site

The study site is in the province of Cuando Cubango in southeast Angola, 10 km west of the Cubango River. The mean annual precipitation is 732 mm, and the mean annual temperature is 22.5° C, with a mean of 17 frost days per year (Weber 2013e). The region has a dry season from May to September and a growing season from November to April (Weber 2013e). The soils are predominantly arenosols, consisting of a thick layer of Kalahari sands, which have been deposited by aeolian transport (Groengroeft et al. 2013).

Literature about the vegetation of southern Angola is sparse. The main vegetation types are closely related to those of the Kavango woodlands of northern Namibia as described by Burke (2002) and Strohbach & Strohbach (2004). A related vegetation type sharing many tree species is the 'chipya' vegetation of Zambia (Lawton 1978). Other sources classify the study region as *Baikiaea* woodland but lack phytosociological data (Werger & Coetzee 1978). Recent classification of the vegetation of southeast Angola defines the region as *Baikiaea-Burkea* woodland (Revermann & Finckh 2013a). Land use in this open woodland is restricted to timber cutting and small-scale livestock farming for local needs. Fire events play a major role in this vegetation unit (Stellmes et al. 2013c), and many of the present plant species show signs of fire adaptation such as thick corky or peeling bark (Strohbach & Petersen 2007).

While the open *Baikiaea-Burkea* woodlands dominate the landscape of the region, the dense woodland resembles a vegetation unit with a spatially very limited extent and is clearly distinguishable from the surrounding open woodland on satellite images. The dense woodland patch under study (16°43'00''S 17°47'00''E, Figure 37) forms the largest continuous area of this vegetation unit in the region with about 14,800 ha extending for about 20 km in a northwest–southeast direction parallel to the Cubango River. It is not mentioned in the vegetation map of the province of Cuando Cubango (dos Santos 1982) and was first mentioned in 2013 (Revermann & Finckh 2013a). Following an automated classification of topography, based on data from the Shuttle Radar Topography Mission (Iwahashi & Pike 2007), there is no notable difference in topographic position between the dense and open woodlands (Figure S12).

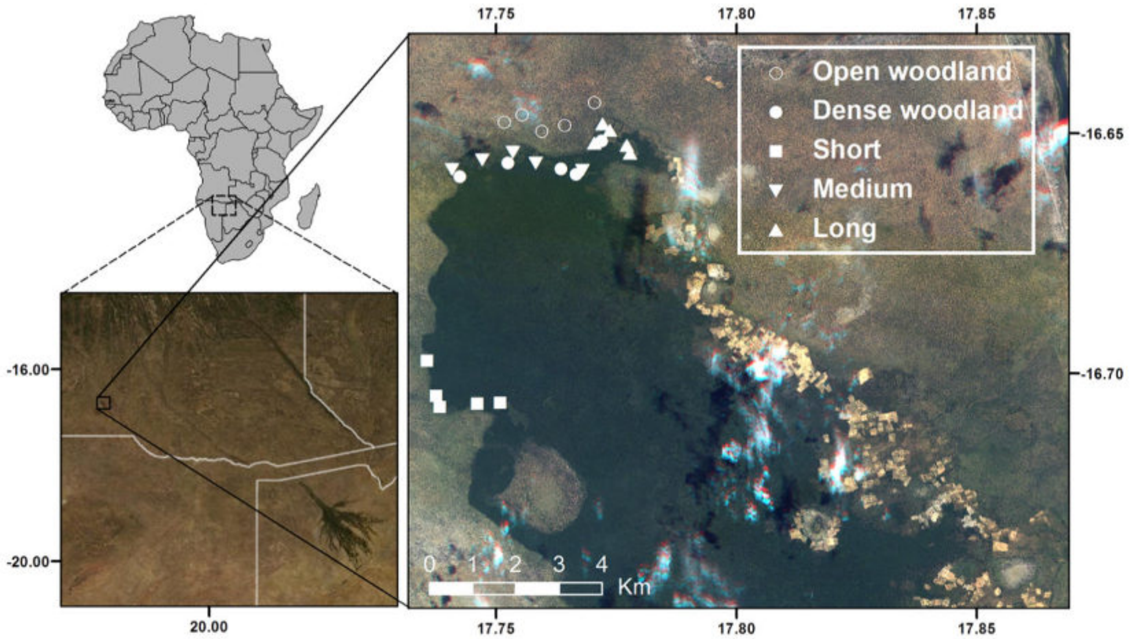


Figure 37 Location of the study site in southeast Angola. Source: Rapid Eye AG (2013); Acquisition date: 03/18/2013; Units: decimal degrees; Map datum: WGS84.

The population density in the region is below 1 person km^2, and the villages are concentrated along the river (Linard et al. 2012). A gravel road follows the Cubango River on its western bank, but the exchange of goods is rather low as there are no nearby cities. The Namibian border is 100 km to the south and the city of Menongue is 230 km to the north. The predominant crops in the fields are a mixed culture of maize or millet with beans and groundnuts. The soil is prepared with hoes and ox-drawn ploughs, and seeds are sowed with the beginning of the rainy season from October to November. The number of years a field is used for cropping strongly depends on how fast soil fertility declines. Typical crop duration is estimated to last two to three years.

Data acquisition

On the satellite images fields are recognizable as rectangular features that appear at the fringes of the dense woodland. To inform site selection we used a time series of satellite images. Based on a combination of Google Earth imagery (Google Inc. 2013), Landsat scenes (NASA Landsat Program 2013), and RapidEye imagery (RapidEye AG 2013) we visually assessed land-use history of the fields in the dense woodland (Table S6). The detected fields differ in the dates when they were first cultivated, but were all abandoned in 2001. Consequently, the fields that are currently fallows were subject to different durations of agricultural use. These fallows were grouped into three categories according to the duration of cultivation: short (ca. 4 y), medium (ca. 9 y) and long (ca. 14 y) periods. Because the available time series does not provide suitable images for each year, it is possible that some fields have not been used continuously during the periods in question. For field investigations, five random points were generated for each of the three disturbed vegetation types: 'short use/fallow', 'medium use/fallow', and 'long use/fallow', as well as for the two types of undisturbed vegetation: 'open woodland' and 'dense woodland' (Figure 38). Field investigations took place in February 2013, when fallows had an age of 12 years.

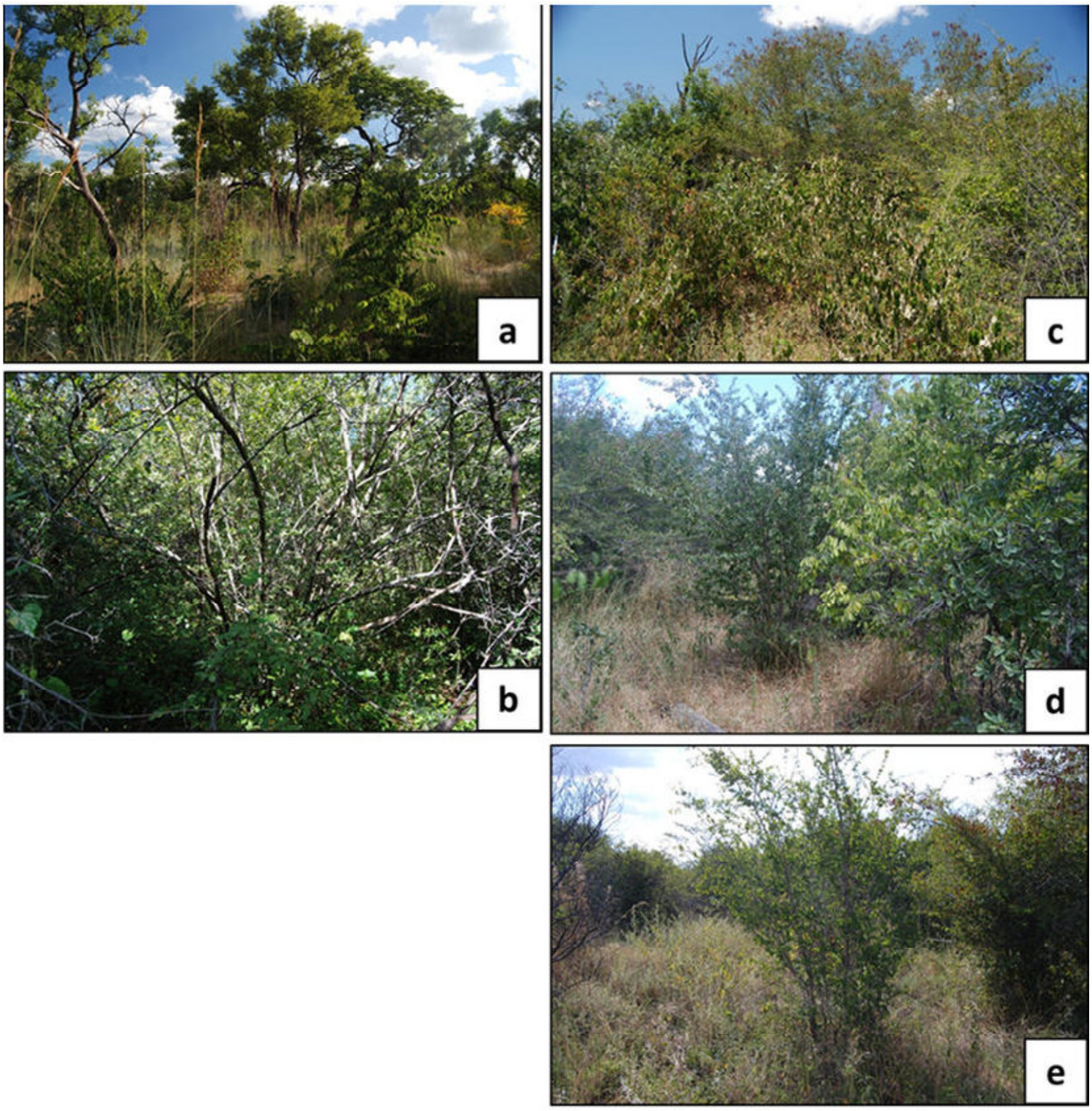


Figure 38 Photos of the five categories. a = open woodland (24202), b = dense woodland (24178), c = short use/fallow (24188), d = medium use/fallow (24170), e = long use/fallow (24166).

On vegetation plots sized 20 m × 50 m, we took an inventory of all vascular plant species and estimated the vertically projected cover of all species. We followed the taxonomy of Figueiredo and Smith (2008). We collected herbarium specimens for species not identifiable in the field. Specimens were deposited at the Instituto Superior de Ciencias da Educação in Lubango (LUBA), Angola, and Herbarium Hamburgense at the Biocentre Klein Flottbek (HBG), Germany.

We measured vegetation structure by estimating total vegetation cover per plot and the percentage covered by plants in the following strata: 0-0.5 m, 0.5-2 m, 2-5 m, 5-10 m and 10-20 m. Additionally, cover values for mosses, lichens, soft litter (leaves), and hard litter (twigs, stems) were recorded. We measured the maximum height and the height of the lower 95% of the vegetation ('main height') in order to exclude single emergent trees. We estimated the duration since the last fire in the categories 1, 2, 5, 10, >10 y based on indicators such as presence of annual species, burned culms of grasses or bark of trees, and charcoal on the ground and in the soil. Signs of grazing animals such as browsed culms and traces were noted. We took hemispherical photos to determine the site-specific Leaf Area Index (LAI) at five locations (distance 12.5 m) per plot at a height of 1.3 m. The LAI was calculated after Lang (Lang 1987) with the software Hemisfer (Schleppi et al. 2007). The threshold was detected automatically after Nobis and Hunziker (2005) and adjusted manually if the automatic detection failed. The correction for non-linearity and slope was used (Schleppi et al. 2007). Because hemispherical photography cannot differentiate woody and leaf material, the LAI is more appropriately described as plant area index (PAI, Greve 2010). As a proxy for standing woody biomass we recorded the height and the diameter at breast height (DBH) of all trees with a DBH > 5 cm. In order to capture the biomass of shrubs and small trees with DBH < 5 cm, all stems higher than 2 m were recorded in a nested subplot of size 10 m × 10 m. Based on the DBH measurements, we calculated the basal area (BA) per hectare according to equation 4. BA was calculated separately for trees with DBH > 5cm (BA_{trees}) and saplings and shrubs with a DBH < 5 cm (BA_{shrubs}).

Equation (4) $BA=\Sigma(\pi\times DBH_i/2)^2)\times 10$

With BA = Basal area in m^2 per hectare; DBH = diameter at breast height in m; for trees on the 1,000 m^2 plot result was multiplied by 10, and for shrubs on 100 m^2 plot by 100, to convert BA to the value for one hectare.

A comprehensive analysis of the edaphic conditions was carried out to assess whether differences in vegetation arise from different abiotic conditions. At every plot four soil samples were taken at standardized depths: 0–10 cm, 25–45 cm, 70–90 cm, and 180–200 cm. The following physical and chemical soil properties were assessed for each sample: conductivity, pH in a 0.01 M $CaCl_2$ solution, grain size according to the USDA classification, and nutrient contents for potassium, calcium, magnesium, and sodium via a 1 M NH4–acetate–EDTA extraction, and phosphorus via a 0.001 M sulphuric acid extraction.

Data analysis

We carried out an indicator species analysis using the indicspecies package in R (De Cáceres & Legendre 2009; R Development Core Team 2013) to identify characteristic species of each vegetation category. For each species we calculated the *phi* value in order to test for the strength of a species' association with each category. The *phi* value ranges from -1 to 1. Positive *phi* values indicate that the species and the vegetation unit jointly occur more frequently than expected by chance(Chytrý et al. 2002). To compare plant diversity of the five categories we calculated diversity profiles. Instead of calculating a few arbitrary selected diversity indices, the diversity profiles have the advantage that they allow a more complete picture of the multidimensional term diversity (Tóthmérész 1995). The scale parameter α can be mathematically converted to common diversity indices. Low α values represent diversity indices focusing on species richness, while with increasing α more weight is given to the aspect of evenness, e.g. α=0 is related to species richness, while α=1 to the Shannon diversity index, and α=2 to the Simpson index (Kindt & Coe 2005). When two profiles do not intersect, the profile with the higher $H\alpha$ values can be considered more diverse. The diversity profiles were calculated with the vegan package (Oksanen et al. 2013) in R 3.0.1 (R Development Core Team 2013).

We used a detrended correspondence analysis (DCA) to investigate the variation within the species composition. The DCA is known to avoid the arch effect common in multivariate vegetation data. The arch effect occurs in a standard correspondence analysis when data sets that are missing the same species data are considered more similar than data sets that share a common species pool (McCune, Grace & Urban 2002). DCA was computed in PC-Ord 5 with 26 segments, rescaled axes, and down-weighted rare species. We also computed a Principal Component Analysis (PCA) on the matrix of environmental variables to identify the abiotic conditions prevailing in the four categories

(McCune, Grace & Urban 2002). PCA uses the linear distance measure Euclidean Distance, which is suitable for environmental data. We applied Kruskal-Wallis, Mann-Whitney and *t*-tests in PAST 2.16 (Hammer, Harper & Ryan 2001) to test for significant differences in structural and soil variables among the categories.

Results

Floristic composition

A total of 187 species were found within the 25 vegetation plots. 76% of the species were identified to species level, 9% to genus level and 15% remained unidentified. As Figure 3 clearly shows, the five land cover classes / vegetation strata clearly differ in their vegetation composition, with the exception of the young and medium fallows, which were broadly compositionally similar. In the open woodland plots tall trees like Ordeal tree (*Erythrophleum africanum*) and Large false mopane (*Guibourtia coleosperma*) have a high *phi* value and are frequent (Table S7). The shrub layer is characterised by tall shrubs such as Horn-pod tree (*Diplorhynchus condylocarpon*), Peeling plane (*Ochna pulchra*) and Bicoloured bushwillow (*Combretum collinum*). The herb layer is defined by different grasses of the genera *Trachypogon*, *Hyparrhenia*, *Eragrostis*, *Aristida* and *Digitaria,* and sedges of the *Cyperaceae* family. Some herbs such as *Tephrosia lupinifolia* and the small shrub *Dichapetalum rhodesicum* are characteristic of the open woodland. In contrast, the dense woodland is a mixture of tall-growing (ca. 6 m), multi-stemmed shrub species like Satin-bark corkwood (*Commiphora tenuipetiolata*) and Jesse-bush bushwillow (*Combretum celastroides*) and tall (ca. 11 m) single-stemmed species, mainly Zambezi teak (*Baikiaea plurijuga*) and single individuals of Kalahari apple-leaf (*Philenoptera nelsii*). In the understorey several herbs occur, e.g. Creeping foxglove (*Asystasia gangetica*), *Alectra picta*, *Ocimum* sp. and *Hibiscus* cf. *mastersianus* as well as lianas of the Apocynaceae family and *Ipomoea dichroa*. The small spiny tree species Flame thorn (*Acacia ataxacantha*) and Sicklebush (*Dichrostachys cinerea*) are characteristic and frequent in short and medium use/fallows. A few herbs are indicative of certain fallow types, such as *Hermannia eenii* which mainly occurs on short use/fallows, *Justicia bracteata* on medium use/fallows and Gemsbok cucumber (*Acanthosicyos naudinianus*) on long use/fallows. In the dense woodland, grasses are nearly absent, but grass species of the genera *Panicum*, *Digitaria* and *Urochloa* are characteristic of short use, long use and the combination of short and medium use/fallows respectively. *Eragrostis cylindriflora s.lat.* is characteristic of the combination of all three fallow types.

Detrended Correspondence Analysis (DCA) visualizes the differences in the species composition among the vegetation plots (Figure 39). The length of the first axis (standard deviation, SD = 5.68) is larger than a single complete turnover in species composition (i.e. > 4 SD) (McCune & Mefford 2011) and illustrates a strong separation of the open from the dense woodland. The three fallow categories cluster near their original state (i.e. dense woodland) in the first axis. The second axis (SD = 2.46) mainly displays the difference in species composition between the dense woodland and the long use/fallows, whereas the medium and short use/fallows are not separated. The distances between plots within each of the undisturbed categories (i.e. dense and open woodland) are less than within the fallow categories, indicating more homogeneity of the undisturbed woodlands.

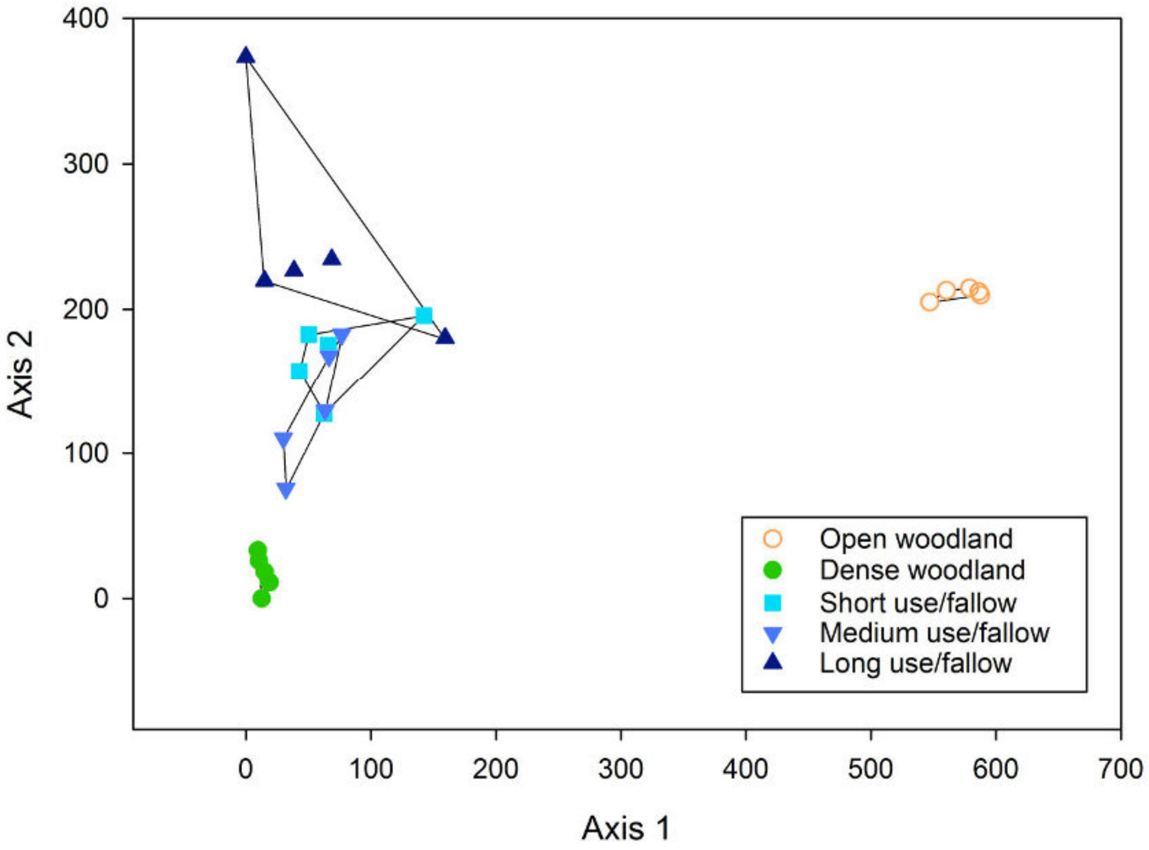


Figure 39 Detrended Correspondence Analysis showing groups of vegetation plots, marked by convex hulls. Ordination diagram with axis 1 and 2 (standard deviation*100); convex hulls were drawn post-hoc.

In general, species diversity is relatively high (Figure 40), with Shannon diversity ($\alpha = 1$) ranging from 2.5 in the dense woodland to 2.9 for long use/fallows, 3.0 for medium use/fallows and open woodland, to 3.2 for the short use/fallows. Diversity profiles show that the categories in general are similar for low α-values and diverge with increasing α. Differences are not significant for species richness (Kruskal Wallis: H = 3.2, df = 4, P = 0.528) but increase if abundances of species are taken into account. The Hα-values are consistently lower in the dense woodland than in the other categories. Short use/fallows have a higher diversity than the other fallow categories and the open woodland, except for species richness. The remaining line comparisons intersect.

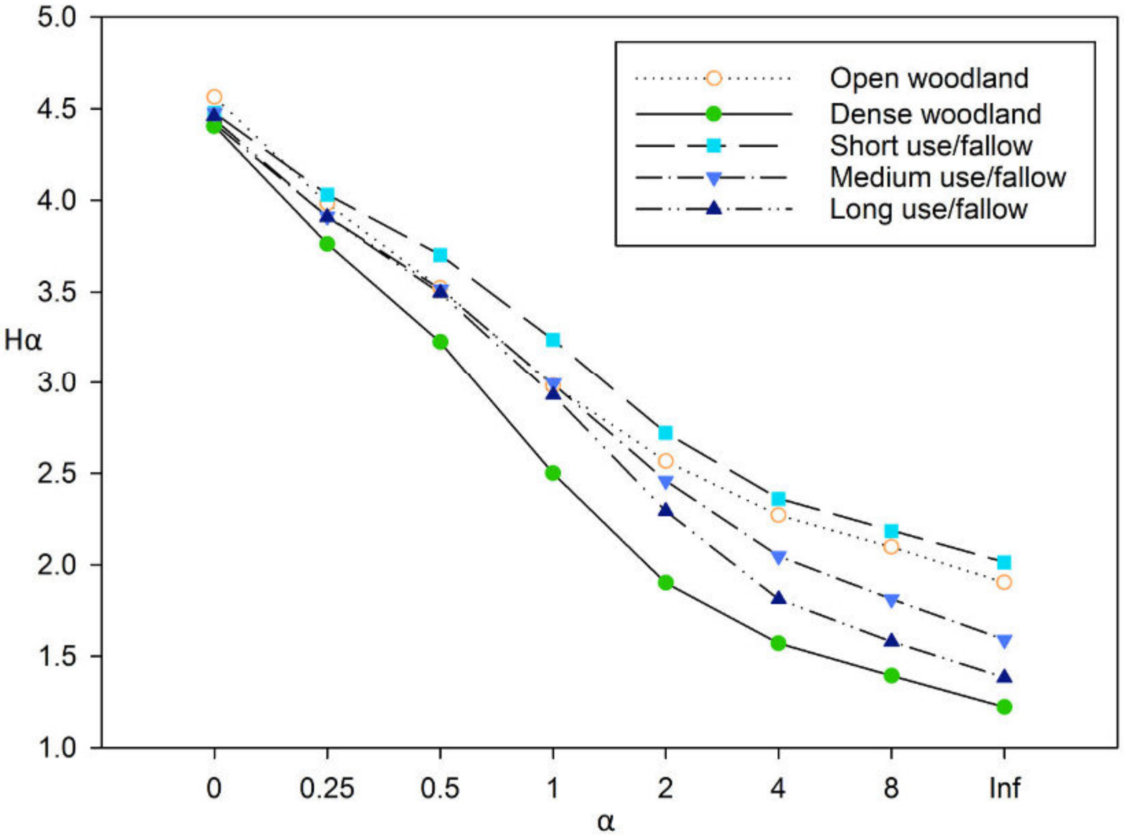


Figure 40 Diversity profiles of five vegetation plot categories using Renyi's diversity (Hα). The scale parameter (α) gives the order of Renyi's diversity; α = 0 is the logarithm of species richness, α = 1 equals the Shannon diversity index, α = 2 is the logarithm of the reciprocal Simpson diversity index, α = Inf refers to the proportion of the most abundant species.

Vegetation structure and soil conditions

The first axis of the PCA (Figure 41) explains 17.2% of the total variance and separates the dense woodland from the other categories. Although this value seems low, it can be explained by the large amount of parameters (=84) that entered the PCA. The LAI, the cover of the shrub stratum 2–5 m, soil sand content, and the soil pH explain the variation in the first axis. The open woodland is clearly separated from the other categories along the second axis, explaining 14.8% of the total variance. This axis is characterised by a strong grazing gradient, fewer nutrients and lower values for total vegetation cover and herb cover. The three fallow categories cannot be clearly separated via the PCA. Generally, the variation within a category is lower for the undisturbed habitats compared to the fallow categories. For correlations of all variables with the first three axes of the PCA and full names of variables, see Table S8.

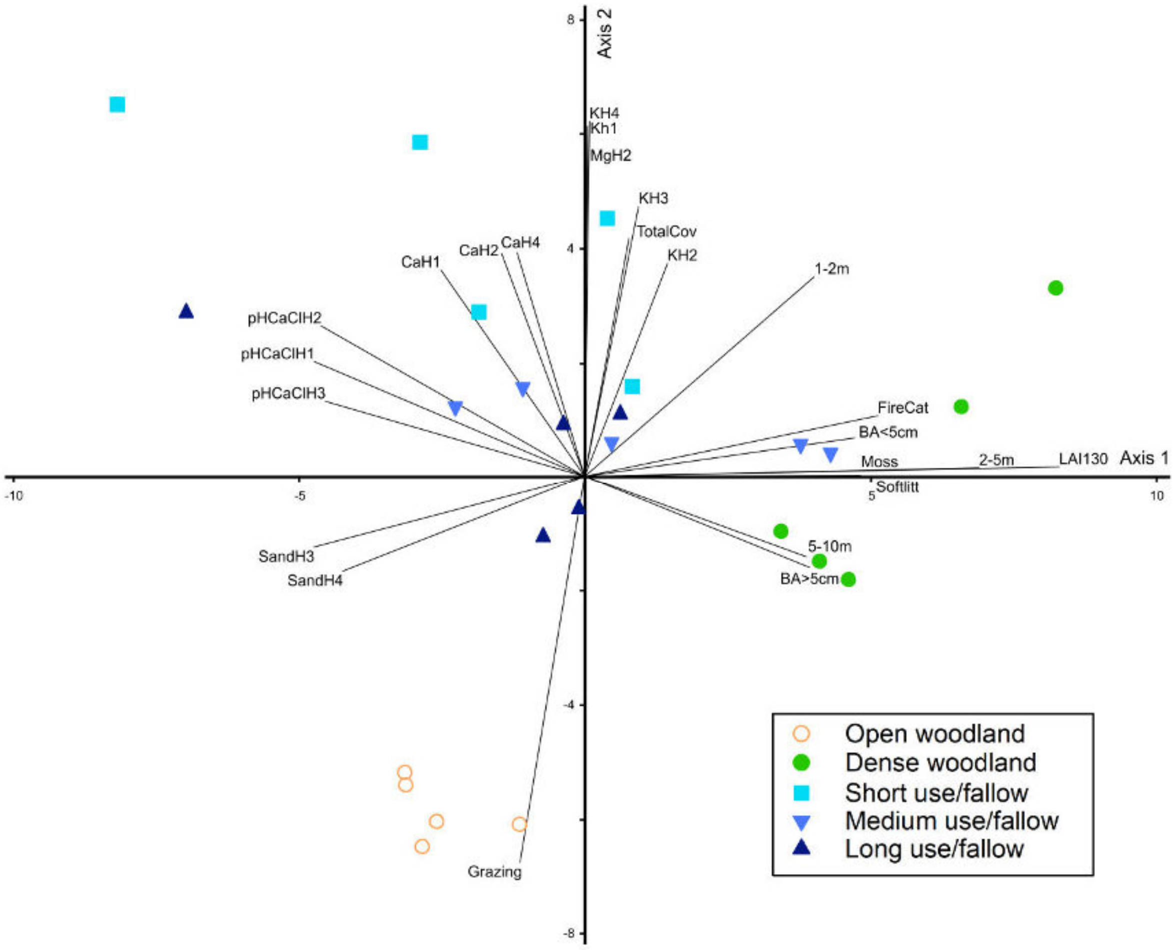


Figure 41 Principal Component Analysis of structural and soil variables. Scores calculated by weighted averages (Euclidean distance); only variables with an R² > 0.4 for the joint plot are shown; for details of variables see Table S8.

The open woodland is characterised by lower total cover values (ca. 60%, Table S4), lower cover values in all strata, and a low LAI (0.8). The basal area for trees and the main height is relatively tall (9.5 m). The open woodland exhibits grazing and frequent fire events; mosses and lichens are not present. The soils are sandier in the open woodland compared to the other categories (Table S5). In general, the soils are nutrient- poor.

The dense woodland is characterised by close vegetation, with the 2–10 m cover and total cover values reaching 97%, the highest of all sites; LAI are also relatively high with a mean of 2.8. The dense woodland exhibits a high BA for the shrubs, the highest BA value for trees and the tallest trees. Furthermore, the dense woodland reaches the highest values for soft litter, moss and lichen cover (Table S4). Additionally, no fire enters the dense woodland (high value for FireCat). For its soil properties, clay ($t = 5.05$, $df = 19$, $P < 0.001$) and silt ($t = 2.32$, $df = 19$, $P < 0.05$) contents are significantly higher than in the open woodland.

The fallows have a relatively high total vegetation cover (79%–87%) due to their dense shrub layer (Table S4). The basal area in the fallows is low with high variablity. The LAI in the fallows ranges from 1.2 to 1.6 with a high standard deviation (0.5–0.9). Nutrient contents for potassium (K^+), calcium (Ca^{2+}) and magnesium (Mg^{2+}) are higher in some fallows (Figure 41). Tests on differences show that Ca_{2+} is significantly higher for short use/fallows than in the other groups (Mann-Whitney: $U = 2$, $n = 5$, $P < 0.05$), but there are no significant differences among the other groups. The Mg^{2+} content is significantly higher for short use/fallows than for the open woodland (t-test for equal variance: $t = 6.27$, $df = 4$, $P < 0.01$, Table S5).

Significant differences were found for potassium among the categories (Kruskal-Wallis: $H = 54.6$, $df = 4$, $P = 3.5 \cdot e^{-11}$) except for the dense woodland and medium use/fallows (Figure 42). The open woodland (56–111 mg kg^{-1}) has a lower concentration of potassium than the dense woodland (250–325 mg kg^{-1}). The potassium values for the fallows show a gradient from short use/fallows to long use/fallows. Compared to the dense woodland, the short use/fallows have higher potassium values (360–570 mg kg^{-1}), the medium use/fallows are at the same level (196–243 mg kg^{-1}) and the long use/fallows have lower values (134–159 mg kg^{-1}, Figure 42).

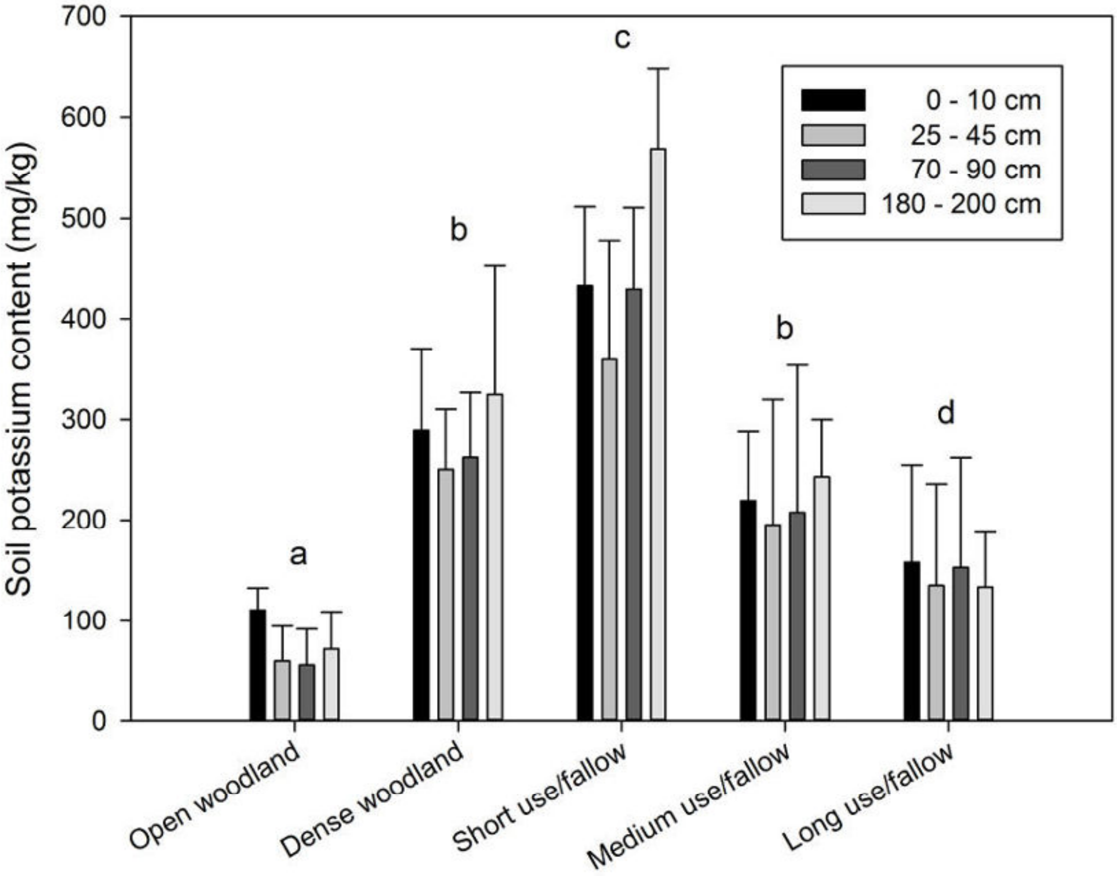


Figure 42 Soil potassium content of the vegetation categories for different soil depths. Whiskers display standard deviation; letters indicate significant differences between categories with $p < 0.05$ according to Mann-Whitney pairwise comparisons.

Discussion

Species composition, structure and diversity of the dense woodland

Woodland species composition and structure

The analysis of the species composition shows an almost complete species turnover from open to dense woodland. This is especially interesting, as there was no apparent environmental gradient or notable ecotone separating the two woodland types.

The open woodland is similar in species composition to the Kavango woodlands of northern Namibia (Burke 2002; Strohbach & Strohbach 2004), where nutrient-poor soils, seasonally dry conditions and frequent fires are the main ecological drivers (Correira & Bredenkamp 1986; Burke 2002). Many species show adaptations to fire, such as woody species with thick corky or peeling bark, or perennial grasses forming dense tufts, which protect the buds and allow for resprouting after fires. In contrast, in the dense woodland the upper canopy is formed almost exclusively by Zambezi teak (*Baikiaea plurijuga*) which has a rather thin bark and is regarded as fire sensitive (DFSC 2001). Kalahari apple-leaf (*Philenoptera nelsii*) is the second tree species reaching the lower canopy.

Furthermore, the dense woodland supports a dense shrub layer formed by species such as Satin-bark corkwood (*Commiphora tenuipetiolata*), Lavender croton (*Croton gratissimus*), and Jesse-bush bushwillow (*Combretum celastroides*). The closed canopy creates a self-sustaining, cooler and more humid micro-climate, with shady conditions for specialized herbs, climbers, and large quantities of mosses and liquens. These microclimatic conditions conserve moisture, favour plant growth, and hinder ground fires. The absence of high grass coverage also impedes the spread of ground fires (Gambiza et al. 2005). Our field observation that wild fires never entered the dense woodland in the recent past is also supported by Frantz et al. (Frantz et al. 2013), recording no fire in the dense woodland within the years 2001-2012, based on the MODIS burned area product.

Woodland species diversity

Plant species diversity in the open woodland was higher in both species richness and evenness aspects than in the dense woodland, probably due to frequent disturbance by fire and grazing (Figure 40). The dense woodland can be regarded as undisturbed by large herbivores, allowing a clear and homogenous vegetation structure to develop. A few species dominate, resulting in a lower evenness than in the open woodland. In contrast, the species richness does not differ between the woodland types with mean values of 48.6 species per 1000 m² for the dense woodland and 50.2 for the open woodland. These values are slightly higher than those cited for plots of equal size in the Kavango woodlands of northern Namibia, with 43.8 species for the observatory Mile 46 and 42.5 for Mutompo (Jürgens et al. 2010).

Differences in environmental factors among open and dense woodland

What are the environmental factors facilitating the occurrence of dense woodlands? Because our results are not conclusive with regard to this question, we can only speculate about the determining environmental factors. However, we can report some salient features: the sharp transition from open to dense woodland, the changes in vegetation taking place within a few metres; the lack of notable differences in elevation or topographic position; and a notable change in soil texture, which indicates geogenic differences in soil conditions. Furthermore, there are clear differences in grazing and browsing regime and in the frequency of fire events. In contrast to the open woodland, grazing as well as fire are literally absent from the dense woodland. Both factors have been shown to be major determinants of vegetation patterns in Southern Africa (Sankaran, Ratnam & Hanan 2004; Bond & Keeley 2005). However, in this case we consider them not as the primary drivers, but as factors sustaining the current state of the distribution of the two coexisting vegetation units, as discussed below.

The dense woodland has a significantly higher silt (6.4 %) and clay (4.9 %) content than the open woodland (2.8 % and 1.0 % respectively), thus providing a higher moisture retention capacity. This is an important factor as rainfall is seasonal (Weber 2013e) and water for vegetative growth needs to be stored. Furthermore, the higher content of potassium in the dense woodland soils offers better growing conditions. This level of potassium can be explained in two ways. Firstly, the higher clay content enhances cation exchange capacity and thus favors nutrient retention. Secondly, the lack of fire events in the dense woodland means that plant material is not volatilized but instead decomposed. In contrast, low potassium contents in the open woodland can be explained by losses through volatilization, ash convection, and erosion, as well as leaching after frequent burning processes (Kauffman et al. 1995; Giardina et al. 2000). The content of organic carbon in the soil, although it was not measured, is expected to be higher in the dense woodland due to being undisturbed by fire. A higher content of soil organic carbon might also increase moisture retention capacity and nutrient retention. The macro nutrient nitrogen was not measured, and for phosphorus no trend was found and the values showed a high standard deviation (Table S5). Although the differences in soil properties between open and dense woodland are small, these differences are important in a very nutrient-poor environment.

Similar vegetation types from the Zambezian phytoregion

A similar type of 'cryptic' dense woodland is known from northern Zambia: the Itigi-Sumbu thickets. They have a very similar structure, have sharp borders with the surrounding vegetation, and feature very shady, moist conditions (White 1983). They even share the species Jesse-bush bushwillow (*Combretum celastroides*) with the dense woodland in our study. An additional similarity is the preference for agriculture in these patches. Although this is a different ecosystem, with higher precipitation and surrounded by Miombo forests, the underlying biophysical conditions may be similar. White (1983) links the occurrence of those Itigi-Sumbu thickets to an impermeable duricrust beneath a sandy soil of 0.6–3 m. In our case such an impermeable underlying structure would restrain infiltration and facilitate accessible groundwater reservoirs. It has been shown that available soil volumes over calcrete crusts, in combination with rooting depth, determine vegetation composition in the Kavango region of northern Namibia (Kindt & Coe 2005). Sicklebush (*Dichrostachys cinerea*), a species we found in the dense woodland and fallows, is mentioned by Burke (Burke 2002) as a species profiting from hard subsoil structures and shallow soils. However, we did not find a hard crust within the two metres of soil depth analyzed.

Dense vegetation patches or thickets occur occasionally in the whole Zambezian phytoregion (White 1983). They are often related to secondary vegetation created by human activity (e.g. livestock farming). However, both the Itigi-Sumbu thickets and the dense woodland of this study represent seemingly undisturbed vegetation. A contrasting hypothesis for the origin of the dense woodland would be a relict ecosystem resulting from the transformation of the surrounding landscape. However, such a change in environmental conditions would have to occur on a very long time scale, as the shape and boundaries of the dense woodland on satellite images have been constant since the oldest available Landsat images in 1972 (Path: 178, Row: 072).

Benefits of the dense woodland for agriculture

Several factors make the dense woodland more attractive for agriculture than the open woodland. As discussed above, soils in the dense woodland offer slightly better growing conditions. Furthermore, the basal area – which is an approximation for standing woody biomass – is higher in the dense woodland. In the basal area of shrubs, we found a more than tenfold increase, from 0.4 m^2 ha^{-1} in the open woodland to 4.7 m^2 in the dense woodland. The shrubs burn easily and add ash and nutrients to the soil, in contrast to trees with larger stems, which are not easily burned. Furthermore, the LAI is almost three times higher in the dense woodland. The larger amounts of leaves and accumulated soft litter mean that more nutrients are released during the slash and burn process and fertilize the soil (Giardina et al. 2000).

Farming in dense woodland sites promises better yields than in the surrounding open woodland. The described advantages apparently outweigh the additional effort in terms of labor and also access: the sites are a distance of about 8–10 km from the river, village and road. To compensate, during the cropping season people move their homes to the hinterland and organize daily water supplies via oxcart.

Impact of duration of agricultural use on regeneration

Diversity of fallows

Compared to the woodlands, the regenerating fallows are more heterogeneous in species composition, vegetation structure, and soil composition, and therefore have a higher species diversity than the undisturbed state.

In our study, species diversity responded to land-use duration, especially for more evenness-based indices (i.e. $\alpha > 1$, see Figure 40). All fallows had a higher diversity than the dense woodland. Short use/fallows showed higher diversity than medium and long use/fallows. This pattern is in line with the predictions of the intermediate disturbance hypothesis (IDH). However, the generality of the IDH is still debated, as studies from dry tropical woodlands show (Bongers et al. 2009) and do not show support for the IDH (Williams et al. 2008). Positive effects of shifting cultivation on diversity at a landscape scale were found in semi-deciduous forests in Ivory Coast (Kassi N'Dja & Decocq 2008), dry floodplain woodlands in Kenya (Oba, Stenseth & Weladji 2002), and in Miombo woodlands of Tanzania (McNicol, Ryan & Williams 2015). The remaining diversity profiles intersect and hence are 'non-comparable' (Tóthmérész 1995) or 'non-separable' (Liu et al. 2007)].

Species composition of fallows

In contrast to Luoga et al. (2004) we found no evidence of resprouting trees from trunks above ground, therefore regeneration has to originate from seed banks, rhizomes, or dispersal from plants surrounding the fallow. This promotes fast-growing grasses and herbs, which are usually the first colonizers (Strang 1974; Bazzaz & Carlson 1982). Sicklebush (*Dichrostachys cinerea*) and Flame thorn (*Acacia ataxacantha*) are spiny plants, an adaptation to herbivory that might hamper grazing on the fallows. As the species composition of all fallows is much closer to the dense than to the open woodland, a return to dense woodland in the long term is likely. However, to verify a successional pathway to dense woodland vegetation, additional data on later stages are needed.

This regeneration pathway may actually never be realised, as economic development and population growth increase demand for agricultural land (Power 2012). Recent work has shown substantial forest cover losses related to agricultural expansion in Angola over the last decade (Hansen et al. 2013; Schneibel et al. 2013c). Based on the time series of satellite images (Table S6) we could show that the cultivation in the dense woodland started in 1986 and was more or less static at 3% from 1986 to 2000. Since then it has increased exponentially, with 17% under cultivation or in recent fallow stages in 2013. Consequently, field fallow cycles will likely shorten, meaning the area of the dense woodland could shrink rapidly in the near future.

Our data indicate that land-use duration affects fallow regeneration of dense woodlands. Long use/fallows differ more strongly in species composition from intact woodlands than fallows with shorter land-use duration (Figure 39). The species composition of the medium and short use/fallows is closer to the original vegetation. Consequently, plant community regeneration in the long use/fallows will take longer, which may be due to a reduced seed pool (Pickett, Collins & Armesto 1987; Guariguata & Ostertag 2001). Mwampamba and Schwartz (2011a) show for tropical woodlands in Tanzania that regeneration is impeded by long cultivation durations exceeding 16 years. For shorter time spans, as in our case, they did not find a straightforward relationship among diversity, basal area, and stand complexity. Similarly, studies from Ivory Coast (de Rouw 1993), Madagascar (Randriamalala et al. 2012) and South America (Guariguata & Ostertag 2001) found slower species regeneration in tropical forests due to more intense and/or prolonged land use. However, a comparison of studies from different tropical regions is difficult because of site-specific differences in regeneration time, type of land use, biotic and abiotic conditions, and the different units used for measuring diversity and regeneration. For example, land-use history for most study sites is vague because exact information about past land use is often not available (Omeja et al. 2012).

Structure and soil properties of fallows

In vegetation structure and soil composition, the fallows did not differ much, according to the PCA. A negative effect of land-use duration on the regeneration of basal area, stem density, and biomass, as shown in other tropical regions (Uhl 1987; Guariguata & Ostertag 2001; Mwampambaa & Schwartz 2011b; Randriamalala et al. 2012), could not be found, but a closer look at each variable revealed differences in the case of potassium. The slash and burn process volatilizes nutrients. Most nitrogen and a large share of phosphorus are lost. However, some nutrients, especially potassium (K^+), are conserved in the ash and act as a fertilizing pulse (Giardina et al. 2000). Our results show that after a short period of land use and twelve years of fallow regeneration, this fertilizing effect is still detectable for K^+ but not for phosphorus. Interestingly, with longer land use the K^+ content decreases and eventually reaches values below the original state (Figure 42). Therefore, a longer cultivation period has a negative effect on the K^+ content, probably due to potassium export with crops. K^+ was shown to be a crucial factor for maize cropping in other tropical regions (Loganathan, Dickson & Isirimah 1995; Lopez & Vlek 2006). This could be the reason why fields can only be cultivated for short time spans before yield reduction makes cultivation unattractive.

Implications for conservation

We have shown that the dense woodland strongly differs in species composition from the prevailing open woodland. In contrast to the open woodland, the dense woodland is protected against fire events. However, it is targeted for agriculture, as its soils are slightly more fertile and the higher woody biomass produces a higher nutrient pulse when burned for shifting cultivation. The usage of the dense woodland for agriculture has increased exponentially since the year 2000. Consequently it can be expected that a new emerging cultural landscape will be created. Such a landscape, with a mixture of fields and fallows, would create a higher plant diversity (Padoch & Pinedo-vasquez 2010; McNicol, Ryan & Williams 2015). However, specialized species closely associated with the dense woodland may become less abundant. Furthermore, increasing demand for arable land, as described for the adjacent region (Röder et al. 2015), may lead to prolonged use of agricultural fields, influencing species composition and diversity in the regenerating fallows as well as negatively impacting soil fertility. Eventually, increased agricultural usage may lead to substantial loss of soil fertility, and consequently cropping conditions in the former dense woodland will no longer be superior to those in the open woodland.

Supplementary Materials available in the Appendix of the thesis

Table S4 Variables on vegetation structure for each category showing the average (AVG) and standard deviation (SD). Cover according to vegetation strata; main height is the maximum height of the lowest 95 % of the vegetation; basal area shrubs = sum of BA of all stems with DBH < 5 cm, basal area trees = sum of BA of all stems with DBH > 5 cm; species richness given for all vascular plants and for trees with a DBH > 5 cm. Table S5 Average (AVG) and standard deviation (SD) values for the soil variables of the four soil depths and the five soil profiles for each category. Table S6 Calculation of fallow age and field duration with a satellite image time series. Source of Imagery given for Landsat, Google Earth and Rapid Eye; categories: S = short use/fallow, M = medium use/fallow, L = long use/fallow; values for land-use intensity: 0 = not used, 0.5 = partly used, 1 = used, E = stripes on the picture (error in Landsat sensor), C = clouds. Table S7 Vegetation table showing the results of the indicator species analysis for open woodland, dense woodland and the three fallow categories short, medium and long usage. Life form (LF) is given for every species according to

Raunkiaer: P = phanerophyte, Ch = chamaephyte, H = hemicryptophyte, Cr = cryptophyte, T = therophyte, brackets indicate uncertain categorization. *Phi* values are given for every species indicating the strength of a species' association to each category or combination of categories. The *phi* value ranges from -1 to 1, however, only significant *phi* values > 0.5 are shown and cells are left empty otherwise. In the case that a species is indicative for more than one category, the highest value is shown in bold. Frequency of occurrence ranges from 1 (low) to 5 (high) and is displayed in the column next to the *phi* values. FNR = field number. Table S8 Pearson correlation of the variables with the first three axes of the Principal Component Analysis. R values shown; Soil depths: H1 = 0–10 cm, H2 = 25–45 cm, H3 = 70–90 cm, H4 = 180–200 cm. Figure S12 Geomorphological landscape units derived from the global digital elevation model SRTM (Shuttle Radar Topography Mission, USGS 2004) following the automated classification of topography developed by Iwahashi & Pike (2007). Classification was done by Jan Wehberg; Grid cell of 90 m; Units: decimal degrees; Map datum: WGS84. 'Valley bottom level 1' denotes the current river bed of the Cubango River, 'Valley bottom level 2' the floodplain, 'Slope' the area showing a gentle slope towards the stream network, and 'Sandveld' the sandy plain of the hinterland with only very subtle differences in terrain.

Acknowledgements

We thank Antonio Kangumbe for his support in the field. Further, we thank the Faculdade de Ciências Agrárias and the Instituto de Investigação Agronómica in Huambo, especially Dr. Santos Quizembe João da Costa, Jorge João Delfim and Fernando Luis for soil analysis. The Future Okavango Project (TFO) provided the financial and infrastructural background for this study. TFO is funded by the German Ministry of Education and Research (BMBF). Finally, we acknowledge the DLR for the provision of data from the Rapid Eye Science Archive.

CHAPTER 8

Synthesis

Rasmus Revermann

In the following I will summarise and discuss the key findings of the thesis with respect to the overarching objectives. For this purpose I will also draw on the results of four co-authored publications that were not included as separate chapters in the printed thesis. Furthermore, results presented at the Conference of the International Society of Biogeography in 2015 are included in the discussion. At the end of each section I will highlight new perspectives for future research.

This chapter is organised according to the main aims of the thesis. These were (1) to analyse species composition of the understudied woodlands of the upper reaches of the Okavango Basin in Angola and to identify representative vegetation communities, (2) to investigate environmental drivers of vegetation patterns, (3) to quantify plant diversity and to analyse spatial patterns of plant diversity in the Okavango Basin, (4) to explore methodological tools to link ecological field data to continuous remote sensing data in order to predict ecosystem properties of unsurveyed areas, (5) to assess the impact of land use on vegetation composition, plant diversity and regeneration of dry tropical woodlands.

(1) Species composition

For the first time a comprehensive, quantitative overview of the vegetation of the Angolan part of the Basin has been presented. The results were based on a vegetation survey using standardised vegetation plots and aiming at sampling all major vegetation units (**Chapter 2**). Using the recently developed vegetation classification algorithm ISOPAM, I provided a first classification of the terrestrial vegetation of the Cubango Basin, the major tributary of the Okavango River. In total, 12 woody vegetation communities were identified and described regarding their species composition (**Chapter 3**). Within the Miombo region four types of woodlands and forests could be discerned as well as two open formations dominated by Poaceae and geoxylic suffrutices.

Within the *Baikiaea* woodlands of the southern parts of the Cubango Basin six woody vegetation communities were described. Among these vegetation types the woody plant community termed *Combretum celastroides-Baikiaea plurijuga* had not been described in the literature before. A detailed characterisation was provided for the first time (**Chapter 3** and **7**).

Furthermore, a vegetation map, depicting the six major vegetation units and 20 subunits with a 250 m spatial resolution, was developed in collaboration with colleagues from the TFO project. The map was based on unsupervised classification of land surface phenology metrics of the MODIS enhanced vegetation index (see **Chapter 5**) and the vegetation units were interpreted using vegetation plots and quick vegetation assessments carried out in the Okavango Basin. The map and a summary of the vegetation description has been provided in the introduction in **Chapter 1**, for full details please refer to the publications Stellmes, Frantz, Finckh & Revermann (2013a) and Revermann & Finckh (2013a).

The thesis presented here has laid the foundations for future work on the ecology of the Angolan dry tropical woodlands. Once all herbaceous species collected are identified a full phytosociological classification of the Miombo and *Baikiaea* woodlands of the Cubango Basin in Angola will be possible. Phytosociological classifications can play a major role in defining objectives of conservation and spatial planning. As such, the core of environmental legislation in Europe, the Habitats Directive of the European Union, based its habitat types on phytosociological units (Luther-Mosebach et al. 2012; European Commission 2013). Furthermore, the numerical classification of the vegetation-plot database will allow underpinning the vegetation map of the Okavango Basin (see above) with detailed information on vegetation composition and vegetation structure.

(2) Environmental drivers of vegetation patterns

Climate

Given the clear climatic gradient in the Basin, it is not surprising that climate emerged as the major driver of vegetation patterns at the regional scale of the Basin. The Miombo woodlands and forests require higher amounts of precipitation and longer rainy seasons and are thus restricted to the sub-humid upper reaches of the Okavango Basin. With decreasing annual precipitation towards the south of the Basin typical Miombo species fade out. Dominant species of the Angolan Central Plateau such as *Brachystegia spiciformis* and *Cryptosepalum exfoliatum* ssp. *pseudotaxus* do not occur in areas with less than approximately 900 mm of annual precipitation. At the foothills of the Angolan Central Plateau precipitation drops to around 700 mm per year. This is where the *Diospyros batocana*-*Julbernardia paniculata* woody plant community forms the southern margin of the Miombo belt. Gradually, all typical Miombo species disappear and give way to the *Baikiaea* woodlands (**Chapter 3**). The latter differ not only in their species composition but also exhibit a distinct vegetation structure with a discontinuous canopy and a rich grass and shrub layer.

Frost as driver of vegetation patterns in tropical Highlands

Although climate has been identified as governing factor for species composition at the regional scale, it was shown in **Chapter 4** that at the local scale micro-climatic conditions strongly influence vegetation patterns. At the TFO core study site of Cusseque, situated on the Angolan Central Plateau, I installed a network of micro-climatic data loggers in cooperation with colleagues from the TFO project. The measurements revealed that night frosts regularly occurred during the dry season. The frost events were mainly restricted to the open slopes and valley bottoms and the wooded elevated areas rarely experienced frost. On the slopes and at the valley bottom frost occurred in 37, 44, and 37 nights in the years 2012, 2013 and 2014 respectively.

The occurrence of the night frosts can be explained by the prevailing clear skies during the dry season supporting thermal radiation. Although air temperatures rise to well above 30°C during the day, temperature drops with the onset of night and can reach freezing level towards the end of the night lasting until sunrise. Due to the short duration of the frost event soil temperature always remained well above freezing level. A flow of cold air following the topography can be observed and the cold air accumulates in depressions and valleys (Revermann & Finckh 2013c). Interestingly, global climate data sets do not show this high frequency of frost events (see Figure 3c in the introduction).

On the one hand, these findings give important hints for agriculture and the suitability of frost sensitive crops at certain areas in the landscape. On the other hand, they sparked a new debate on the evolutionary drivers of geoxylic suffrutices with their distributional centre in the Zambezian phytoregion. The reasons for the development of this specific lifeform have been debated since their first mentioning by Davy in the year 1922 (Davy 1922). In 2014, Maurin et al. (2014) dated the evolutionary onset of the geoxyles back to the Miocene and suggested increased fire frequency as the evolutionary trigger. However, appropriate paleoclimate data and fossil records to support this hypothesis are lacking. Current landscape patterns and microclimatic condition highlight frost in tropical highlands as one important driver. However, frost is often neglected as it is not evident from gridded climate products. Therefore, investigating the frost sensitivity of pairs of closely related trees and geoxyles may provide further support for the frost hypothesis (see also Sanguino 2015).

Climatic variables as predictor variables in ecological modelling

Although climate (temperature and precipitation) was identified as determining factor for vegetation patterns on the regional scale, climatic predictor variables were not suitable to produce realistic maps of plant α-diversity in a statistical modelling framework (**Chapter 5**). In spite of high model performance, the maps, predicted by statistical models, exhibited a lot of artefacts. Instead, land surface phenology metrics captured the variation of plant α-diversity in the landscape much better and produced realistic maps.

Topography

In the modelling approach, predictor variables concerning the topography, i.e. topographic wetness index, topographic position index and topographic ruggedness index, had only moderate to low variable importance. This concurs with the findings in **Chapter 3** where topography was shown to be of relevance only in the rolling landscape of the Angolan Central Plateau. Here, topographic position is decisive as it determines pedogenesis, mediates the flow of cold air, and governs the availability of water.

Soils

The vegetation survey was accompanied by an extensive soil sampling approach. Three samples were taken at each plot in the depths 0 to 10 cm, 45 to 55 cm and 70 to 90 cm. However, the analysis of soil properties (**Chapter 3**) revealed that throughout the Basin there is little variation within the soils of the woodlands and forests. However, small differences in the content of clay and silt in the (sub) soil often are the determining factor of species compostion at the local scale.

The predominant soil types were acidic Arenosols with low nutrient levels. Clay and carbonate rich soils were encountered on the old and recent floodplains of the middle reaches of the Cubango River. The investigation of the enigmatic dense *Baikiaea* woodland which is restricted to the communal area of Savate in the Cuando Cubango Province in **Chapter 7** revealed a slight difference with regards to the substrate. The dense woodland type showed slightly higher contents of silt and clay.

Furthermore, different soil conditions were found at the azonal vegetation types of the Basin. The riverine peatlands of the Angolan Central Plateau featured Histosols with peat layers reaching several meters of depth (Revermann et al. 2013). The vegetation communities dominated by geoxylic suffrutices also exhibited soil properties deviating from the surrounding woodlands. The plant community *Cryptosepalum maraviense-Cryptosepalum exfoliatum ssp. suffruticans* generally occurred on shallow ferralitic soils with slightly higher content of fine material. Moreover, extensive elevated plains with impeded drainage exist in the extreme north of the Basin supporting edaphic grasslands on peaty mineral soils (**Chapter 3**).

(3) Plant diversity in the Okavango Basin

When preparing the first checklist of vascular plants in Angola, Figueiredo and Smith (2008) compiled information from hardcopy, electronic and herbarium specimen to generate an overview of the entire flora of the country. In total, they recorded 6,735 indigenous species. This corresponded to an increase of 20% in comparison to the previous estimate (Figueiredo, Smith & César 2009). The checklist "Plants of Angola – Plantas de Angola" was a very important step for any work on vegetation ecology in Angola.

While the work of Figueiredo and Smith (2008) was largely based on old studies and herbarium specimen that were, in their large majority, collected in the pre-independence era, the field work carried out within the framework of the presented thesis was the first systematic survey within the last decades in southeast Angola. In total, 2099 specimen were collected and over 450 different taxa were identified (**Chapter 2**). Due to the lack of field guides and keys for the flora of Angola, some of the collected material still has to be identified. The vegetation database of the Okavango Basin (Revermann et al. 2016b) contains over 11,000 observations of vascular plant species in the Angolan part of the Okavango Basin. This equals almost the number of records of vascular plants currently entered in the GBIF online database for the entire country (Figure 6). At the study site of Cusseque 154 woody species were recorded within 100 km^2 (**Chapter 2**). In comparison, Monteiro (1970) provided a list of 166 woody species for the entire province of Bié, thus emphasising the need of future surveys to grasp the full plant diversity of the country.

Using non-parametric species richness estimators, the pool of woody species for the Miombo region of the Cubango Basin was estimated to 302±11 woody species and to 262±20 woody species for the *Baikiaea* woodlands (**Chapter 3**). The highest density of vascular plant species was found in the northern parts, in the Miombo region, with more than 60 vascular plant species within one vegetation plot of 1,000 m^2 (**Chapter 5**). Hence, the highest diversity occurs precisely in the area with the highest rate of deforestation and accelerating land use change (see Figure 2).

Species new to science

In addition, one grass species new to science was discovered in the riverine peatlands of the Angolan Central Plateau when identifying the collected plant material from the vegetation survey (Figure 43). What was first believed to be a rediscovery of S*typpeiochloa catherineana* Cope & Ryves of the subfamily of the Arundinoideae later turned out to be a different taxon. Morphological measurements showed that the collected specimens deviated in a range of taxonomically important measures. Subsequently, the inspection of leaf anatomy showed that the putative new species exhibited Kranz anatomy and therefore excluded the placement with the Arundinoideae. Microhairs analysed by scanning electron microscope revealed that the putative new species had microhairs of the ‘chloridoid type’. Subsequent molecular analysis confirmed the morphological studies and indicated closest relationship to *Bewsia biflora* of the subfamily of the Chloridoideae. Further molecular analyses will reveal if the new species as well as *Styppeiochloa catherineana* will need to be placed in a new genus of the

Chloridoideae or if it should be included in an existing genus; a publication is in preparation.

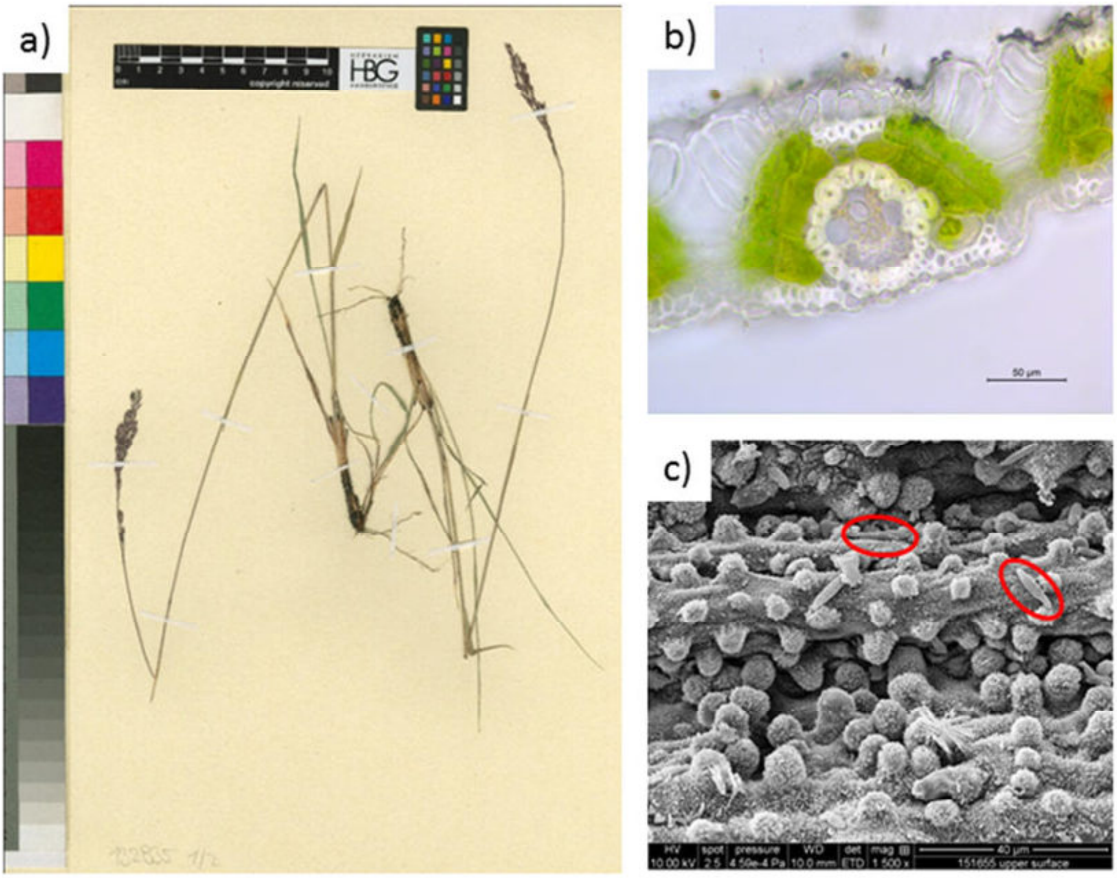


Figure 43 New grass species discovered in the riverine peatlands along a tributary of the Cusseque River on the Angolan Central Plateau. a) herbarium specimen of the new species, b) cross-section of a basal leaf under the light microscope with 40 times magnification, c) SEM image of the upper leaf surface at 1,500 times resolution showing microhairs of the chloridoid type denoted by red circles.

During the TFO vegetation survey specimens of *Schistostephium crataegifolium* (DC.) Fenzl ex Harv. (Asteraceae, Figure 44) were collected and represent the first generic records from Angola (Gonçalves, Tchamba & Goyder 2016). Altogether, this indicates that the vegetation of Angola is clearly understudied and that new surveys, be they based on old herbarium specimen or new field surveys are likely to reveal range extensions of species formerly not known to occur in the country or even detect new species. As such, it is also most likely that further work on the collected plant material during the TFO vegetation survey will reveal further findings.

Figure 44 The Asteraceae *Schistostephium crataegifolium* (DC.) Fenzl ex Harv. recorded during the TFO vegetation survey for the first time in Angola (Gonçalves, Tchamba & Goyder 2016)

(4) Linkage of ecological field data with remote sensing

Predicting plant α-diversity

Globally, a decline of biodiversity has been recorded (Butchart et al. 2010). To halt the loss of biodiversity, there is an urgent need of spatially explicit data on diversity patterns to enable spatial conservation planning. As shown in **Chapter 5,** the amalgamation of ecological site data and continuous remote sensing data can play a prominent role in this regard. In this chapter it was shown that land surface phenology (LSP) metrics derived from coarse scale MODIS enhanced vegetation index data proved to be good explanatory variables to predict α-diversity derived from the vegetation-plot database of the Okavango Basin (**Chapter 2**). In spite of their lower model performance, models based on LSP metrics provided more realistic maps than models using climatic variables.

Land surface phenology metrics in species distribution modelling

Using remote sensing information in species distribution modelling (SDM) is still a rather recent but promising trend in biogeography (Cord et al. 2014; He et al. 2015). To illustrate the potential of combining vegetation-plot database and remote sensing LSP metrics in SDM studies, I will briefly present results not included in the preceding chapters. The study was presented on the conference of the International Biogeography Society in 2015 (Revermann et al. 2014), and a manuscript is in preparation.

To predict tree species distributions in the Okavango Basin, I used the same predictor variables as presented in **Chapter 5**. The response variables, a presence-absence dataset of all frequent woody species of the Basin, were derived from the vegetation-plot database (**Chapter 2**) and from forest inventory plots in Namibia (De Cauwer 2013). Using boosted regression trees the distribution of the 105 most frequent woody species of the Okavango Basin were predicted, see Figure 45 for examples of the maps for three common species. 10-fold cross validation showed good model performance according to the true skill statistic (TSS) and Nagelkerke's R^2 and excellent performance according to the area under the curve (AUC) statistics. Due to their comparatively high resolution these maps provide detailed information on the distribution of the common woody species of the Basin and hence can support conservation and management of the woody resources in the Okavango Basin.

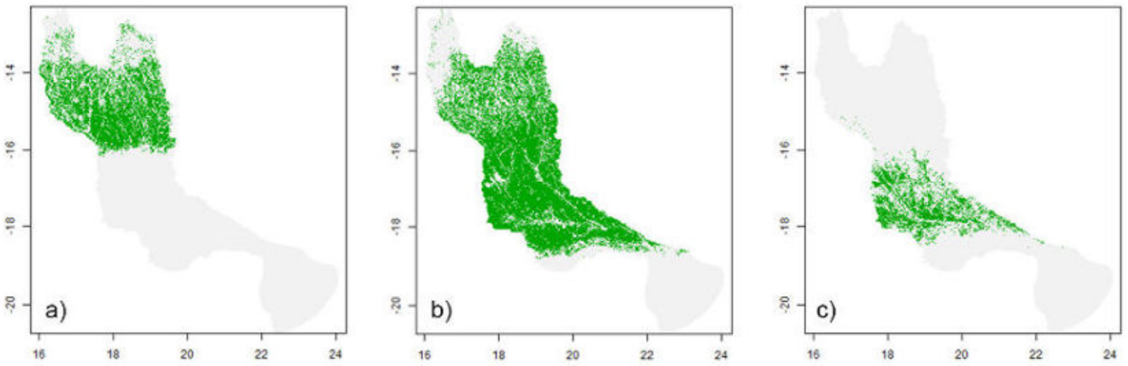


Figure 45 Modelled tree species distributions in the Okavango Basin of a) *Julbernardia paniculata*, b) *Burkea africana*, and c) *Baikiaea plurijuga*. Model type: BRT, data set: MODIS EVI LSP metrics and climate data (see Chapter 5). Green indicates predicted presence of the species according to the conversion of predicted probabilities using the threshold 'predicted prevalence equal to observed prevalence'.

Case study: Distribution of *Pterocarpus angolensis* DC under climate change

Due to the nature of the LSP predictor variables, it is not possible to predict changes in the distributional range of species caused by a changing climate. In a study led by Vera de Cauwer (De Cauwer et al. 2014) we investigated the impact of a changing climate on the economically valuable timber species *Pterocarpus angolensis* DC in southern Africa. Based on presence records from herbaria, own fieldwork and literature MaxEnt models were developed for current climate conditions and two climate scenarios. Predictions indicated that *Pterocarpus angolensis* may disappear from Namibia and Botswana by the year 2080. However, slight expansions of the distributional range were predicted for Zambia (Figure 46).

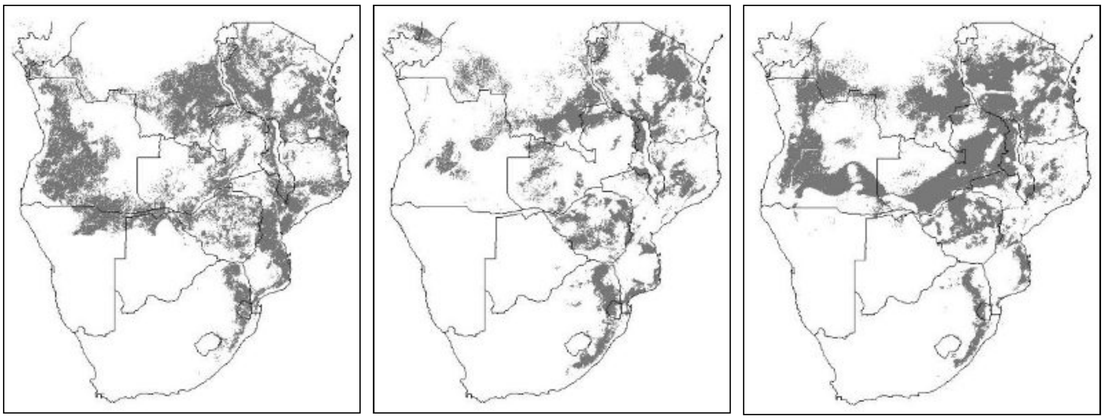


Figure 46 Current and future (2080s) distribution scenarios for Pterocarpus angolensis. Left is the current distribution, the middle uses emission data from emission scenario A2a and the right from emission scenario B1. A minimum threshold of 10% percentile on occurrence probabilities was applied to delineate species distribution. Reprinted from Forest Ecology and Management, 315, V. De Cauwer, B. Muys, R. Revermann, and A. Trabucco, Potential, realised, future distribution and environmental suitability for Pterocarpus angolensis DC in southern Africa, 211-226, 2014, with permission from Elsevier.

LSP in vegetation ecology

Chapter 3 illustrates how, the other way round, remote sensing data can enrich studies in vegetation ecology. In the classification of the woody vegetation of the Cubango Basin LSP metrics were used to infer ecological properties of the derived woody vegetation communities. The variable 'LargeIntegral', for example, gives an indication of the total aboveground biomass, whereas temporal metrics can shed light on the timing of vegetation development such as start, end or duration of the growing season.

Future perspectives of the usage of LSP

Future research in deriving LSP metrics from medium resolution remote sensing products, i.e. Landsat data, may improve the matching of ecological site data and the remote sensing information and hence lead to an even better representation of landscape heterogeneity.

Until now the derivation of LSP metrics from Landsat has been problematic due to the low revisit frequency of the sensor platform. To generate reliable LSPs a time series consisting of at least one image per 16 days is required (Archibald & Scholes 2007) which is not feasible in Landsat as it only provides one image in a 16 day interval. In the tropics, there is virtually no chance to gather enough suitable images during the wet season due to the frequent cloud covers obscuring the images. However, new approaches combining coarse and medium resolution imagery using information of the local pixel neighbourhood are very promising (Frantz et al. 2016). This approach will yield LSPs on a regional scale with spatial refinement of MODIS LSP by Landsat reflectance data. This will enable the prediction of plant diversity and vegetation composition on regional scales with unprecedented detail.

(5) Impact of land use on vegetation composition, plant diversity and regeneration.

Agriculture and commodification of natural resources

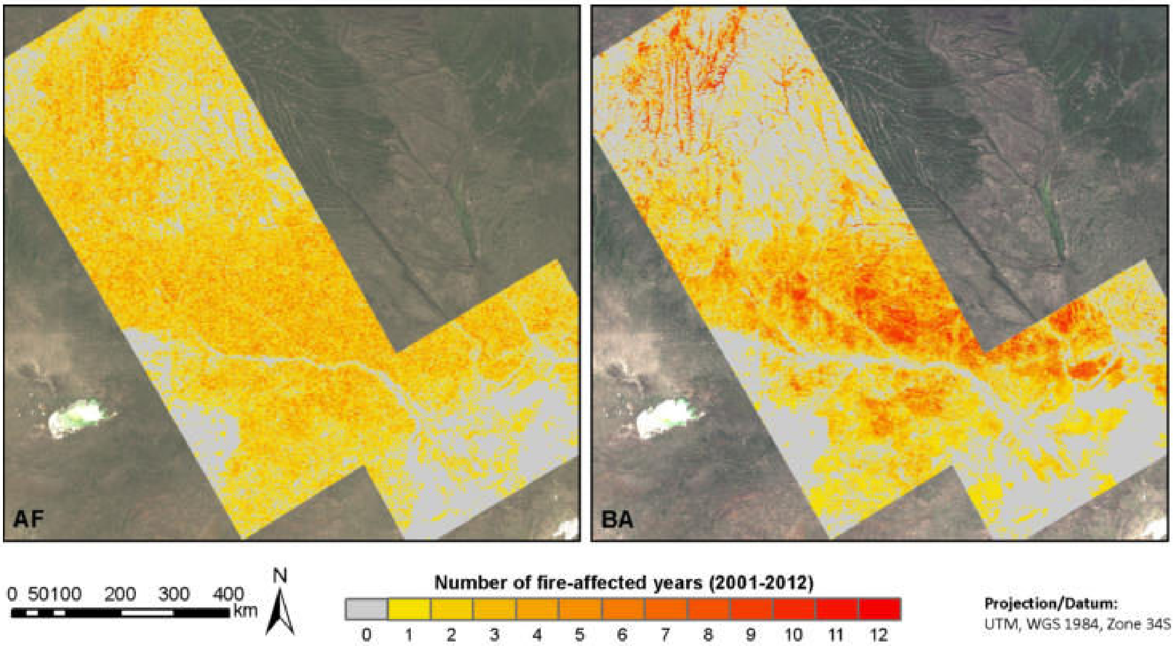
The most imminent changes of the natural environment are not caused by climate change but by socio-economic changes. As detailed in the introduction, the entire African continent is subject to global drivers causing dramatic local land use changes. Furthermore, the steadily increasing population leads to higher demands of agricultural area for small-holder subsistent farmers, too. In the past, shifting cultivation was an appropriate method to deal with low soil fertility and has been successfully applied as fertility management practise. Clearing woodlands and subsequent burning of the biomass generates a nutrient pulse and the field can be used for approximately five years. This is usually followed by a regeneration period of several decades. (Abdelli & Jouen 2012; Domptail et al. 2013). However, decreasing land availability will lead to shorter fallow periods or longer usage of cleared fields (Pröpper et al. 2015). In the study presented in **Chapter 7**, we revealed how longer duration of the usage of agricultural fields in shifting-cultivation has negative repercussions on the regeneration of fallows. In the light of reduced land abundance and increasing need of agricultural area for a growing population this highlights the importance to find ways to improve yields of the small-holder dominated agricultural system. Conservation agriculture, a form of sustainable intensification (Godfray & Garnett 2014), is a promising approach for the low-nutrient systems of the Okavango Basin and merit further thorough scientific research (Pröpper et al. 2015).

The so called 'global change' exerts also strong indirect pressures on rural communities. New aspirations and desires of formerly subsistent farmers promote the commodification of natural resources, i.e. in form of agricultural products, timber and non-timber related forest products (Pröpper et al. 2013). The study on the cross-border contrast between Angola and Namibia in **Chapter 6** showed that spatially diffuse forms of land use have a measureable impact on plant diversity, too. Woody species were affected more strongly than herbaceous ones.

As a co-author, I also contributed to three publications dealing with two other important factors impacting on vegetation: fire and road infrastructure. In the following, I will provide a brief recapitulation of the main key findings of these articles.

Fire regime in the Okavango Basin

In the article entitled "Fire frequency, fire seasonality and fire intensity within the Okavango region derived from MODIS fire products" (Stellmes et al. 2013c) the prevailing fire regime in terms of fire frequency, timing and intensity were analysed based on the MODIS burnt area and MODIS active fire products (Figure 47). It was shown that fire frequency is related to land cover type and fire management. Closed Miombo woodlands, due to their high tree cover (Hennenberg et al. 2006; Archibald et al. 2009), are largely fire resistant while the two types of geoxylic grasslands also occurring in the upper reaches of the Basin are burned almost every year. The *Baikiaea* woodlands of the middle reaches were also prone to frequent fires and more than 50% of the extent of these woodlands were affected by fire in the twelve year period analysed. The fact that the fire season is inversely timed to the thunderstorm season suggested that the large majority of fires were of anthropogenic origin.



Data source/background:
The datasets are based on the MODIS active fire product (MOD14A1 and MYD14A1) and the MODIS burned area product (MCD45A).
The background of the maps are MODIS reflectance images. All products courtesy of EOSDIS (NASA) and the University of Maryland.

Figure 47 Number of fires per year detected within the active fire product (AF, left hand side) and the burnt area product (BA, right hand side) in the period 2001 to 2012. Source: Stellmes et al. 2013.

High fire return rates of less than five years impede the regeneration of woodlands. The reoccurring fires permanently capture tree saplings in the so called 'fire trap' and preclude their outgrowing of the danger zone of ground fires (Sankaran, Ratnam & Hanan 2004; Bond & Keeley 2005). Once they reach maturity many woodland and savanna tree species develop a thick, corky bark that makes them less susceptible to fires (see also **Chapter 4**).

Road infrastructure

The articles "Agricultural expansion during the post-civil war period in southern Angola based on bi-temporal Landsat data" (Schneibel et al. 2013c) and "Evaluating the trade-off between food and timber resulting from the conversion of Miombo forests to agricultural land in Angola using multi-temporal Landsat data" (Schneibel et al. 2016) both investigated the impact of road infrastructure on the surrounding woodlands based on time series of Landsat imagery. Moreover, the latter article puts an emphasis on investigating the spatiotemporal patterns of land cleared for agriculture (Figure 48).

In total, 5.6% of the forested area were cleared in the time period between 1989 and 2013 (Schneibel et al. 2016). Road infrastructure clearly channelled land use activities: 93% of the agricultural area was situated in a buffer zone of 5 km around roads, and almost 50% was located in a distance of less than 1 km to the next road. Furthermore, a clear interrelation with the quality of the roads was documented: Tar-sealed roads attracted more clearance of woodlands than unsealed roads (Schneibel et al. 2013c). Thus, spatial planning and infrastructure development have a direct impact on the clearance of woodlands. Based on a denser time series of Landsat imagery in Schneibel et al. (2016) it became evident that agricultural land is rarely reused after a resting period. Instead, new land was cleared. This emphasises again the need of introducing agricultural methods preserving soil fertility and improving yields.

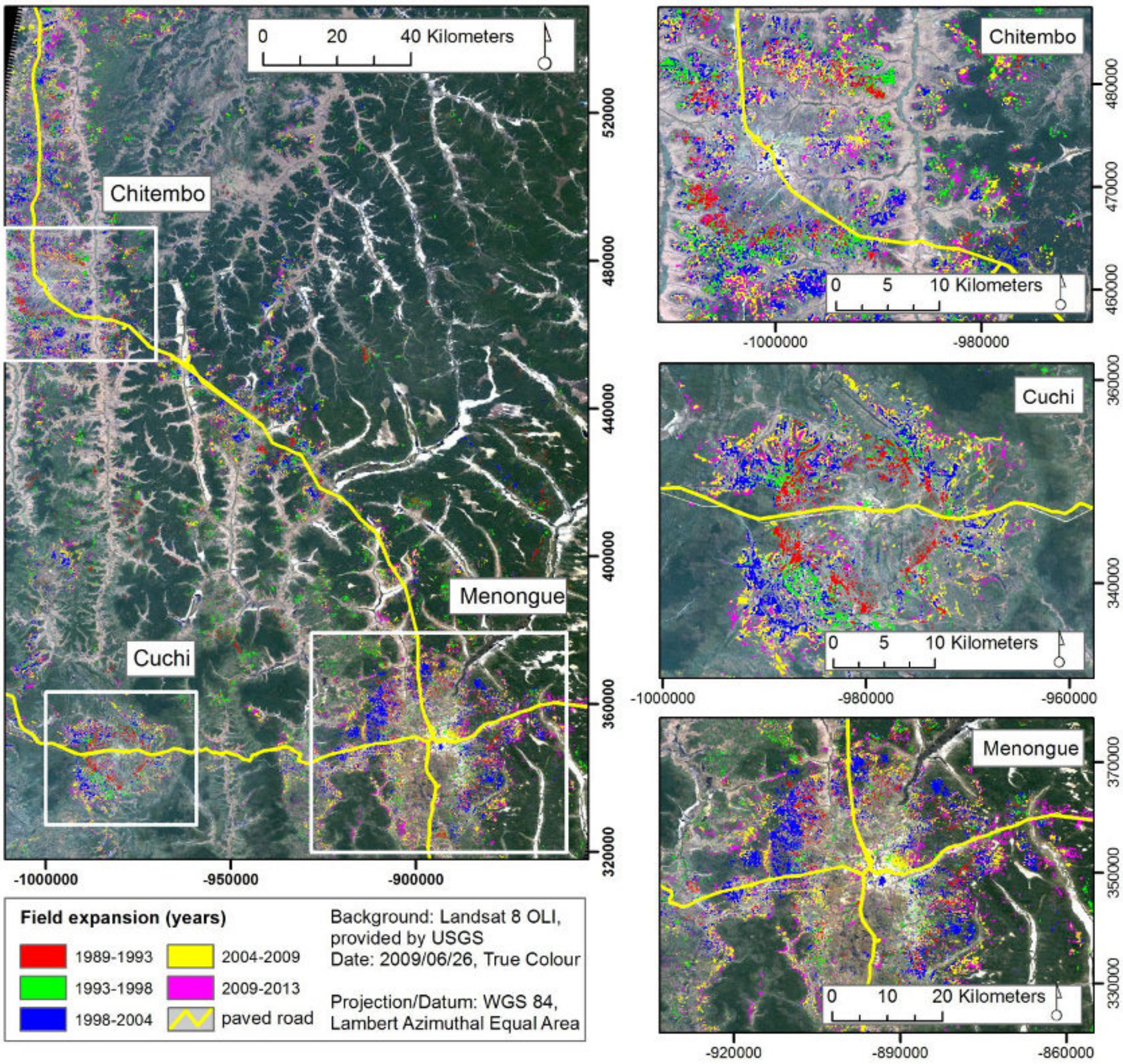


Figure 48 Map of field expansion for each time step from 1989–2013 with additional close-up for the three cities Chitembo, Cuchi and Menongue. Reprinted from Science of the total environment, 548-549, A. Schneibel, M. Stellmes, A. Röder, M. Finckh, R. Revermann, D. Frantz, and J. Hill, Evaluating the trade-off between food and timber resulting from the conversion of Miombo forests to agricultural land in Angola using multi-temporal Landsat data, 390-401, 2016, with permission from Elsevier.

Conclusion

The presented study has contributed to foster the understanding of vegetation and diversity patterns of the dry tropical woodlands of the Okavango region. The thesis provided the first comprehensive account of plant species composition and plant diversity of the Angolan part of the Basin. A classification scheme of the woody vegetation communities of the Cubango Basin has been developed. The communities were characterised in regard to their species composition and underlying abiotic conditions.

One grass species was identified as new to science and its placement in the subfamily of the Chloridoideae was discussed. Further work on the collected material will most likely reveal further range extensions of described species and potentially also new species discoveries. Studies on the vegetation of Angola remain a challenging task due to the diverse flora, the lack of local experts and the outdated and incomplete identification keys. However, the foundations for future, detailed work on the vegetation of the upper Okavango Basin have been laid.

Frost during clear nights in the dry season has been documented as a regular feature of the tropical highlands in Angola. The data collected from the micro-climatic measurement network during three years sparked the debate on the evolution of the geoxyle life form in the Zambezian Phytoregion and frost was proposed as a strong evolutionary driver.

A modelling framework was presented on how to synergistically use ecological site data and continuous remote sensing products to predict ecosystem properties. This approach is transferrable to other regions and can support natural resource management in providing appropriate, spatial biodiversity data. As such, the study revealed that the Miombo woodlands of the upper reaches of the Okavango River supported the highest plant diversity. At the same time, land use change and forest degradation are severest in this region and there is a clear lack of conservation areas protecting the Miombo vegetation types.

The impact of land use on vegetation was investigated in two case studies. In a cross-border study among Angola and Namibia the impact of spatially diffuse forms of land use was investigated. Higher land use intensities resulted in lower species richness. In another study the impact of shifting cultivation on the regeneration of dense *Baikiaea* woodlands was analysed. Duration of land use negatively impacted diversity and hampered regeneration of species composition to the original state.

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AUTHOR CONTRIBUTIONS

Chapter 1: Manuscript, data analysis and figures were all prepared by the author of the thesis. Where material from co-authored papers was included proper reference is made to these articles.

Chapter 2: a) Vegetation Database of the Okavango Basin: I was among the principal contributors of vegetation plots to the database and jointly manage the database with the co-custodian. I prepared the factsheet for the database and wrote the manuscript. The co-author critically revised the manuscript.

b) I carried out the fieldwork and identified the majority of the species that were included in the checklist. All co-authors also carried out field work at the Cusseque study site and contributed to the species list. I analysed the data and prepared figures and tables, and wrote the first draft of the manuscript.

Chapter 3: I conceived the study and pathway of analysis; methods and scope were subsequently discussed among co-authors. I carried out fieldwork and also identified the species. Furthermore, I performed data analysis as well as the preparation of figures and tables. All co-authors contributed to the final version of the manuscript.

Chapter 4: The micro-climatic logger network was designed and maintained together with Manfred Finckh. I carried out the data analysis and prepared the figures and tables. The first draft of the manuscript for "Microclimate – Cusseque" was prepared by myself. Manfred Finckh drafted a first outline of the response to the article of Maurin et al. (2014). We wrote the manuscript together and Marcos Aidar provided input on the advanced manuscript.

Chapter 5: The study is a brainchild of mine and I developed the study design. Furthermore, I carried out the majority of the field work in the Angolan part of the study area. Ben Strohbach contributed most of the plot data from Namibia. David Frantz and Marion Stellmes carried out the analysis of the MODIS EVI time series and provided the

LSP metrics. Climate data were provided by Torsten Weber and Thomas Weinzierl; downscaling to the working resolution of the study and the calculation of bioclimatic variables was done by me. I elaborated the modelling framework and run all calculations. Furthermore, I prepared all figures and tables and wrote the first draft of the manuscript; all authors commented on later stages of the manuscript and helped to improve the manuscript throughout the review process.

Chapter 6: I had the initial idea for the study and lead the field work. Data analysis, preparation of figures and the first draft of the manuscript was carried out by me. Johannes Wallenfang supported the field work. Jens Oldeland critically accompanied the statistical analysis. All authors discussed the results and contributed to the manuscript.

Chapter 7: The study was conceived by Johannes Wallenfang and me and we performed the field work together. The data analysis was carried out by Johannes Wallenfang in close collaboration with the co-authors. He also wrote the first draft of the manuscript and I contributed a lot to sharpen the line of arguments. Johannes Wallenfang and I implemented the suggestions made by the reviewers and prepared the response.

Chapter 8: The entire chapter was written by me. The content included in this section from the four co-author papers is clearly marked as such. In these papers I had significant contributions in the interpretation of the results and in the writing of parts of the manuscripts.

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APPENDIX

Note S1 Technical note on the climate logger network in the Cusseque Valley, Bié Province, Angola.

The study site is located in the Cusseque valley on the Angolan Plateau in the province of Bié. In the main valley and the tributaries 21 microclimatic measuring stations were installed. The stations are located along three catenas extending from the hills down to the valley bottoms (Figure 19). Each station was equipped with a Gemini Tinytag® PLUS 2 data logger measuring temperature at a height of 0.3 m above the ground. Data loggers were mounted below a wooden board protecting them from direct sunlight. Selected stations were fitted with soil probes at 0.1 m depth measuring soil temperature. The measuring interval was set to one recording every 15 min. Measurements started in November 2011 and are continuing to date. For further details please refer to Revermann & Finckh (2013).

Table S1 Annual minimum air temperatures at 0.3 m above ground, number of frost days and length of frost period (date of first and last frost in the course of the year) during the years 2012–2014. The logger network occasionally suffered from fire and vandalism, therefore data is not available (n/a) for all stations in all years. For locations of measuring stations please refer to Figure 19.

		2012			**2013**			**2014**		
Logger ID	**habitat**	**Tmin**	**n° of frost days**	**frost period**	**Tmin**	**n° of frost days**	**frost period**	**Tmin**	**n° of frost days**	**frost period**
TT07	forest	0.8	0	no frost	2.6	0	no frost	3.6	0	no frost
TT06	forest	-2.7	2	18.07. - 19.07.	0.3	0	no frost	n/a	n/a	n/a
TT09	forest	1.4	0	no frost	2.7	0	no frost	4.0	0	no frost
TT14	forest	-4.4	12	12.06. - 26.07.	-1.0	3	12.07. - 14.07.	0.1	0	no frost
TT20	forest	n/a	n/a	n/a	1.3	0	no frost	2.2	0	no frost
TT05	ecotone	-4.0	9	11.06. - 24.07.	-0.8	2	12.07. - 13.07.	0.0	0	no frost
TT21	ecotone	n/a	n/a	n/a	-1.1	3	12.07. - 14.07.	-0.4	4	13.07. - 18.07.
TT02	grassland	n/a	n/a	n/a	-4.0	38	27.05. - 31.07.	-3.1	24	21.06. - 04.09.
TT03	grassland	n/a	n/a	n/a	-3.4	31	27.05. - 31.07.	n/a	n/a	n/a
TT04	grassland	-6.3	20	04.06. - 24.07.	-2.6	9	29.05. - 15.07.	-1.5	9	05.07. - 27.08.
TT08	grassland	-7.5	37	25.05. - 27.07.	-3.5	18	17.06. - 31.07.	-3.8	31	02.06. - 25.07.
TT10	grassland	-4.7	16	04.06. - 26.07.	-0.7	3	12.07. - 14.07.	n/a	n/a	n/a
TT12	grassland	n/a	n/a	n/a	-3.0	28	29.05. - 07.08.	n/a	n/a	n/a
TT13	grassland	n/a	n/a	n/a	-3.7	39	27.05. - 07.08.	-3.2	21	06.07. - 05.09.
TT15	grassland	-6.8	34	25.05. - 24.07.	-2.3	7	29.05. - 14.07.	-0.8	2	05.07. - 06.07.
TT16	grassland	n/a	n/a	n/a	-3.0	24	25.05. - 31.07.	-1.6	16	08.06. - 04.09.
TT23	grassland	n/a	n/a	n/a	-3.6	44	29.05. - 10.09.	-3.1	22	08.07. - 05.09.
TT01	peatland	-4.7	19	05.06. - 26.07.	-2.0	9	10.06. - 21.07.	-1.5	10	13.07. - 03.09.
TT11	peatland	-4.8	21	08.06. - 08.08.	-2.8	44	27.05. - 07.08.	-1.8	15	07.06. 04.09.
TT17	peatland	n/a	n/a	n/a	-1.2	11	12.07. - 06.08.	n/a	n/a	n/a
TT22	peatland	n/a	n/a	n/a	-1.4	4	12.07. - 15.07.	-1.1	8	13.07. - 04.09.
	max/min	**-7.5**	**37**	**25.05. – 08.08.**	**-3.6**	**44**	**25.05. – 10.09.**	**-3.8**	**31**	**02.06. – 05.09.**

Table S2 Validation results for the two model types boosted regression trees (BRT) and randomforest (RF) on the three subsets of the predictor variables (a) remote sensing and topography 'RSTOPO' (b) only climate data derived from CRU and ARC2 'CLIMATE CRU/ARC2', (c) all data'ALL2' ('RS TOPO and 'CLIMATE CRU/ARC2'). The following performance measures were calculated: explained variance (expl. var. [%]), Pearson's correlation coefficient (rp) between observed and predicted values, coefficient of determination (R2), the root mean square error (RMSE, in species per 10^3 m^2) and the RMSE normalized by the mean, the relative root mean square error (rRMSE in per cent).The results for training and testing data are displayed (training 80% of the data and testing 20%).

		expl. var.	**correlation (r_p)**		**R^2**		**RMSE**		**rRMSE**	
		train	**train**	**test**	**train**	**test**	**train**	**test**	**train**	**test**
BRT	RS TOPO	54	0.78	0.69	0.61	0.48	10.1	11	30.2	31.9
	CLIMATE RU/ARC2	64	0.85	0.78	0.73	0.61	8.5	9.8	24.3	27.0
	ALL2	67	0.86	0.76	0.74	0.57	8.3	10.3	23.8	28.5
RF	RS TOPO	43	0.94	0.70	0.89	0.49	5.9	10.9	17.2	30.4
	CLIMATE RU/ARC2	50	0.93	0.79	0.87	0.62	5.9	9.6	17.0	26.4
	ALL2	54	0.95	0.78	0.90	0.61	5.5	9.7	15.8	26.8

Table S 3 Results of the GLMs for the effect of fire, distance to main road and the interaction of distance to road and country (Angola vs. Namibia) on three diversity indices: species richness (S), Shannon index (H'), and Shannon evenness (J'). Results are shown for four data (sub)sets: all species pooled, woody species, herbaceous species, and grass and sedge species. For the formula of the GLM see eq. (3). The intercepts and the slopes of the regression for the variable distance to road are given for each country separately. P-values <0.05 are marked with an asterisk "*" and p-values <0.01 with a dot "•".

		all species		trees and shrubs		forbs and herbs		grasses and sedges	
		estimate	p-value	estimate	p-value	estimate	p-value	estimate	p-value
S	Intercept Angola	2.436	*<0.001	2.028	*<0.001	1.048	*<0.001	1.024	*<0.001
	Slope Angola	0.030	0.139	0.017	0.477	0.027	0.544	0.026	0.354
	Intercept Namibia	2.179	0.131	1.795	0.256	1.929	* 0.023	0.878	0.532
	Slope Namibia	0.046	0.482	0.028	0.700	0.009	0.743	0.044	0.571
	Fire	-0.041	0.188	-0.020	0.592	-0.075	0.278	-0.073	• 0.092
H'	Intercept Angola	39.759	*<0.001	15.859	*<0.001	17.805	*<0.001	6.095	*<0.001
	Slope Angola	1.812	* 0.006	0.698	0.019	0.825	• 0.074	0.289	0.102
	Intercept Namibia	44.912	0.342	20.383	• 0.071	18.666	0.824	5.863	0.877
	Slope Namibia	0.322	• 0.056	-0.103	* 0.025	0.099	0.190	0.326	0.861
	Fire	-1.618	0.102	-0.443	0.324	-0.341	0.628	-0.835	* 0.003
J'	Intercept Angola	0.661	*<0.001	0.732	*<0.001	0.367	*<0.001	0.596	*<0.001
	Slope Angola	0.001	0.826	-0.003	0.655	0.003	0.813	-0.001	0.955
	Intercept Namibia	0.574	* 0.040	-0.591	* 0.019	0.684	* 0.007	0.509	0.452
	Slope Namibia	0.011	0.091	0.012	0.077	-0.001	0.780	0.009	0.562
	Fire	-0.004	0.633	-0.001	0.940	-0.018	0.373	0.007	0.726

Table S4 Variables on vegetation structure for each category showing the average (AVG) and standard deviation (SD). Cover according to vegetation strata; main height is the maximum height of the lowest 95 % of the vegetation; basal area shrubs = sum of BA of all stems with DBH < 5 cm, basal area trees = sum of BA of all stems with DBH > 5 cm; species richness given for all vascular plants and for trees with a DBH > 5 cm.

	Open woodland		Dense woodland		Short use/fallow		Medium use/fallow		Long use/fallow	
	AVG	SD	AVG	SD	AVG	SD	AVG	SD	AVG	SD
Total Cover (%)	61.0	11.4	96.6	2.3	87.0	2.7	79.0	10.8	86.6	7.6
0.0-0.5 m Cover (%)	41.0	9.6	43.0	6.7	67.0	24.9	47.2	14.5	68.0	22.5
1-2 m Cover (%)	21.6	9.1	64.0	13.4	62.0	13.0	48.0	13.5	43.0	18.6
2-5 m Cover (%)	18.0	9.1	73.0	8.4	35.4	23.8	51.0	7.4	32.2	19.1
5-10 m Cover (%)	15.2	7.6	28.0	10.4	4.0	6.2	10.6	4.4	10.2	5.7
10-20 m Cover (%)	5.8	6.4	10.8	5.4	0.0	0.0	0.0	0.0	0.4	0.9
Main Height (m)	9.5	3.2	11.7	1.1	4.6	0.5	5.5	0.4	4.4	2.7
Leaf Area Index	0.8	0.2	2.8	0.4	1.3	0.9	1.6	0.5	1.2	0.8
Soft litter Cover (%)	23.0	26.8	82.0	11.0	29.0	20.1	12.6	7.0	12.0	9.0
Mosses Cover (%)	0.0	0.0	1.4	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Lichens Cover (%)	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Basal Area shrubs (m^2/ha)	0.42	0.15	4.69	1.65	2.41	1.63	3.32	1.67	2.12	2.37
Basal Area trees (m^2/ha)	7.50	3.11	12.42	2.57	2.22	1.20	3.63	1.33	2.66	2.14
Species richness	50.2	3.8	48.6	2.9	50.6	4.1	50.4	5.5	46.0	5.8
Species richness (>5 cm DBH)	9.2	2.2	7.4	2.4	5.2	1.6	6.2	0.4	4.4	2.1
Grazing signs	Y		N		N		N		N	
Fire signs	Y		N		N		N		N	

Table S5 Average (AVG) and standard deviation (SD) values for the soil variables of the four soil depths and the five soil profiles for each category.

	Open woodland		Dense woodland		Short use/fallow		Medium use/fallow		Long use/fallow	
	AVG	SD	AVG	SD	AVG	SD	AVG	SD	AVG	SD
$CaCO_3$ content (g kg^{-1})	0.5	0.6	0.7	0.9	0.8	0.5	0.4	0.4	1.0	0.6
Clay content (%)	1.0	1.2	4.9	2.3	1.9	1.2	6.9	1.5	5.7	1.6
Silt content (%)	2.8	1.0	6.4	4.6	3.2	0.8	4.9	1.3	4.3	1.1
Sand content (%)	96.2	2.1	88.8	5.5	94.9	1.1	88.1	1.2	89.9	2.7
pH ($CaCl_2$)	4.4	0.1	4.3	0.1	4.7	0.5	4.8	0.5	4.8	0.6
Conductivity (µs cm^{-1})	7.3	1.8	17.0	9.0	13.2	1.7	15.0	2.5	15.0	2.7
Potassium (mg kg^{-1})	74.7	25.1	281.5	76.2	447.6	61.1	216.3	93.5	145.1	56.4
Sodium (mg kg^{-1})	22.3	2.6	28.1	11.0	35.0	6.6	30.3	15.0	20.5	1.8
Calcium (mg kg^{-1})	70.1	14.4	105.8	58.3	416.8	174.4	160.9	79.7	133.7	123.0
Magnesium (mg kg^{-1})	0.89	0.32	1.53	0.79	2.09	0.29	1.58	0.62	1.37	0.62
Phosphorus (mg kg^{-1})	0.32	0.09	0.29	0.21	0.46	0.43	0.31	0.15	0.19	0.12

Table S6 Calculation of fallow age and field duration with a satellite image time series. Source of Imagery given for Landsat, Google Earth and Rapid Eye; categories: S = short use/fallow, M = medium use/fallow, L = long use/fallow; values for land-use intensity: 0 = not used, 0.5 = partly used, 1 = used, E = stripes on the picture (error in Landsat sensor), C = clouds.

Plot	Category	Fallow ID	1984 LT51780721984166AAA03	1986 LT51780721986315AAA03	1987 LT51780721987030AAA03	1990 etp178r72_5t19900412	1993 LT51780721993158JSA00	1996 LT51780721996039JSA00	1997 LT51780721997233JSA00	1999 LE71780721999263EDC00	2000 LE71780722000186EDC00	2001 LE71780722001028EDC00	2002 elp178r072_7t20010808	2003 LE71780722003354ASN01	2004 LE71780722004117ASN02	2007 Google Inc.	2011 LT51780712011032JSA00	2012 LE71780722012155ASN00	2013 Rapid eye	years since cultivation	fallow age (years)	duration of cultivation (years)
24186	S	1	0	0	0	0	0	0.5	1	1	0	0	0	0	E	0	0	0	0	17.0	13	**4.0**
24188	S	2	0	0	0	0	0	0.5	1	1	0.5	0	0	0	E	0	0	0	0	17.0	12	**5.0**
24190	S	2																				
24184	S	3	0	0	0	0	0	0.5	1	1	0	0	0	C	E	0	0	0	0	17.0	13	**4.0**
24182	S	4	0	0	0	0	0	0	0.5	1	0.5	0	0	0	E	0	0	0	0	16.0	12	**4.0**
24176	M	12	0	0	0	0.5	0.5	0	1	1	0.5	0	0	E	0	0	0	0	0	23	13	**10.0**
24172	M	15	0	0	0	0.5	1	0.5	1	1	0.5	0	0	0	0	0	0	0	0	23.0	13	**10.0**
24170	M	16	0	0	0	0	1	0.5	1	0.5	0.5	0	0	0	E	0	0	0	0	20.0	13	**7.0**
24168	M	18	0	0	0	0.5	1	0.5	1	0.5	0.5	0	0	0	E	0	0	0	0	23.0	13	**10.0**
24180	M	20	0	0	0	0	0.5	0.5	0.5	1	0.5	0	0	E	E	0	0	E	0	20.0	13	**7.0**
24156	L	21	0	0.5	0.5	0.5	0.5	0	0.5	1	0.5	0	0	C	0	0	0	0	0	27.0	13	**14.0**
24158	L	22	0	0.5	0.5	1	1	1	1	1	1	0	0	0	E	0	0	E	0	27.0	13	**14.0**
24160	L	23	0	0.5	0.5	0.5	1	1	1	1	1	0	0	E	0	0	0	0	0	27.0	13	**14.0**
24164	L	24	0	0.5	0.5	1	1	1	1	1	1	0	0	E	0	0	0	0	0	27.0	13	**14.0**
24166	L	24																				

Table S7 Vegetation table showing the results of the indicator species analysis for open woodland, dense woodland and the three fallow categories short, medium and long usage. Life form (LF) is given for every species according to Raunkiaer: P = phanerophyte, Ch = chamaephyte, H = hemicryptophyte, Cr = cryptophyte, T = therophyte, brackets indicate uncertain categorization. *Phi* values are given for every species indicating the strength of a species' association to each category or combination of categories. The *phi* value ranges from -1 to 1, however, only significant *phi* values > 0.5 are shown and cells are left empty otherwise. In the case that a species is indicative for more than one category, the highest value is shown in bold. Frequency of occurrence ranges from 1 (low) to 5 (high) and is displayed in the column next to the *phi* values. FNR = field number.

Species name	**LF**	**Open**		**Dense**		**Short**		**Medium**		**Long**		**Dense + Short**		**Short + Medium**		**Short + Medium + Long**	
Tephrosia lupinifolia DC.	Ch	**1.000**	5														
Trachypogon spictatus (L.f.) Kuntze	H	**0.930**	5														
Ochna pulchra Hook.	P	**0.905**	5														
Dichapetalum rhodesicum Sprague & Hutch.	Ch	**0.898**	5														
Schizachyrium jeffreysii (Hack.) Stapf	H	**0.894**	5														
Chamaecrista sp.	(T)	**0.873**	4														
Cyperus margaritaceus Vahl	H	**0.873**	4														
Grewia falcistipula K.Schum.	P	**0.868**	5														
Diplorhynchus condylocarpon (Müll.-Arg.) Pichon	P	**0.843**	5														
Eragrostis cimicina Launert	(H)	**0.841**	5														
Erythrophleum africanum (Welw. ex Benth.) Harms	P	**0.831**	5														
Tristachya superba (De Not.) Schweinf. & Asch.	H	**0.818**	5														
Acrotome cf. *angustifolia*	T	**0.792**	5														
Asparagus sp. FNR 133172	Ch	**0.792**	5														
Combretum psidioides Welw.	P	**0.791**	5														

Species name	LF	Open		Dense		Short		Medium		Long		Dense + Short		Short + Medium		Short + Medium + Long	
Pseudolachnostylis maprouneifolia Pax	P	**0.791**	5														
Terminalia brachystemma Welw. ex Hiern	P	**0.765**	4														
Guibourtia coleosperma (Benth.) J. Léonard	P	**0.764**	5								1						1
Perotis leptopus Pilg.	T	**0.739**	3														
Dialium engleranum Welw. ex Baker	P	**0.730**	4														
Aristida stipitata Hack.	H	**0.724**	4				1		2				1		2		1
Combretum collinum Fresen.	P	**0.706**	5														
Tricalysia cocondensis Hiern	P	**0.706**	4														
Evolvulus alsinoides (L.) L.	Ch	**0.682**	5														
Commelina sp. FNR 136442	T	**0.671**	5														
Hymenocardia acida Tul.	P	**0.634**	4														
Xenostegia tridentata (L.) D.F.Austin & Staples	Ch	**0.632**	4								2						1
Clerodendrum ternatum Schinz	Ch	**0.624**	4				1						1		1		1
Digitaria eriantha Steud.	H	**0.621**	5														
Acrotome inflata Benth.	T	**0.620**	3														
Indigofera daleoides Benth. ex Harv.	Cr	**0.582**	5								2						1
Lannea gossweileri ssp. *gossweileri* Exell & Mendonça	Ch	**0.560**	3														
Baikiaea plurijuga Harms	P		3	**0.948**	5		4		4		4	0.557	5		4		4
Commiphora tenuipetiolata Engl.	P			**0.782**	5		4		3		1	0.528	5		4		3

Species name	**LF**	**Open**		**Dense**		**Short**		**Medium**		**Long**		**Dense + Short**		**Short + Medium**		**Short + Medium + Long**	
Erythrococca menyharthii (Pax) Prain	P			**0.769**	5		1		2			0.616	3		2		1
Asystasia gangetica (L.) T.Anderson	Ch		1	**0.739**	4		1		1		1		3		1		1
Alectra picta (Hiern) Hemsl.	T			**0.739**	3								2				
Apocynaceae sp. FNR 136422	Ch		4	**0.718**	4				3				2		2		1
Combretum celastroides Welw. ex M.A. Lawson	P			**0.708**	5		5		5		5	0.520	1		1		5
Climber FNR 136421	Ch			**0.651**	4								2				
Ocimum sp. FNR 136406	T			**0.624**	4				1				2		1		1
Commelina sp. FNR 136400	T			**0.620**	3								2				
Panicum maximum Jaq.	H			**0.615**	5		1		2		1		3		2		2
Creeper FNR 136404	Ch			**0.611**	4				1				2		1		1
Grewia flavescens Juss.	P			**0.605**	4		1		2				3		2		1
Croton gratissimus Burch.	P			**0.600**	5		5		5		5		1		1		5
Combretum engleri Schinz	P			**0.580**	5		5		5		5		1		1		5
Ipomoea dichroa Choisy	T			**0.576**	5		3		3		3		4		3		3
Hibiscus cf. *mastersianus* FNR 136278	T		2	**0.557**	5		4		5		5		5		5		5
Berchemia cf. *discolor* FNR 136423	P			**0.551**	4				1				2		1		1
Fabaceae sp. FNR 136412	P				4	**0.815**	5		4			0.584	5	0.549	5		3
Cyanotis foecunda Hassk.	T				5	**0.800**	5		5		4	0.710	1		1		5
Panicum sp. FNR 136397	(H)				3	**0.770**	5		5		2		4	0.541	1		4
Hermannia eenii Baker	Ch		1			**0.631**	3		1		1		2		2		2
Climber FNR 136408	Ch				4	**0.614**	4		3		1	0.546	4		4		3

Species name	**LF**	**Open**		**Dense**		**Short**		**Medium**		**Long**		**Dense + Short**		**Short + Medium**		**Short + Medium + Long**	
Ochna afzelii ssp. mechowiana R.Br. ex Oliv.	P				5	**0.586**	4		1		1		5		3		2
Malvaceae sp. FNR 136225	(Ch/T)					**0.540**	5		1				3		3		2
Justicia bracteata (Hochst.) Zarb	Ch		1		5		5	**0.754**	5		4		1		1		5
Clerodendrum uncinatum Schinz	Ch						1	**0.639**	4		1		1		3		2
Asteraceae sp. FNR 136391	(T)						3	**0.623**	4		1		2		4		3
Digitaria ciliaris (Retz.) Koeler	H						2			**0.655**	4		1		1		2
Chamaecrista biensis (Steyaert) Lock	(T/Ch)				1		1			**0.639**	4		1		1		2
Acanthosicyos naudinianus (Sond.) C.Jeffrey	Ch						2		5	**0.560**	5		1		4		4
Chamaecrista absus (L.) Irwin & Barneby	T		3						2	**0.533**	4				1		2
Lanzettblatt Fr. rot (Munkudi) 136374	P				3	0.558	5		4		2	**0.574**	4		5		4
Dichrostachys cinerea (L.)	P				1		5		5		3		3	**0.691**	1		5
Acacia ataxacantha DC.	P				5		5		5		4		1	**0.621**	1		5
Baphia massaiensis Taub.	P				5	0.501	5		5		5		1	**0.603**	1	0.601	5
Urochloa brachyura (Hack.) Stapf	T				3		5		5		5		4	**0.583**	1	0.568	5
Setaria pumila (Poir.) Roem. & Schult.	(T)		1		5		5		5		3		1	**0.552**	1		5
Eragrostis cylindriflora s.lat.	H						5	0.521	5		5		3	0.617	1	**0.648**	5
Grewia retinervis Burret	P				2		5		4		5		4		5	**0.577**	5

Table S8 Pearson correlation of the variables with the first three axes of the Principal Component Analysis. R values shown; Soil depths: H1 = 0–10 cm, H2 = 25–45 cm, H3 = 70–90 cm, H4 = 180–200 cm.

PCA name	Variable	Axis 1	Axis 2	Axis 3
TotalCov	Total Cover	0.278	0.645	0.103
0.0-0.5m	0.0-0.5 m Cover	-0.545	0.473	0.109
1-2m	1-2 m Cover	0.634	0.592	-0.128
2-5m	2-5 m Cover	0.832	0.126	-0.069
5-10m	5-10 m Cover	0.624	-0.377	0.016
10-20m	10-20 m Cover	0.431	-0.334	-0.121
MainHeig	Height of the lowest 95 %	0.510	-0.489	-0.241
FireCat	Fire category	0.716	0.325	-0.004
LAI130	Leaf Area Index 130 cm	0.912	0.130	-0.057
Woodlitt	Woody litter Cover	0.263	-0.252	-0.076
Softlitt	Soft litter Cover	0.690	0.000	-0.326
Moss	Mosses Cover	0.695	0.044	-0.180
Lichen	Lichen Cover	0.507	0.029	-0.257
Grazing	Grazing signs	-0.337	-0.823	-0.218
BA<5cm	Basal Area for DBH < 5cm	0.687	0.259	-0.120
BA>5cm	Basal Area for DBH > 5cm	0.627	-0.400	-0.198
ConductH1	Conductivity H1	0.519	0.216	0.013
LimeH1	Lime content H1	-0.177	-0.102	-0.062
ClayH1	Clay content H1	0.429	0.199	0.744
SiltH1	Silt content H1	-0.231	-0.034	0.373
SandH1	Sand content H1	-0.202	-0.131	-0.739
pHCaClH1	pH in $CaCl_2$ H1	-0.688	0.449	0.144
KH1	Potassium content H1	0.068	0.783	-0.487
NaH1	Sodium content H1	0.400	0.391	-0.159
CaH1	Calcium content H1	-0.501	0.602	-0.340
MgH1	Magnesium content H1	-0.010	0.524	-0.106
PH1	Phosphorus content H1	-0.116	0.219	-0.330
ALHH1	Aluminium hydride content H1	0.273	-0.400	-0.199
FluoriH1	Fluoride content H1	0.237	-0.056	-0.150
ChloriH1	Chloride content H1	0.189	-0.022	-0.494
NitratH1	Nitrate content H1	0.463	0.204	-0.309
SulphaH1	Sulphate content H1	-0.097	0.561	0.044
AmoniuH1	Ammonium content H1	0.261	0.383	0.351
ConductH2	Conductivity H2	0.326	0.436	0.290
LimeH2	Lime content H2	-0.174	0.195	-0.048
ClayH2	Clay content H2	0.522	0.035	0.467

PCA name	Variable	Axis 1	Axis 2	Axis 3
SiltH2	Silt content H2	0.149	0.168	0.379
SandH2	Sand content H2	-0.450	-0.103	-0.515
pHCaClH2	pH in CaCl2 H2	-0.679	0.513	0.169
KH2	Potassium content H2	0.381	0.611	-0.448
NaH2	Sodium content H2	0.196	0.439	-0.312
CaH2	Calcium content H2	-0.382	0.625	-0.198
MgH2	Magnesium content H2	0.036	0.741	-0.073
PH2	Phosphorus content H2	-0.381	0.255	-0.419
ALHH2	Aluminium hydride content H2	0.553	-0.262	-0.089
FluoriH2	Fluoride content H2	-0.034	-0.559	-0.155
ChloriH2	Chloride content H2	0.362	0.008	0.010
NitratH2	Nitrate content H2	0.431	-0.106	-0.427
SulphaH2	Sulphate content H2	-0.007	0.351	0.189
AmoniuH2	Ammonium content H2	0.281	-0.094	0.486
ConductH3	Conductivity H3	0.257	0.413	0.615
LimeH3	Lime content H3	-0.067	0.308	-0.108
ClayH3	Clay content H3	0.469	0.381	0.582
SiltH3	Silt content H3	0.629	0.214	0.154
SandH3	Sand content H3	-0.689	-0.354	-0.421
pHCaClH3	pH in CaCl2 H3	-0.674	0.362	0.175
KH3	Potassium content H3	0.307	0.687	-0.453
NaH3	Sodium content H3	0.271	0.158	-0.316
CaH3	Calcium content H3	-0.285	0.565	-0.225
MgH3	Magnesium content H3	-0.233	0.565	-0.468
PH3	Phosphorus content H3	-0.212	0.243	-0.255
ALHH3	Aluminium hydride content H3	0.467	-0.415	-0.350
FluoriH3	Fluoride content H3	0.138	-0.340	-0.493
ChloriH3	Chloride content H3	0.109	0.238	-0.037
NitratH3	Nitrate content H3	0.089	0.222	-0.599
SulphaH3	Sulphate content H3	-0.065	-0.020	0.464
AmoniuH3	Ammonium content H3	0.024	-0.270	0.255
ConductH4	Conductivity H4	0.036	0.308	0.434
LimeH4	Lime content H4	-0.201	0.109	0.083
ClayH4	Clay content H4	0.402	0.381	0.189
SiltH4	Silt content H4	0.544	0.263	0.190
SandH4	Sand content H4	-0.652	-0.408	-0.246
pHCaClH4	pH in CaCl2 H4	-0.553	0.327	0.268
KH4	Potassium content H4	0.089	0.788	-0.484

PCA name	Variable	Axis 1	Axis 2	Axis 3
NaH4	Sodium content H4	0.363	0.453	-0.252
CaH4	Calcium content H4	-0.344	0.626	-0.253
MgH4	Magnesium content H4	-0.418	0.439	-0.155
PH4	Phosphorus content H4	-0.589	0.082	-0.098
ALHH4	Aluminium hydride content H4	0.036	-0.083	0.314
FluoriH4	Fluoride content H4	0.113	-0.374	-0.467
ChloriH4	Chloride content H4	0.465	-0.025	-0.305
NitratH4	Nitrate content H4	0.051	0.099	-0.530
SulphaH4	Sulphate content H4	0.126	0.019	0.386
AmoniuH4	Ammonium content H4	-0.085	-0.286	0.377

Figure S1 Plot design used in the vegetation survey

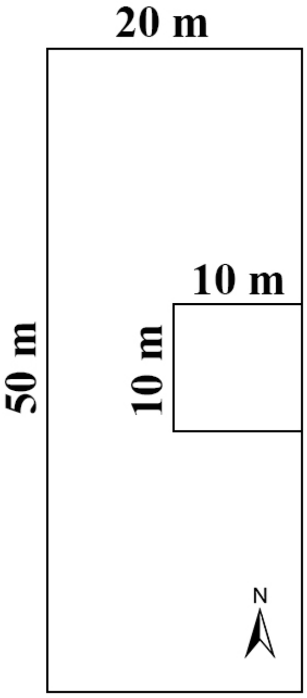


Figure S2 Geographic location of relevés of each plant community in the Cubango Basin.

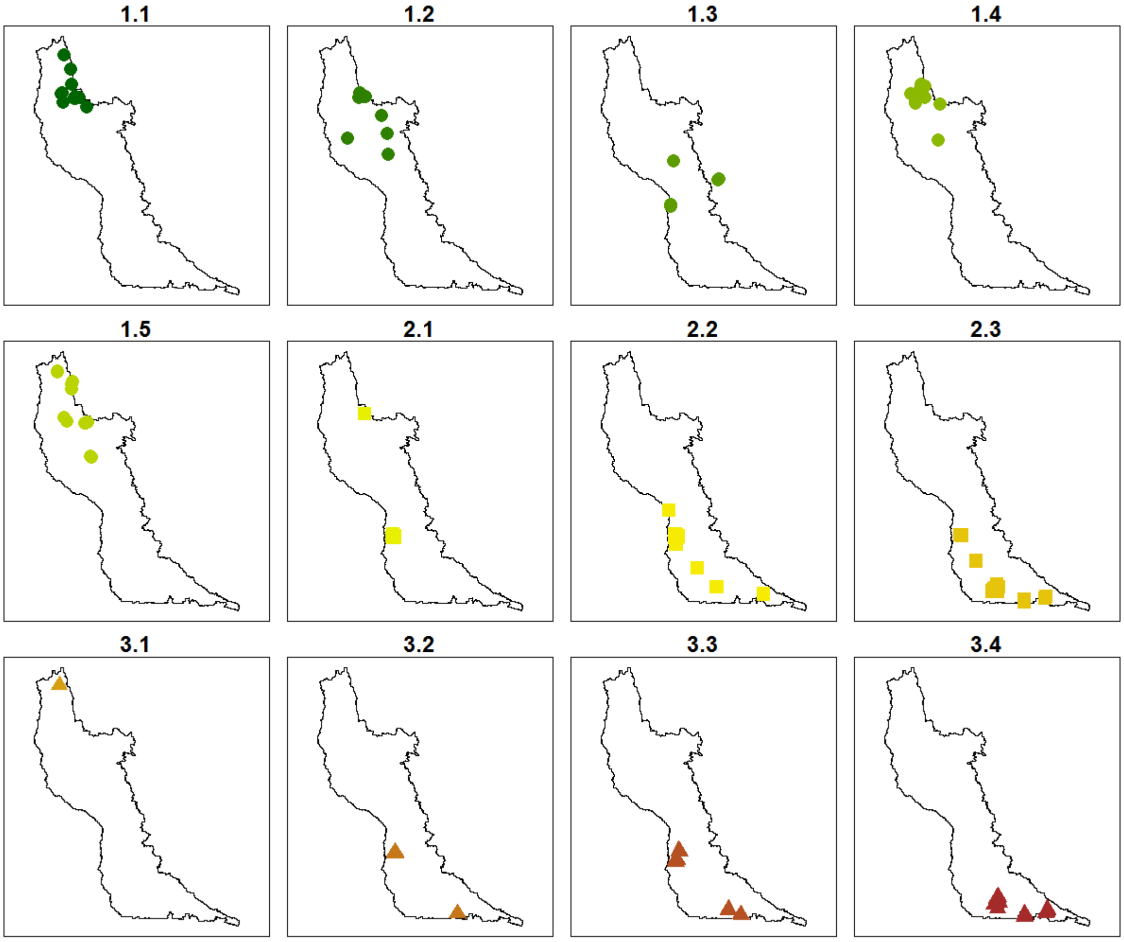


Figure S3 Comparison of the vegetation and environmental parameters of the derived vegetation communities. Differences among the vegetation communities are tested with an ANOVA and Tukey HSD post hoc test; group membership is indicated by letters. a) vegetation diversity and structure b) climate and land surface phenology c) soil 0-10 cm, d) soil 45-55 cm e) soil 70-90 cm.

Figure S3a

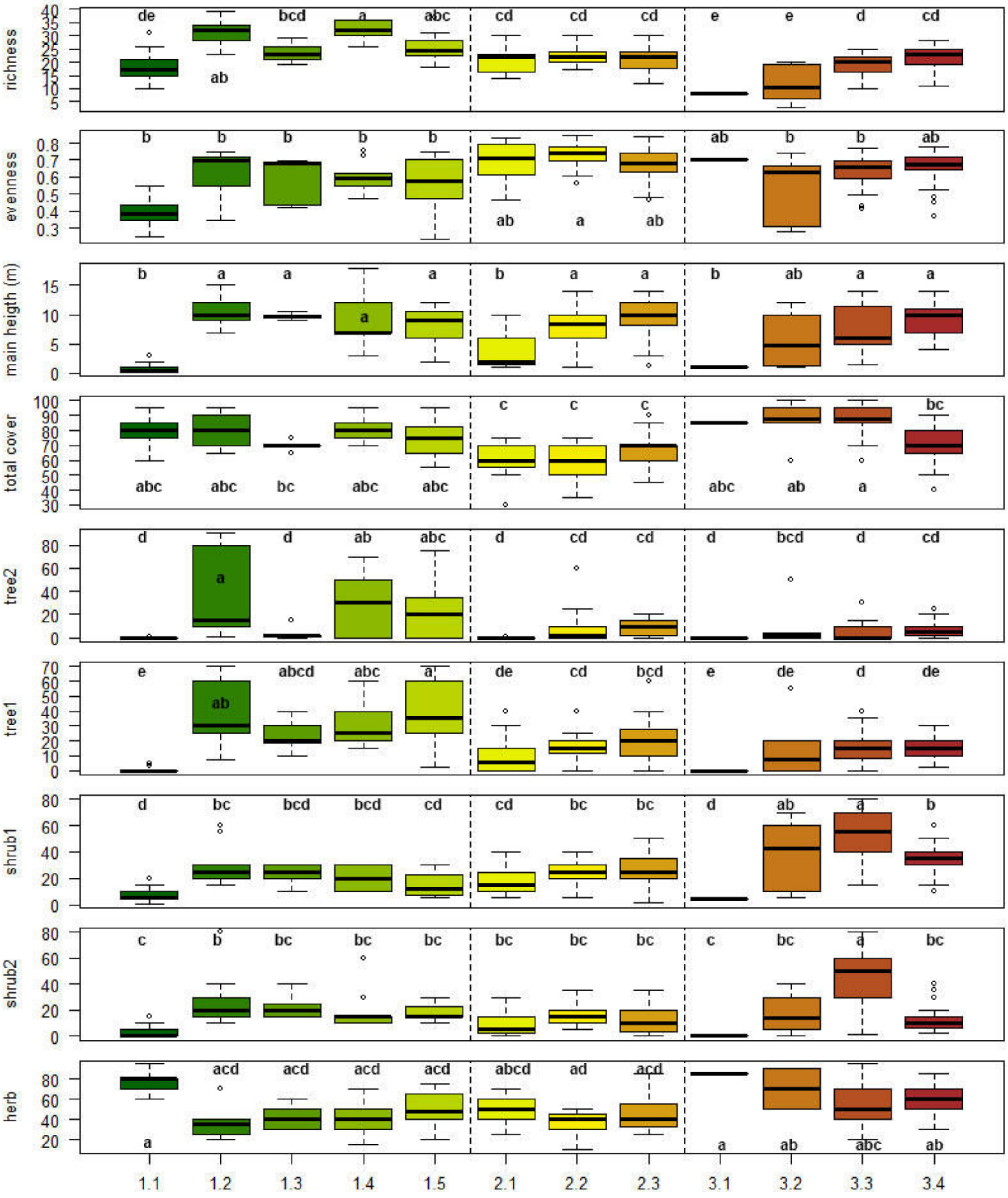


Figure S3b

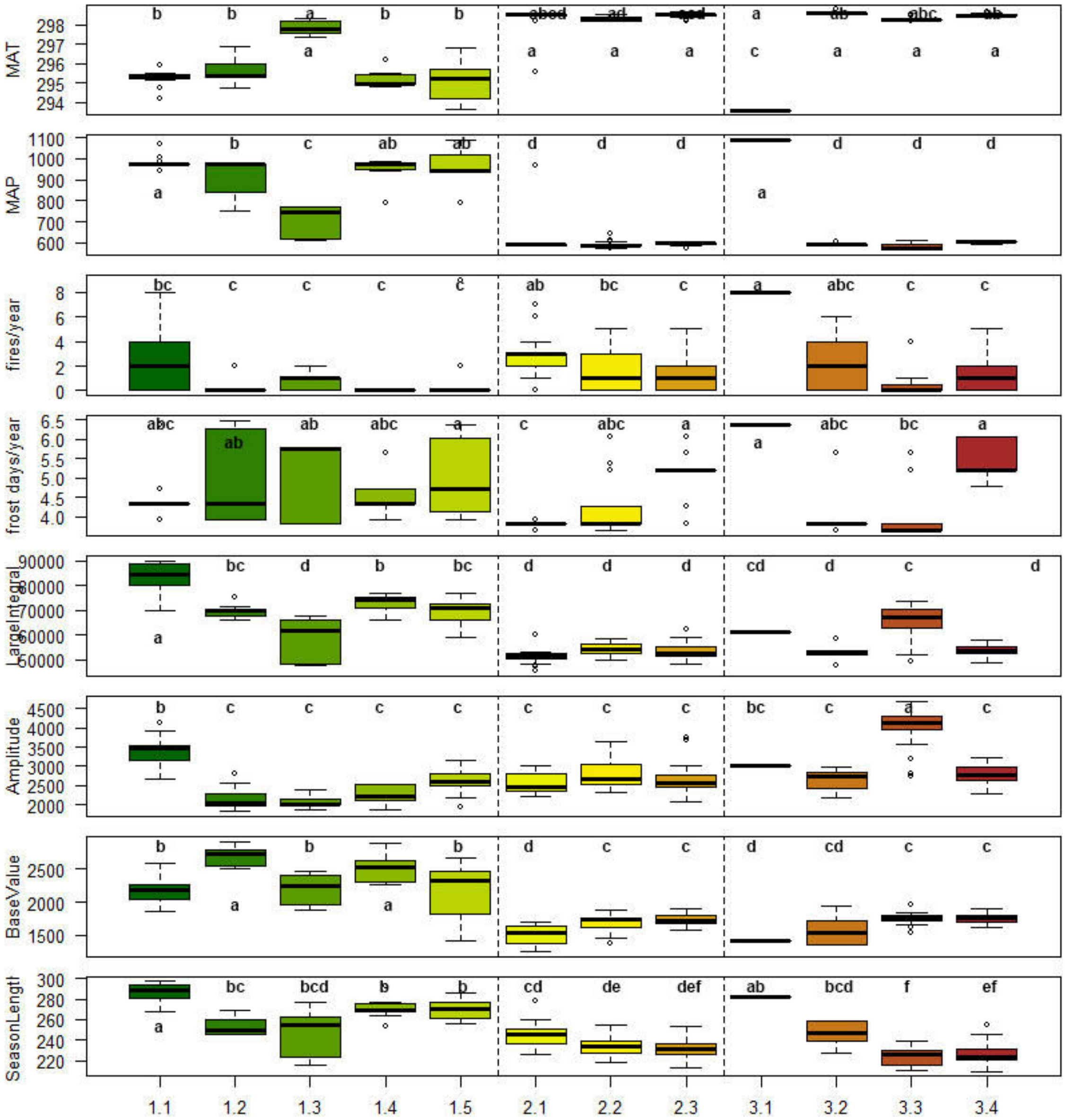

MAT
298
297
296
295
294
b b a b b abcd ad acd a ab abc ab
a a a a c a a a
MAP
1100
1000
900
800
700
600
b c ab ab d d d d d d
a a
fires/year
8
6
4
2
0
bc c c c c ab bc c a abc c c
frost days/year
6.5
6.0
5.5
5.0
4.5
4.0
abc ab ab abc a c abc a abc bc a
a
LargeIntegral
90000
80000
70000
60000
50000
bc d b bc d d d cd d c d
a
Amplitude
4500
4000
3500
3000
2500
2000
b c c c c c c c bc c a c
BaseValue
2500
2000
1500
b b b b d c c d cd c c
a a
SeasonLength
300
280
260
240
220
bc bcd b b cd de def ab bcd f ef
a
1.1
1.2
1.3
1.4
1.5
2.1
2.2
2.3
3.1
3.2
3.3
3.4

Figure S3c)

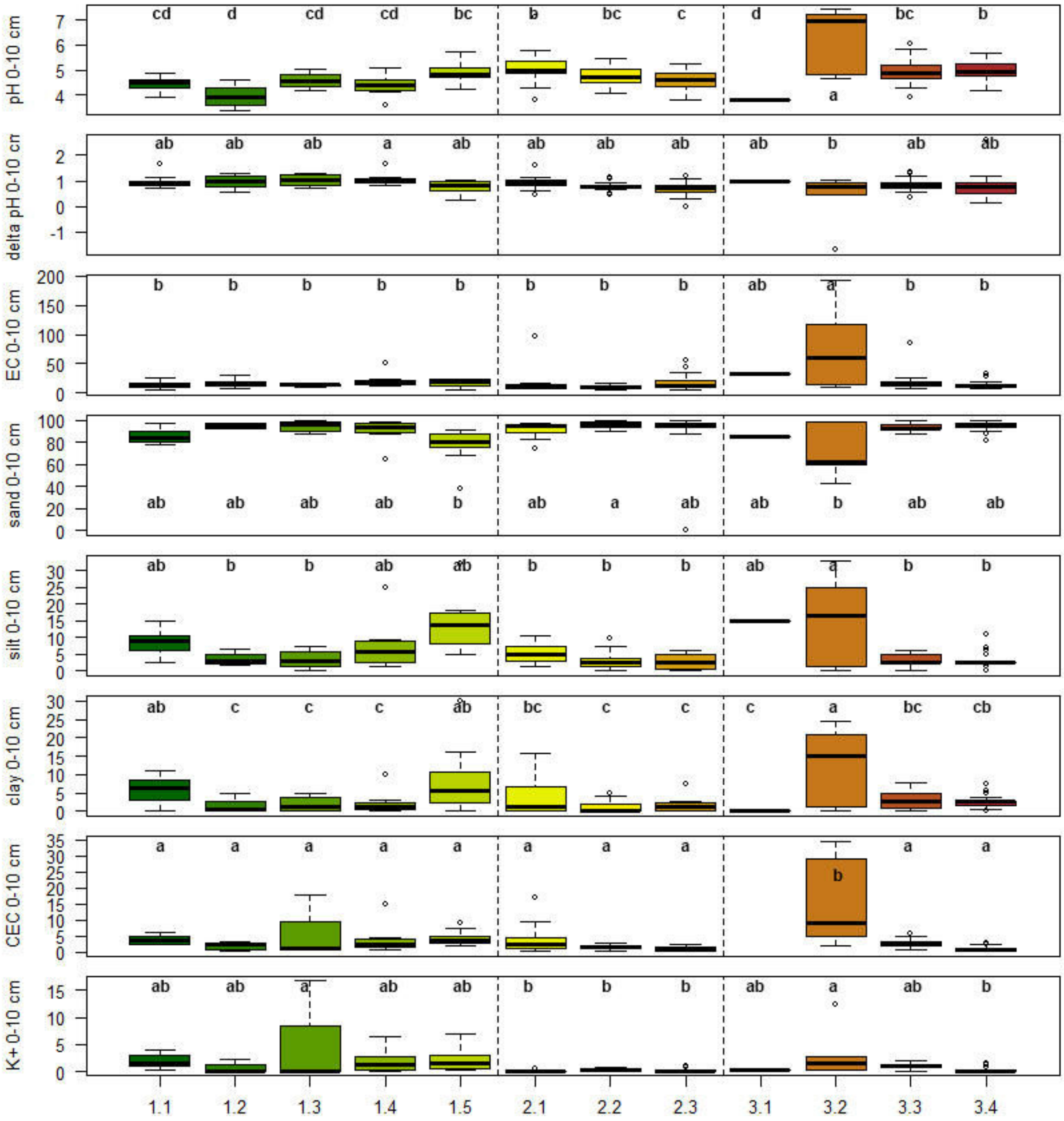

pH 0-10 cm
4
5
6
7
cd d cd cd bc b bc c d bc b
a
delta pH 0-10 cm
-1
0
1
2
ab ab ab a ab ab ab ab ab b ab ab
EC 0-10 cm
0
50
100
150
200
b b b b b b b b ab a b b
sand 0-10 cm
0
20
40
60
80
100
ab ab ab ab b ab a ab ab b ab ab
silt 0-10 cm
0
5
10
15
20
25
30
ab b b ab ab b b b ab a b b
clay 0-10 cm
0
5
10
15
20
25
30
ab c c c ab bc c c c a bc cb
CEC 0-10 cm
0
5
10
15
20
25
30
35
a a a a a a a a b a a
K+ 0-10 cm
0
5
10
15
ab ab a ab ab b b b ab a ab b
1.1
1.2
1.3
1.4
1.5
2.1
2.2
2.3
3.1
3.2
3.3
3.4

Figure S3d

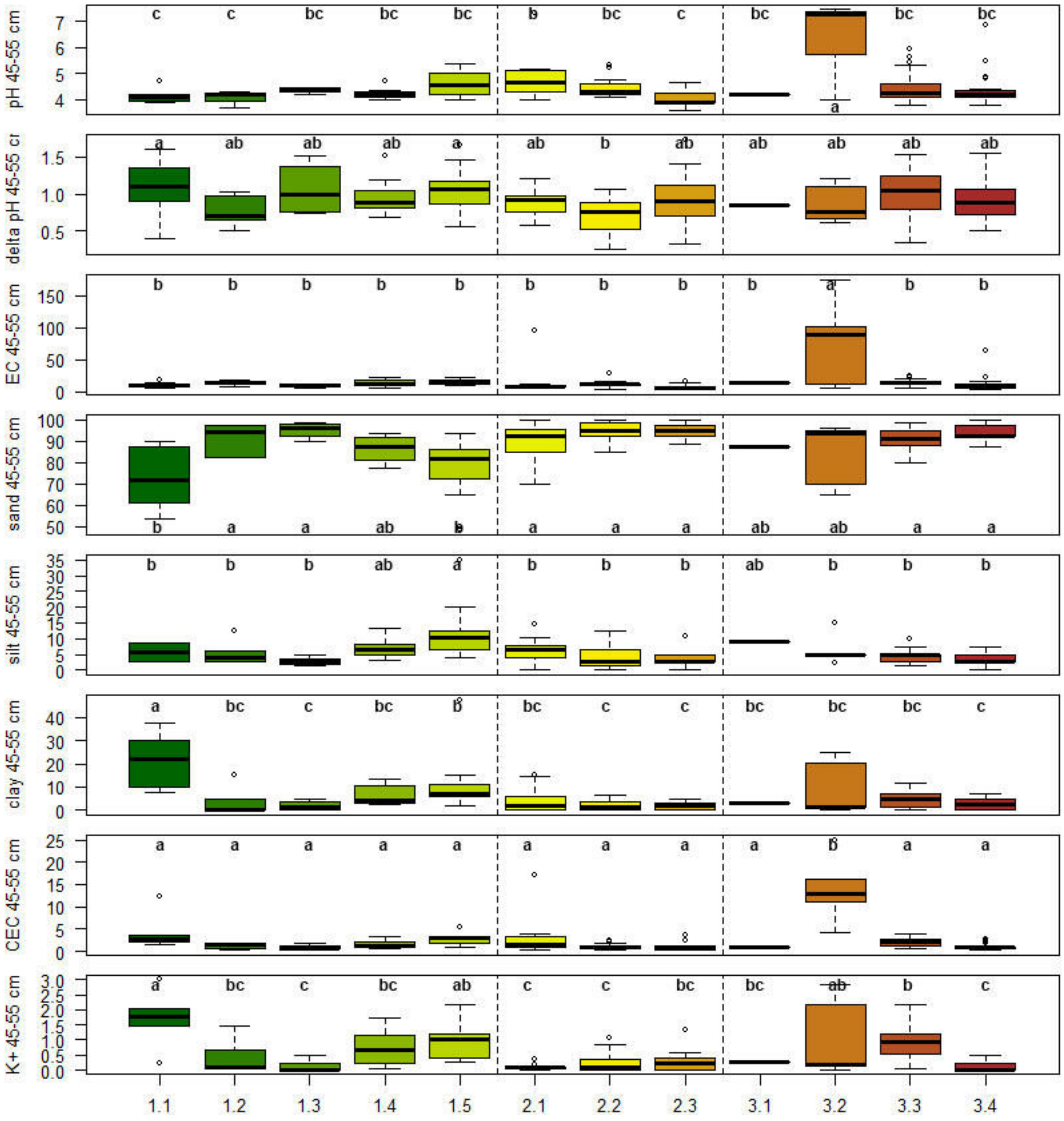

pH 45-55 cm
4
5
6
7
c c bc bc bc b bc c bc a bc bc
delta pH 45-55 cm
0.5
1.0
1.5
a ab ab ab a ab b ab ab ab ab ab
EC 45-55 cm
0
50
100
150
b b b b b b b b b a b b
sand 45-55 cm
50
60
70
80
90
100
b a a ab b a a a ab ab a a
silt 45-55 cm
0
5
10
15
20
25
30
35
b b b ab a b b b ab b b b
clay 45-55 cm
0
10
20
30
40
a bc c bc b bc c c bc bc bc c
CEC 45-55 cm
0
5
10
15
20
25
a a a a a a a a a b a a
K+ 45-55 cm
0.0
0.5
1.0
1.5
2.0
2.5
3.0
a bc c bc ab c c bc bc ab b c
1.1
1.2
1.3
1.4
1.5
2.1
2.2
2.3
3.1
3.2
3.3
3.4

Figure S3e

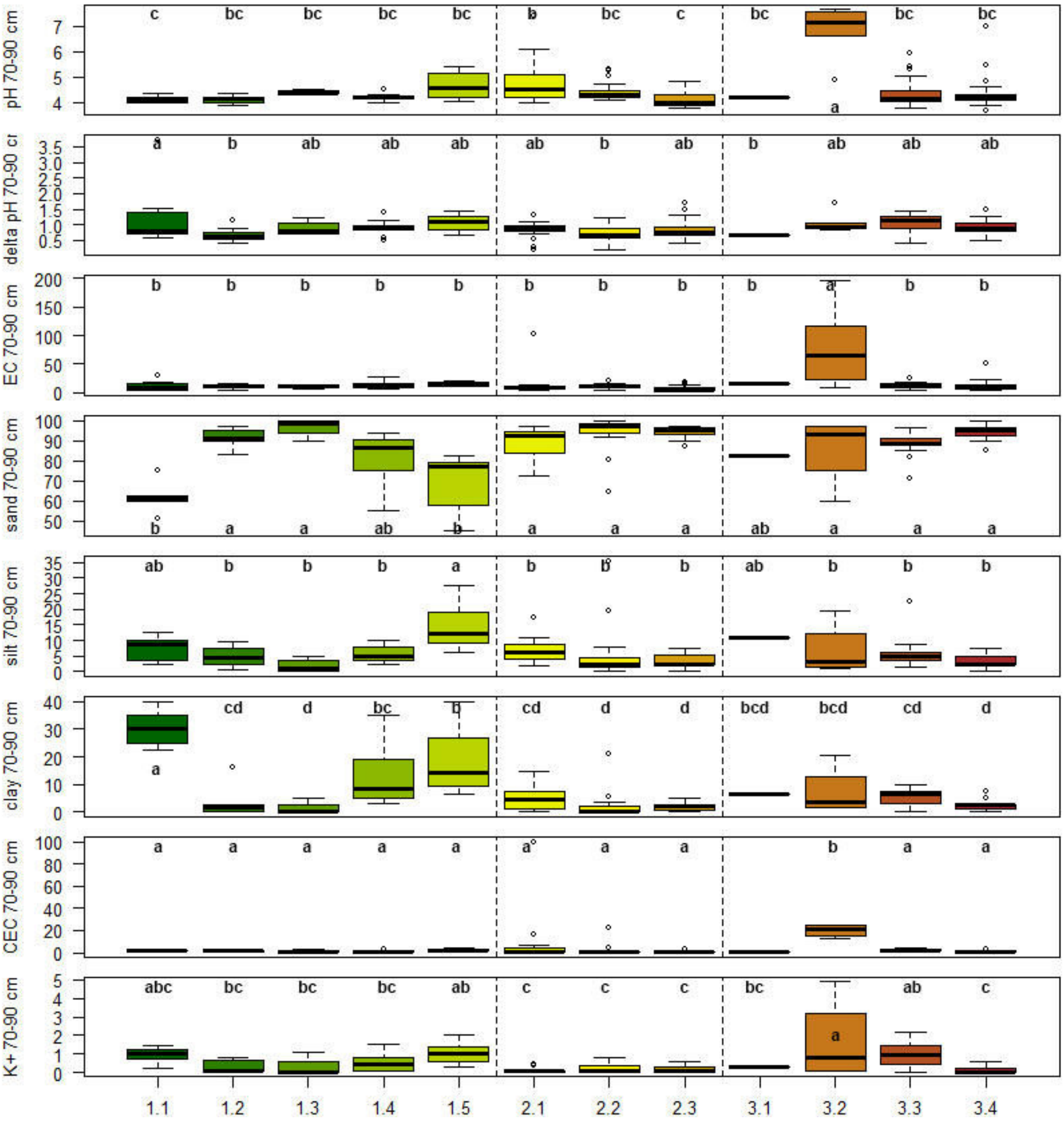

pH 70-90 cm
4 5 6 7
c bc bc bc bc b bc c bc a bc bc
delta pH 70-90 cı
0.5 1.0 1.5 2.0 2.5 3.0 3.5
a b ab ab ab ab b ab b ab ab ab
EC 70-90 cm
0 50 100 150 200
b b b b b b b b b a b b
sand 70-90 cm
50 60 70 80 90 100
b a a ab b a a a ab a a a
silt 70-90 cm
0 5 10 15 20 25 30 35
ab b b b a b b b ab b b b
clay 70-90 cm
0 10 20 30 40
a cd d bc b cd d d bcd bcd cd d
CEC 70-90 cm
0 20 40 60 80 100
a a a a a a a a b a a
K+ 70-90 cm
0 1 2 3 4 5
abc bc bc bc ab c c c bc a ab c
1.1 1.2 1.3 1.4 1.5 2.1 2.2 2.3 3.1 3.2 3.3 3.4

Figure S4 Canonical Correspondence Analysis (CCA) of vegetation data and soil properties for the communities of the *Baikiaea* woodlands without the community of the edaphic grassland 3.1 and the floodplain plant community 3.2.

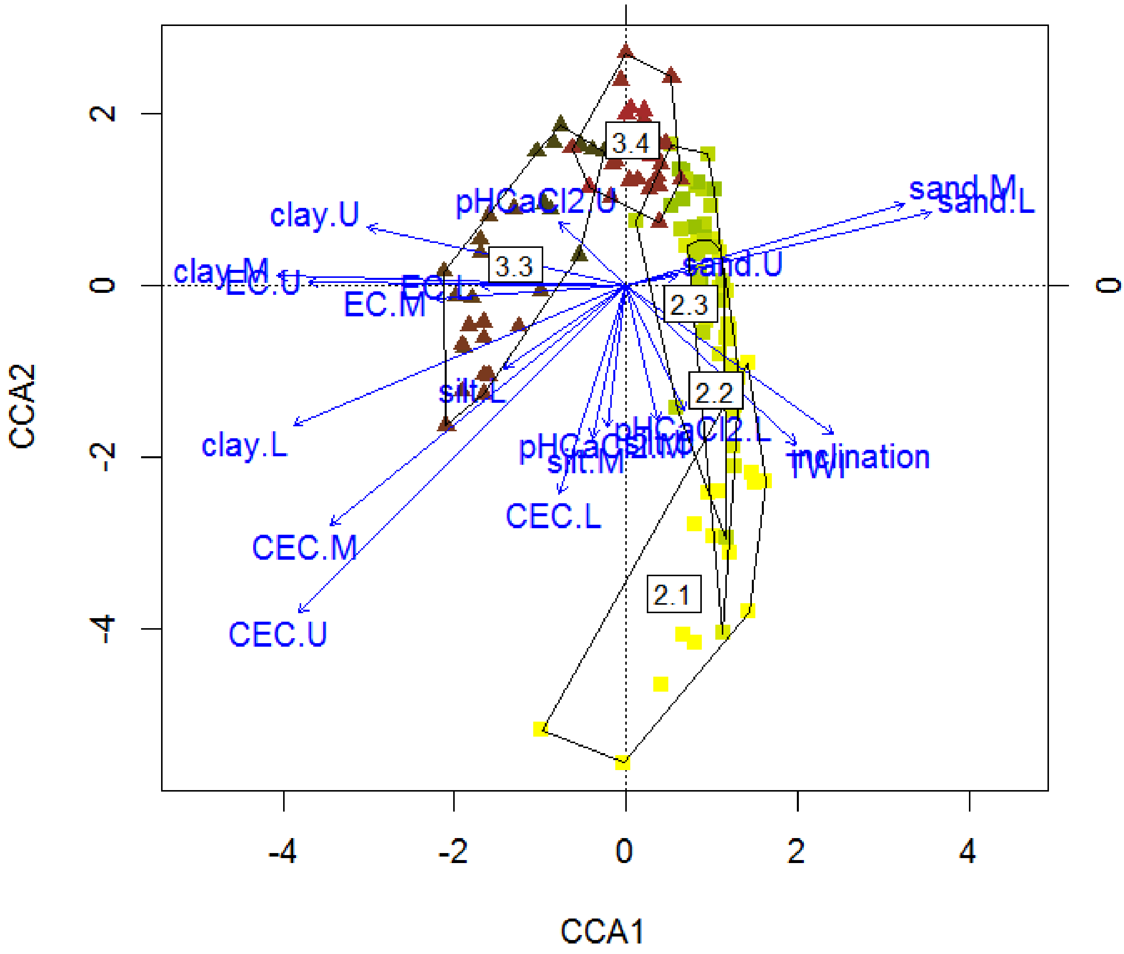


Figure S5 Cross section of the Sovi Valley (A–B, C–D, E–F) and the Cusseque Valley (G–H) indicating forest (green), geoxylic grassland (yellow), peat and wetlands (blue). The dashed lines show the lower tree line and reflects the increasing volume of cold air masses accumulating valley downwards. The *y*-axis indicates the elevation in meters above sea level (meters above sea level).

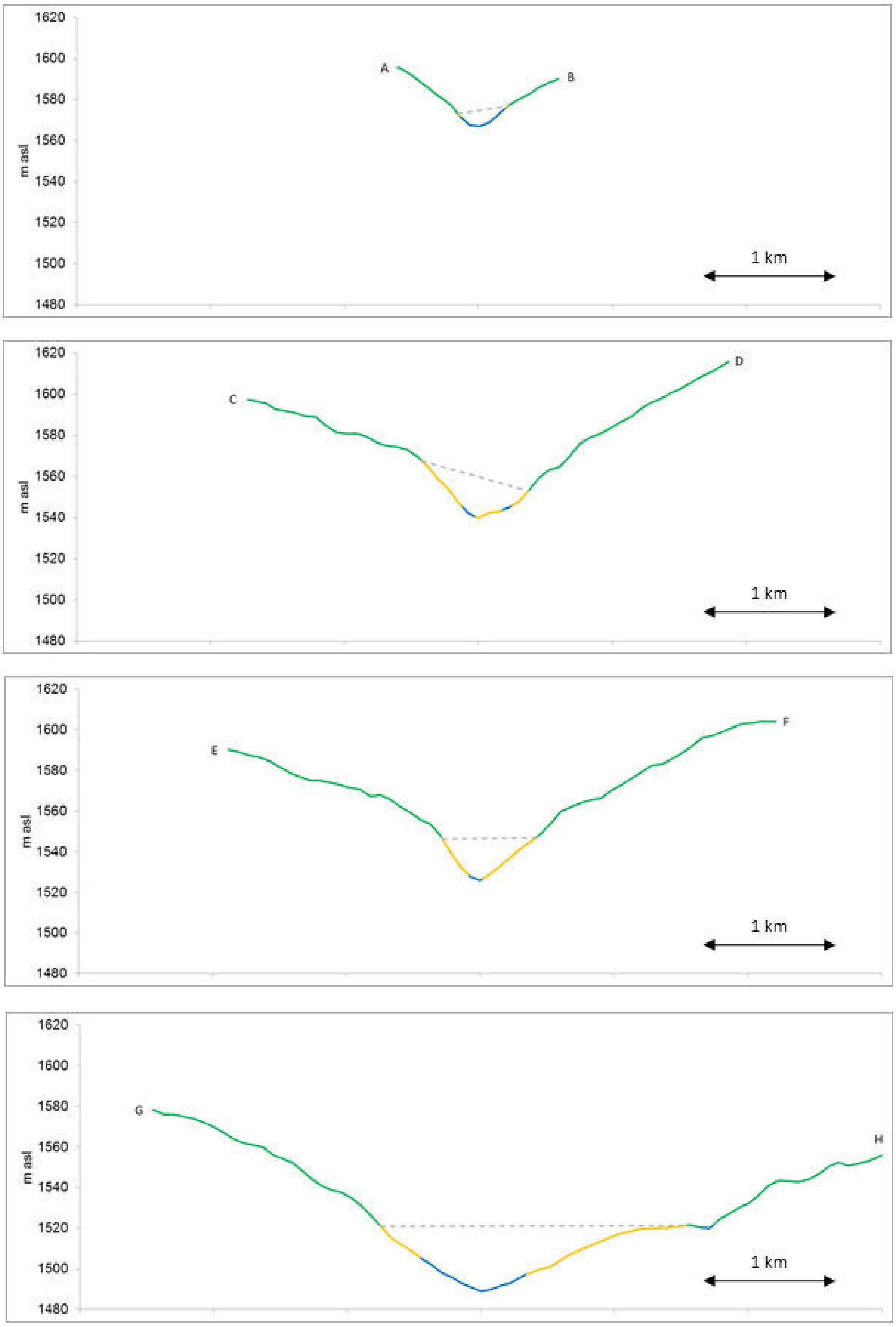


Figure S6 Observed values of alpha diversity plotted against predicted values on training data for (a) BRT on data set 'RS TOPO'; (b) RF on data set 'RS TOPO'; (c) BRT on data set 'CLIMATE'; (d) RF on data set 'CLIMATE'; (e) BRT on data set 'ALL'; (f) RF on data set 'ALL'.

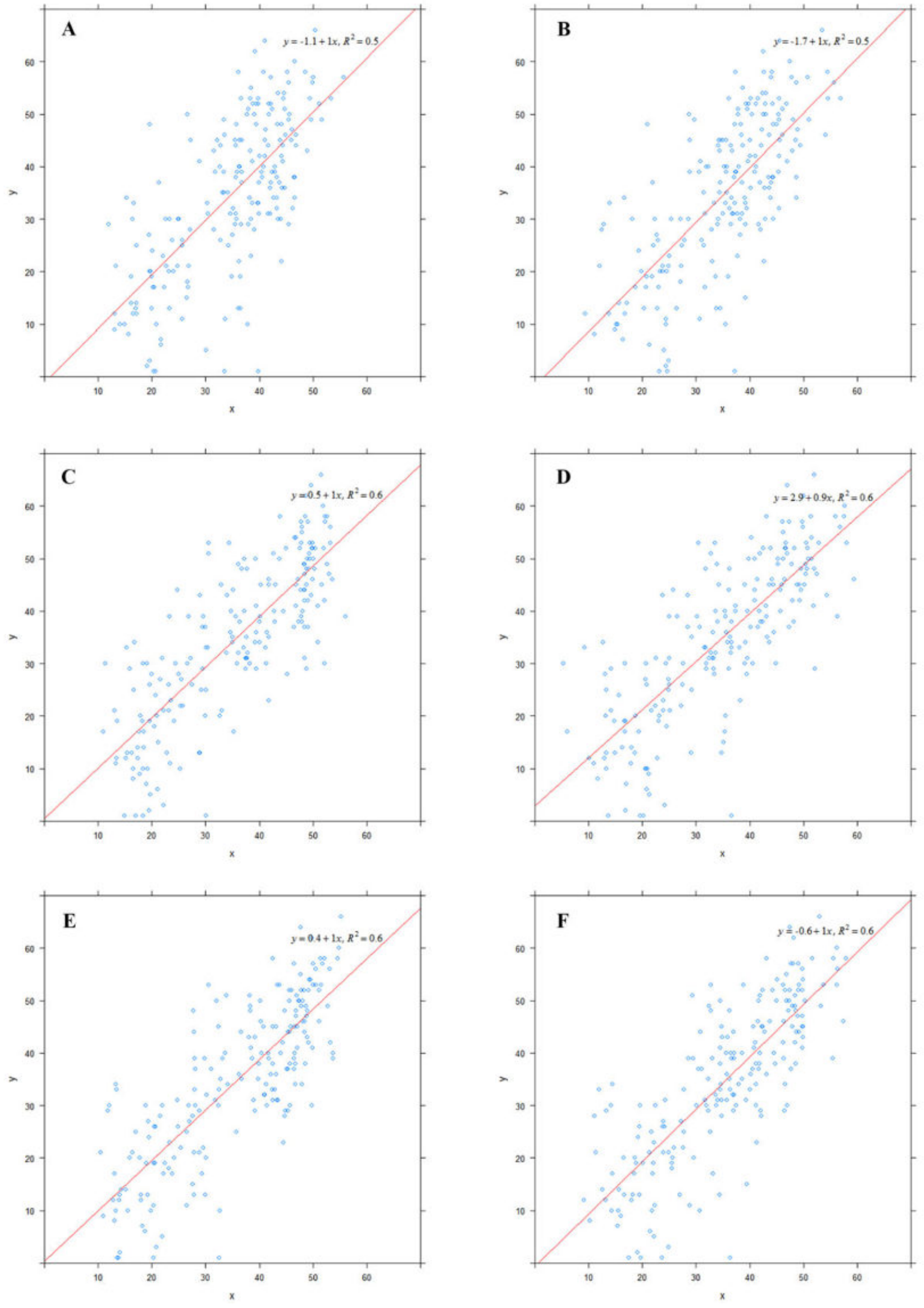


Figure S7 Observed plant alpha diversity (species density per 10^3 m^2). Data is based on 999 vegetation plots sized 20 x 50 m.

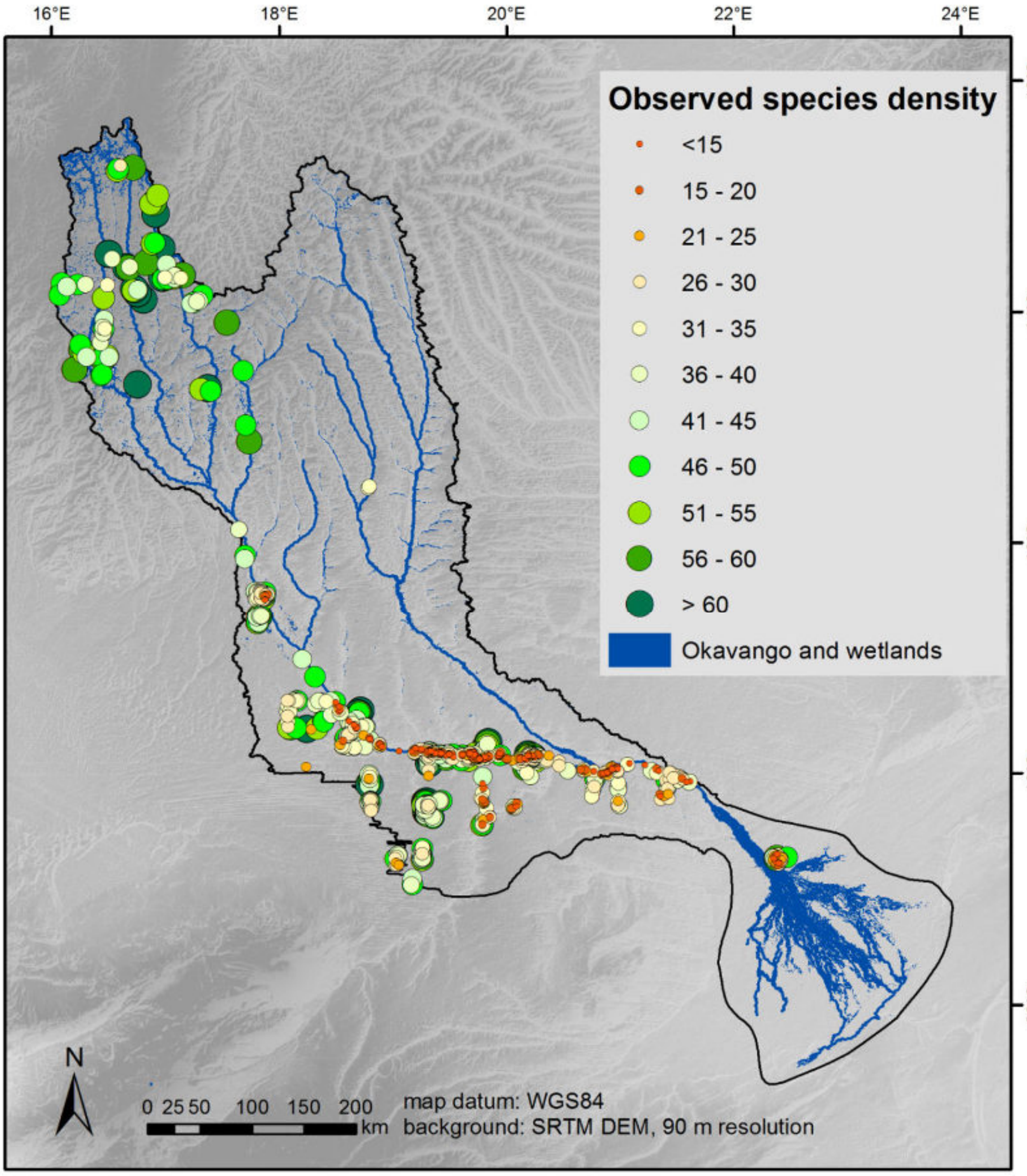


Figure S8 Model residual for the two model types: boosted regression trees (a,c,e) and random forest (b,d,e) on the three datasets: 'RS TOPO' (a,b); 'CLIMATE' (c,d); 'ALL'; (g,h). Furthermore, we calculated variograms to check for spatial autocorrelation but no sever spatial auto correlation was detected.

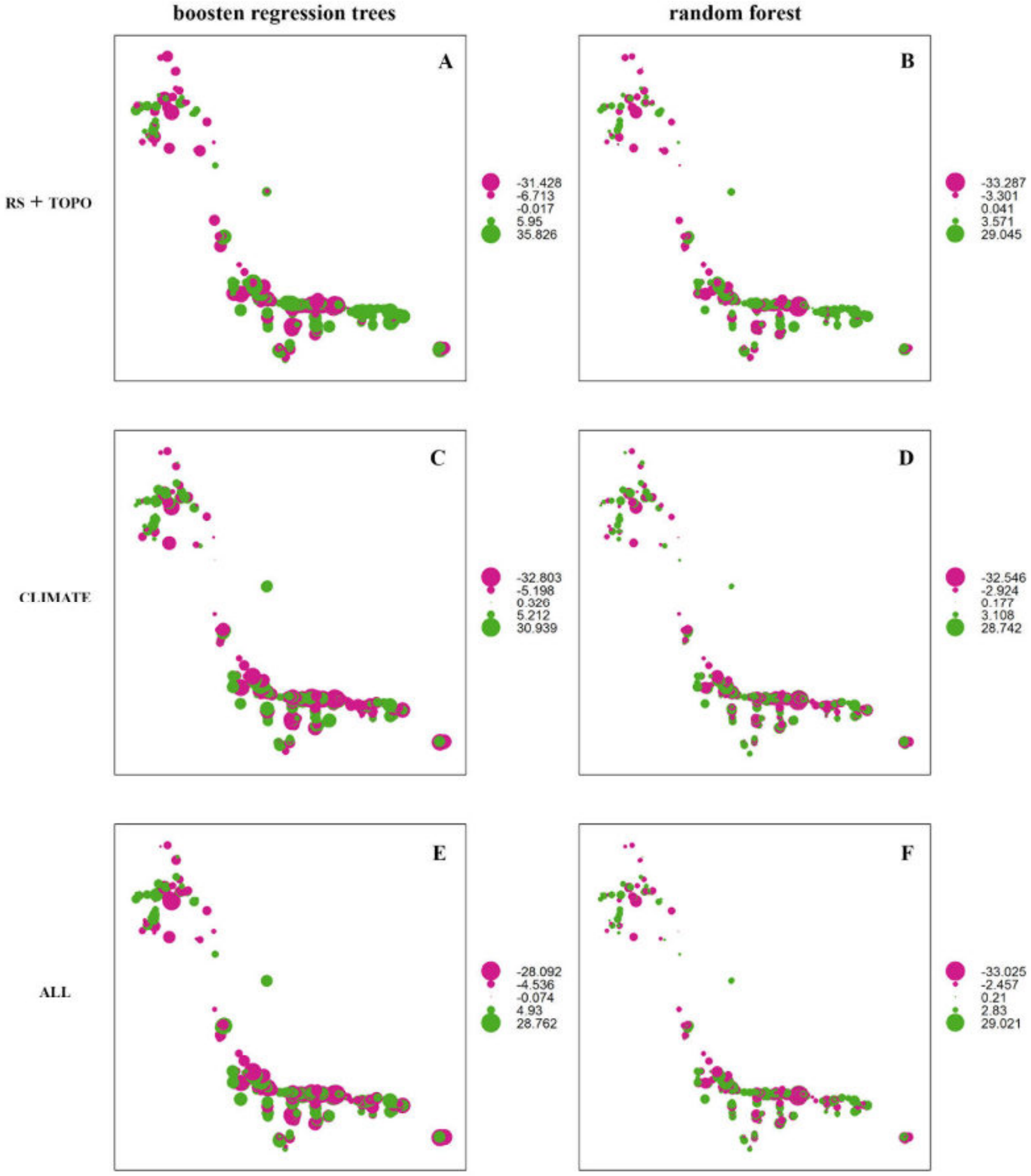
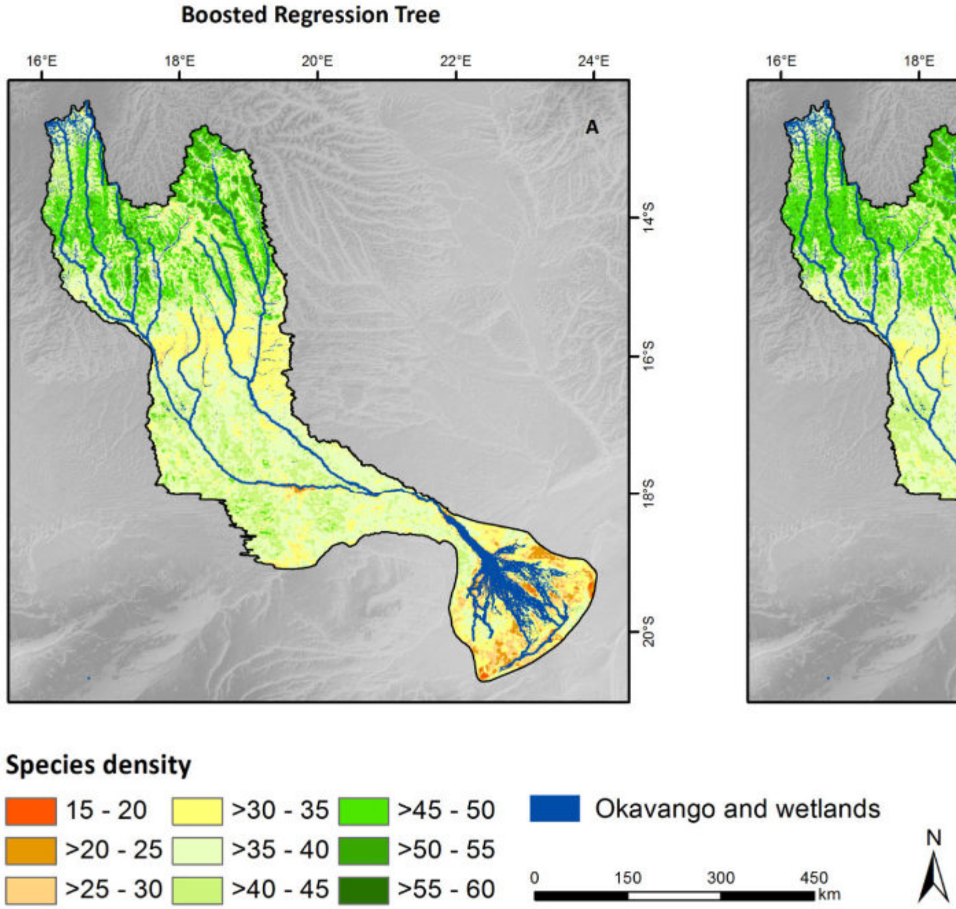
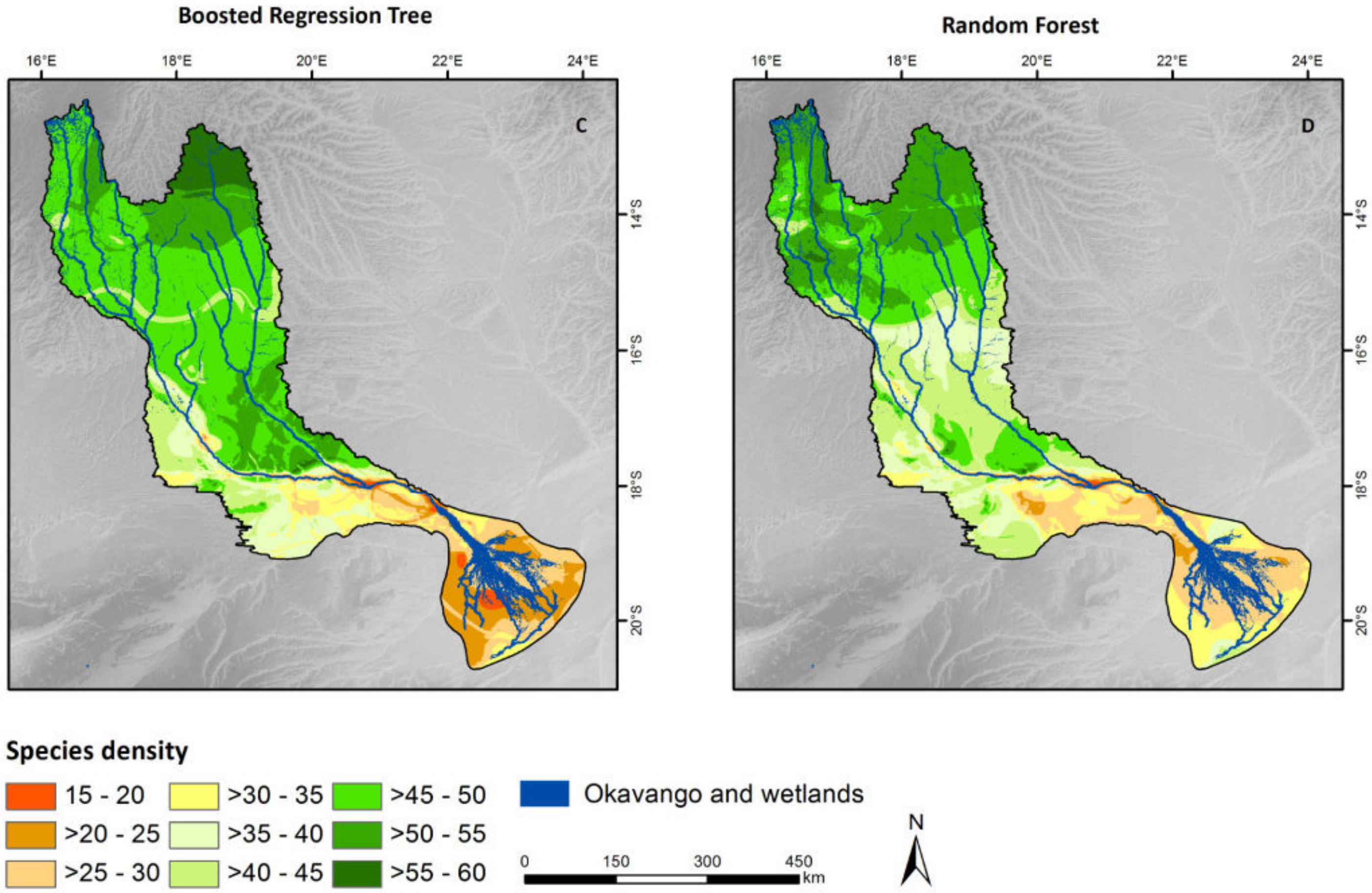


Figure S9 Plant alpha diversity (species density per 10^3 m2) predicted by the two model types: BRT (a,c,e) and random forest (b,d,f) on the three data (sub-)sets: 'RS TOPO' (a,b); 'CLIMATE' (d,e); 'ALL' (e,f).



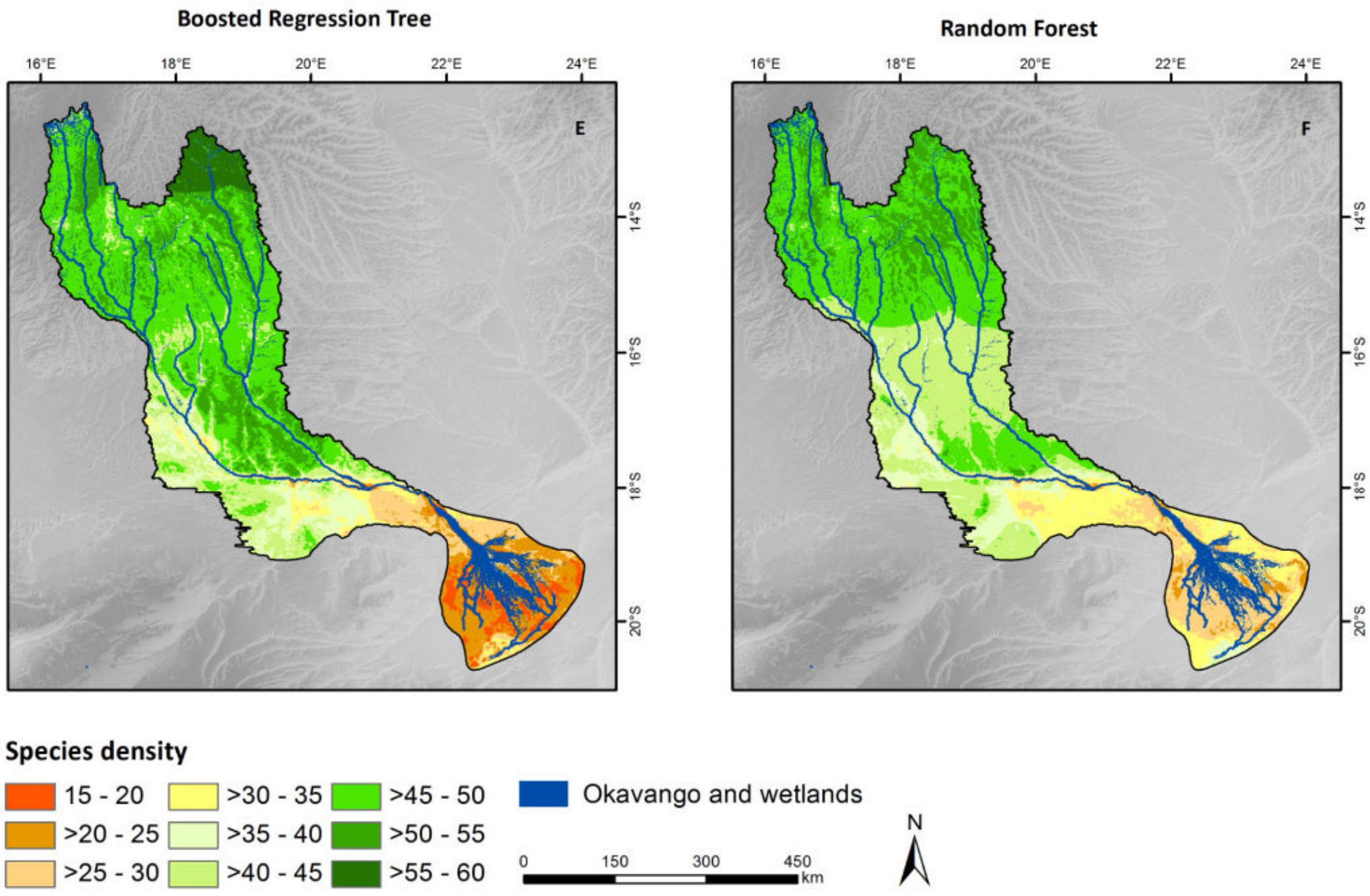
data set: RS + TOPO
map datum: WGS84; background: digital elevation model SRTM, 90 m resolution

Figure S9continued



data set: CLIMATE
map datum: WGS84; background: digital elevation model SRTM, 90 m resolution

Figure S9 continued



data set: ALL
map datum: WGS84; background: digital elevation model SRTM, 90 m resolution

Figure S10 Partial dependence plots of the LSP metrics 'Amplitude' (a,d), 'BaseValue' (b,e), 'LargeIntegral' (c,f) for the two model types BRT (a–c) and RF (d–f).

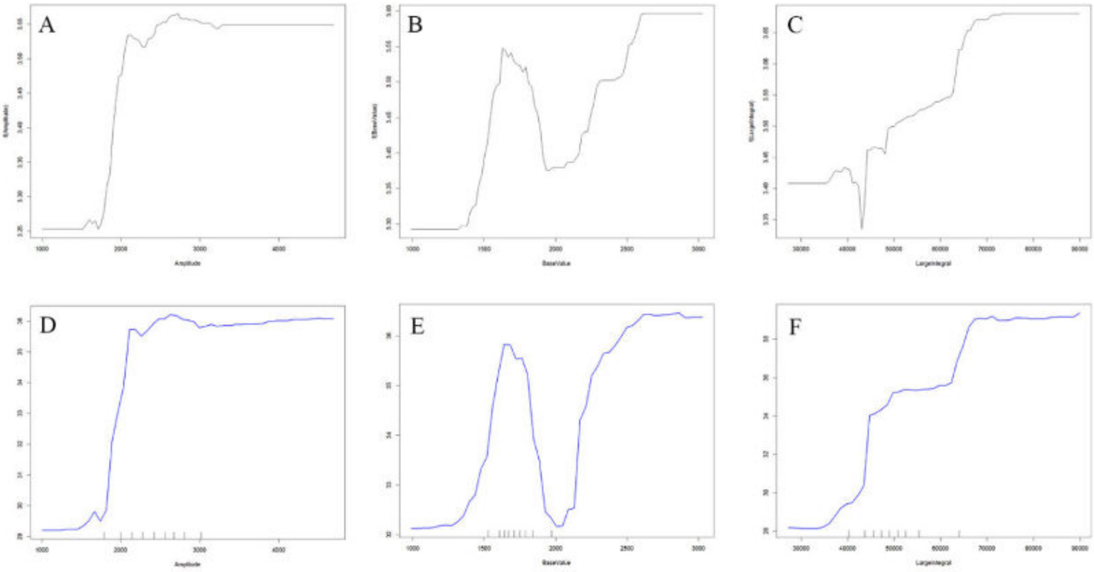
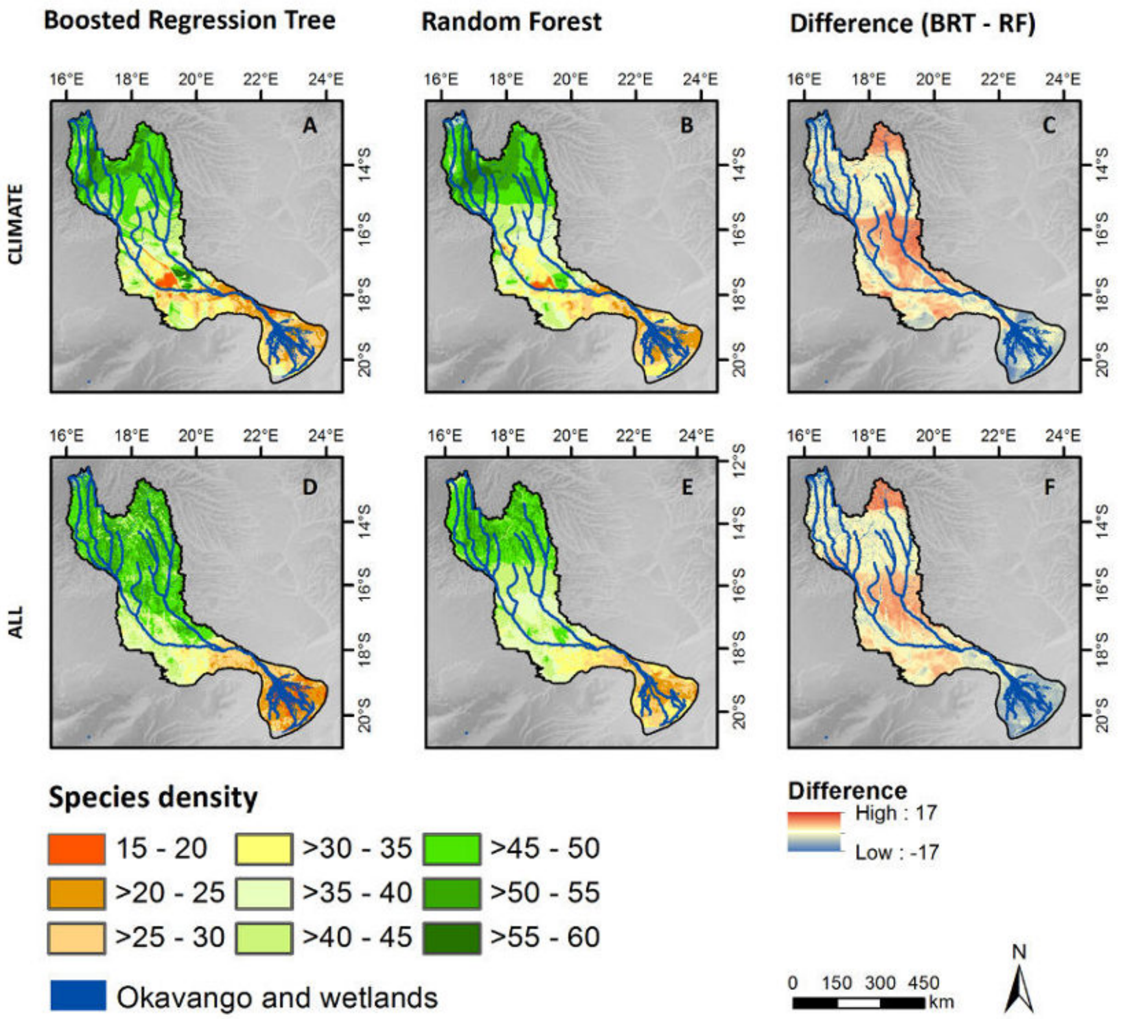
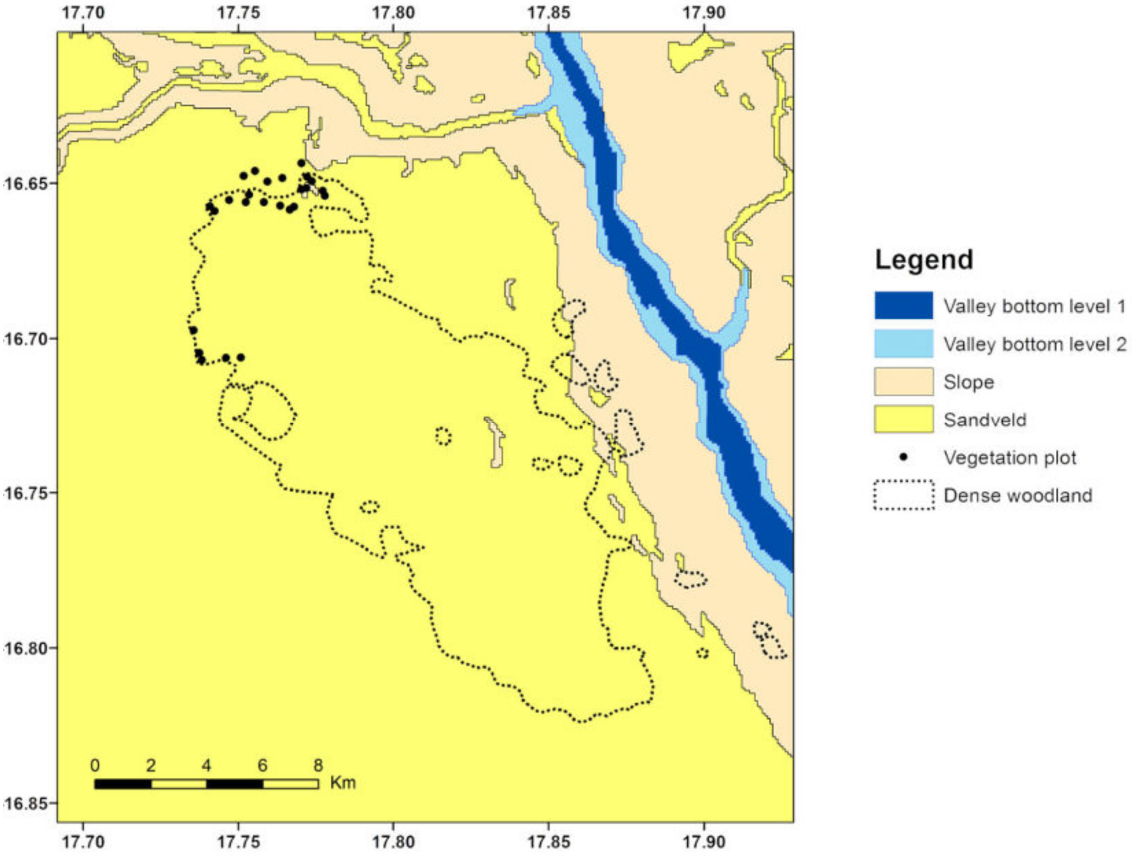


Figure S11 Plant alpha diversity (species density per 10^3 m^2) predicted by the two model types: BRT (a and d) and random forest (b and e) on the second climate data set CRU/ARC2 (a, b); and on the entire data set comprising the second climate data set CRU/ARC2 and remote sensing data (d and e) and the difference between the two model algorithms (c and f).



map datum: WGS84; background: digital elevation model SRTM, 90 m resolution

Figure S12 Geomorphological landscape units derived from the global digital elevation model SRTM (Shuttle Radar Topography Mission, USGS 2004) following the automated classification of topography developed by Iwahashi & Pike (2007). Classification was done by Jan Wehberg; Grid cell of 90 m; Units: decimal degrees; Map datum: WGS84. 'Valley bottom level 1' denotes the current river bed of the Cubango River, 'Valley bottom level 2' the floodplain, 'Slope' the area showing a gentle slope towards the stream network, and 'Sandveld' the sandy plain of the hinterland with only very subtle differences in terrain.



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, den 30.06.2016

(Rasmus Revermann)