

Flora_{et} Vegetatio Sudano-Sambesica



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Flora et Vegetatio Sudano-Sambesica (former "Etudes sur la flore et la végétation du Burkina Faso et des pays avoisinants") is a refereed, international journal aimed at presenting high quality papers dealing with all fields of geobotany and ethnobotany of the Sudano-Sambesian zone and adjacent regions. The journal welcomes fundamental and applied research articles as well as review papers and short communications.

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Biota of the WAP complex – starting a citizen science project for West Africa’s largest complex of protected areas

Received: 2016-11-14; accepted: 2016-11-19

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Summary: To improve data availability and exchange in the area of the WAP complex, West Africa’s largest continuous area of reserves, we set up a citizen science project on the iNaturalist platform, allowing contribution of observations, ideally documented by photographs and/or sounds. Along with the project we created a number of online field guides for the local flora. Within only two months, 852 observations of 312 species have been assembled. We expect this dataset to further grow in the future and complement existing data sets from scientific collections and surveys.

Key words: WAP complex, citizen science, observation data, digital photos

BIOTA OF THE WAP COMPLEX - DÉMARRAGE D’UN PROJET DE SCIENCE CITOYENNE POUR LE PLUS GRAND COMPLEXE D’AIRES PROTÉGÉES EN AFRIQUE DE L’OUEST

Résumé: Afin d’améliorer la disponibilité et l’échange de données dans le domaine du complexe WAP, le plus grand complexe d’aires protégées en Afrique de l’Ouest, nous avons mis en place un projet scientifique citoyen sur la plate-forme iNaturaliste. Parallèlement à ce projet, un certain nombre de guides de terrain ont été créés en ligne pour la flore locale. En deux mois déjà, 852 observations sur 312 espèces ont été rassemblées. Nous espérons pour l’avenir une croissance continue de cette base de données qui sera également complétée par celles existantes au niveau des collections et travaux scientifiques.

Mots clés: Complexe WAP, science citoyenne, données d’observation, photos numériques

BIOTA OF THE WAP COMPLEX - START EINES BÜRGERWISSENSCHAFTSPROJEKTES FÜR DEN GRÖSSTEN KOMPLEX VON SCHUTZGEBIETEN IN WESTAFRIKA

Zusammenfassung: Um Datenverfügbarkeit und -austausch in der Region des WAP-Komplexes, Westafrikas größtem zusammenhängenden Gebiet von Schutzgebieten, zu verbessern, haben wir ein Bürgerwissenschaftsprojekt auf der iNaturalist-Plattform aufgesetzt, zu dem mit Fotos und/oder Klängaufnahmen dokumentierte Naturbeobachtungen hinzugefügt werden können. Projektbegleitend haben wir eine Reihe von Online-Feldführern für die lokale Flora zusammengestellt. Innerhalb von nur 2 Monaten wurden 852 Beobachtungen von 312 Arten beigetragen. Wir erwarten, dass diese Datensammlung in der Zukunft weiterwächst und existierende Daten aus naturwissenschaftlichen Sammlungen und Erhebungen ergänzt.

Schlagnworte: WAP-Komplex, Bürgerwissenschaft, Beobachtungsdaten, Digitalfotos

1 INTRODUCTION

Biodiversity data for West Africa’s savanna region is scarce. Together with the Sahara desert, the drylands surrounding it constitute one of the largest ‘white spots’ remaining on GBIF’s global map of species occurrences (<http://www.gbif.org/occurrence>). This lack of publicly available data is detrimental to biodiversity science as well as to conservation actions in the region (STEPHENSON et al. 2016). As a new approach to improve the situation, we started a citizen science project collecting biodiversity observations within the area of the WAP complex (Fig. 1). Citizen science, presently experiencing increased attention, has a long tradition, and some citizen scientist datasets rank among the world’s largest biodiversity datasets (e.g. eBird <http://ebird.org> with > 500 Mio. records). This project, called ‘Biota of the WAP complex’ (www.inaturalist.org/projects/biota-of-the-wap-complex) was initiated on iNaturalist, an international citizen science platform for sharing biodiversity observations, usually georeferenced photo records.

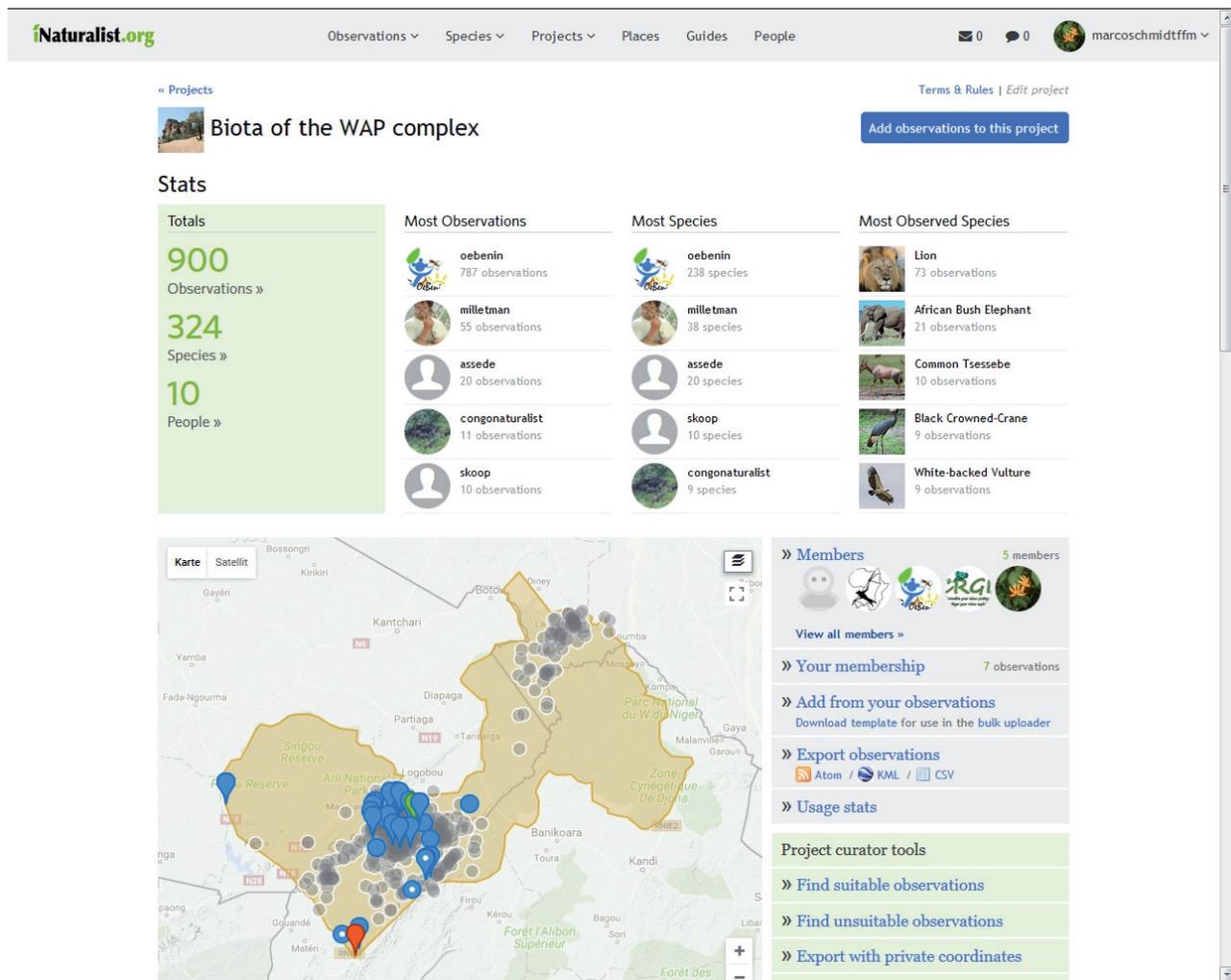


Fig. 1: Screenshot of the project’s start screen, offering an overview of the number of observations, taxa and contributors as well as a map, search and export options. / Capture d’écran de la page d’accueil du projet, montrant un aperçu du nombre d’observations de taxons et contributeurs, ainsi qu’une carte avec les options de recherche et d’exportation. / Screenshot der Startseite des Projekts mit der Zahl der Beobachtungen, Arten und Beitragenden, sowie einer Landkarte, Such- und Exportfunktionen.

The WAP complex is West Africa’s largest continuous area of reserves, including the W Transborder Park (Benin, Burkina Faso, Niger), the National Parks of Arly (Burkina Faso) and Pendjari (Benin) as well as adjacent reserves and hunting concessions (for details on protection status, governance, etc. see KONRAD 2015).

2 METHODS

Starting a project on iNaturalist is straightforward and simple, mainly defining the target taxa and regions as well as options for contributions. Existing data on the platform have been added to the project, hitherto undetermined photo records have been identified, and people have been invited to contribute. iNaturalist relies on standard lists for its taxonomy and nomenclature, e.g. The Plant List (www.theplantlist.org; PATON 2013) for plants and The Clements Checklist (CLEMMENTS et al. 2016) for birds, in order to harmonize taxon names and data exchange with other data providers such as GBIF (www.gbif.org).

Along with the project, we also decided to create guides to the local flora (Fig. 2): while field guides exist for birds (BALANCA et al. 2007) and mammals (LAMARQUE 2004), a

guide book to the plants of the WAP complex is still missing. So we compiled a species list from the checklists of MBAYNGONE et al. (2008), OUÉDRAOGO et al. (2011), NACOUлма (2012) and ASSÉDÉ et al. (2012) and added in a half-automated process (provided by iNaturalist for producing such guides) open access descriptions and illustrations with suitable licences, which were available via Encyclopedia of Life (www.eol.org) or Wikipedia and were in many cases originally from the sites of the Zimbabwe Flora (HYDE et al. 2016) and African Plants – a photo guide (DRESSLER et al. 2014). Several taxa had to be curated or added to iNaturalist’s taxonomic backbone in order to be integrated into the guides. Since the number of taxa for an iNaturalist guide is restricted, we created four separate guides for ferns (www.inaturalist.org/guides/3961), monocots (www.inaturalist.org/guides/3918), legumes (www.inaturalist.org/guides/3962) and other dicots (<http://www.inaturalist.org/guides/3963>).

3 RESULTS

The present GBIF occurrences for the area of the WAP complex (defined as a rectangle from 10.5°N-12.8°N and 0.4°E-

The screenshot shows the iNaturalist.org website interface for the 'Flora of the WAP complex - ferns' guide. At the top, there are navigation links for Observations, Species, Projects, Places, Guides, and People. The user profile 'marcoschmidtffm' is visible in the top right. The main heading is 'Flora of the WAP complex - ferns', with options to 'Enable offline access', 'PDF / Print', and 'Edit'. Below the heading, a brief introduction states that the local flora is divided into four guides: (1) ferns, (2) monocots, (3) legumes, and (4) non-leguminous dicots. A taxonomy sidebar on the left shows 'All' (4 items) and 'Order Polypodiales' (3 items). The main content area lists four species, each with a photo, a search bar, a description, and a distribution map. The species listed are Marsilea minuta, Ceratopteris thalictroides (= C. cornuta), Adiantum philippense, and Pellaea dura.

Fig. 2: Screenshot of the smallest of the four guides to the flora of the WAP complex showing a representative photo, descriptive text and maps of the global distribution of the species. / Capture d'écran de la plus petite des quatre guides de la flore du complexe WAP montrant des photos représentatives d'espèces, les textes descriptifs ainsi que les cartes de distribution de ces espèces. / Screenshot des kleinsten der vier Naturführer zur Flora des WAP-Komplexes mit repräsentativen Fotos, Beschreibungen und Karten zur globalen Verbreitung der jeweiligen Art.

3.5°E) comprise 50,575 records, largest contributors are the National Forest Census of Benin (12871), the West African Vegetation Database (9222, SCHMIDT et al. 2012) and collection records from Naturalis Biodiversity Center (2525), well representing the area due to the work on the Flore du Benin (AKOEGNINOU et al. 2006). The majority of these records is from Benin (36343), followed by Burkina Faso (12017) and Niger (1169). Taxonomically, the largest share of observations is contributed by plants (36949) followed by animals (13545). Not a single record on fungi has been found for the area on GBIF.

Only two months after the start of the Biota of the WAP project, the data consist of 900 observations of 324 species contributed by 10 observers. Integration of data into GBIF takes place by harvesting the ABCD or Darwin Core archives of its contributors in regular intervals, and all research grade records (with at least two identical identifications at species level) will be contributed to GBIF through regular data harvests. This makes data easily available for both the research and conservation community.

4 DISCUSSION

Up to now, most users of the WAP project are scientists rather than amateurs, the usual user group targeted by citizen science approaches. This may be partly due to the fact that internet access, although much improved in the past decade, is still limited and expensive for most people in West African. Platforms like iNaturalist and other citizen science approaches have not yet found the popularity they have in many countries in Europe, North America and Asia. Furthermore, larger citizen associations focusing on conservation and an interest in biodiversity - as existing in many countries in Europe, North America and also South Africa - are missing. Local NGOs/associations including OeBenin (Organisation pour la promotion de l'éducation des filles au Bénin) and ACTAG-PRW (Association des Campements Touristiques pour l'Appui à la Gestion du Parc Régional W) however have been actively contributing observations.

Even though the user community is still small, the basic principle of contributing photo observations and getting assistance in determination is working well and we see good future potential of using the 'Biota of the WAP complex'

project for training local students in the biodiversity and conservation domain and for guides and visitors in ecotourism, providing at the same time a showcase of the protected areas and bringing domain experts and 'citizen scientists' closer together. Since digital cameras with GPS and camera traps have become affordable to the interested public, the number of photo observations is growing rapidly. Such photo observations are in most cases sufficiently documented and well organized by platforms like iNaturalist to allow verification by taxon experts (both scientists and laymen).

The relatively small citizen science community in West Africa further profits from the expertise of a large international platform, especially for taxa with a large group of citizen scientists (e.g. birdwatchers).

For botany, this new source of observation data can be expected to complement existing data sources such as collection data and vegetation plot data. It may close a gap in occurrence data since (1) botanical research activities in the Sudanian savannas are seasonally biased towards the end of the wet season when the majority of plants is identifiable (SCHMIDT 2006, Fig. 9D) and (2) vegetation plot data often miss rare species (SCHMIDT et al. 2010) due to small areas of investigation. Photographers are expected to be more active in the dry season (when the chances to see large mammals in the reserves are high), conspicuous species and species rarely encountered will be better represented than in plot data.

For all taxa, the amount and coverage of data is increased and with sufficient participation may become an important contribution to species monitoring.

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Substitutes for seeds of *Vitellaria paradoxa*, *Parkia biglobosa* and *Adansonia digitata* used for nutrition by five major ethnic groups in Benin, West Africa

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Summary: Non-Timber Forest Products (NTFPs) make a major contribution to the livelihoods and diets of rural households in the savanna ecosystems of West Africa. However, land use change and climatic variability might affect their availability in the future. Based on a survey among 227 households in Northern Benin, we investigated local substitution patterns for the seeds of the three socio-economically most important NTFP-species in the region, *Vitellaria paradoxa*, *Adansonia digitata* and *Parkia biglobosa*, being major sources for protein, fat, and micronutrients in local daily diets. Our study compared substitution patterns between, firstly, three income groups, to assess whether a household's socio-economic status has an influence on the choice of surrogates (low cost vs. more costly options). Secondly, we compared substitution patterns between the five major ethnic groups in the study region (the Fulani, the Bariba, the Ditammarie, the Kabyé and the Yom). The choice of substitutes differed significantly across income groups. However, the poorest households clearly show to be the most vulnerable: up to 30 % of the sampled households stated they would lack an adequate replacement for the NTFPs in question. Furthermore, ethnic affiliation showed to have a considerable impact on the preferred alternative products due to underlying cultural traditions of plant use. Subsequently, aiming at maintaining – and enhancing – the local supply of *V. paradoxa*, *P. biglobosa* and *A. digitata* in order to secure their contributions to local diets, local land use policy should have a particular focus on their ethnic-conditioned use and particularly the specific requirements of the poorest community members.

Key words: Livelihood, non-timber forest products, NTFPs, rural income, forest dependency, West Africa, savanna ecosystem, rural poor

SUBSTITUT DES GRAINES DE *VITELLARIA PARADOXA*, *PARKIA BIGLOBOSA* ET *ADANSONIA DIGITATA* UTILISÉES POUR LA NUTRITION PAR CINQ GROUPES ETHNIQUES MAJEURS AU BÉNIN, AFRIQUE DE L'OUEST

Résumé: Les produits forestiers non ligneux (PFNL) apportent une contribution majeure aux besoins quotidiens et aux régimes alimentaires des ménages ruraux dans les écosystèmes des savanes d'Afrique de l'Ouest. Cependant, le changement de l'occupation du sol et la variabilité climatique pourraient affecter leur disponibilité dans l'avenir. Sur la base d'une enquête menée auprès de 227 ménages du nord du Bénin, nous avons étudié les modèles de substitution locale pour les produits alimentaires des trois espèces de PFNL socio-économiquement les plus importantes de la région, *Vitellaria paradoxa*, *Adansonia digitata* et *Parkia biglobosa*. Leurs graines sont une importante source de protéines, lipides et micronutriments. Notre étude a comparé les schémas de substitution entre, premièrement, trois groupes de revenu afin d'évaluer si le statut socio-économique des ménages aurait une influence sur le choix des substituts (coût faible par rapport aux options plus coûteuses). Deuxièmement, nous avons comparé les modes de substitution entre les cinq principaux groupes ethniques dans la région étudiée (Fulani, Bariba, Ditammarie, Kabyé et Yom). Le choix des substituts différait considérablement d'un groupe de revenu à l'autre. Cependant, les ménages les plus pauvres sont clairement les plus vulnérables: jusqu'à 30% des ménages échantillonnés ont déclaré qu'ils n'auraient pas un remplaçant approprié pour les PFNL en question. De plus, l'appartenance ethnique s'est révélée avoir un impact considérable sur les produits alternatifs préférés en raison des traditions culturelles sous-jacentes de l'utilisation des plantes. Par la suite, dans le but de maintenir - et d'améliorer - l'approvisionnement local de *V. paradoxa*, *P. biglobosa* et *A. digitata* afin d'assurer leur contribution aux régimes alimentaires des ménages ruraux, la politique locale d'utilisation des terres devrait porter une attention particulière à leur utilisation, surtout aux besoins spécifiques des membres les plus pauvres de la communauté.

Mots clés: Ressources de base, produits forestiers non ligneux, PFNL, revenu rural, dépendance des forêts, Afrique de l'Ouest, savane, populations rurales pauvres

UNTERSUCHUNG ZUR SUBSTITUIERUNG DER IN DER ERNÄHRUNG GENUTZTEN SAMEN VON *VITELLARIA PARADOXA*, *PARKIA BIGLOBOSA* UND *ADANSONIA DIGITATA* BEI FÜNF ETHNISCHEN GRUPPEN IN BENIN, WESTAFRIKA

Zusammenfassung: Essbare Wildpflanzen stellen wichtige Nahrungsergänzungen, zu einer ansonsten nährstoffarmen Ernährung ländlicher Nichtholz-Forstprodukte (non-timber forest products, NTFPs) leisten einen wesentlichen Beitrag zu den Lebensgrundlagen und der Ernährung ländlicher Haushalte in den Savannenökosystemen Westafrikas. Landnutzungsänderungen und klimatische Variabilität könnten ihre Verfügbarkeit in Zukunft jedoch beeinträchtigen. Basierend auf einer Befra-

gung von 227 Haushalten in Nord-Benin untersuchten wir die lokalen Substitutionsmuster für die in der Ernährung genutzten Samen der drei sozioökonomisch wichtigsten NTFP-Arten in der Region, *Vitellaria paradoxa*, *Adansonia digitata* und *Parkia biglobosa*, die wesentliche Quellen für essentielle Proteine, Fett und Mikronährstoffe sind. Unsere Studie verglich zunächst die Substitutionsmuster zwischen drei Einkommensgruppen, um festzustellen, ob der sozioökonomische Status der privaten Haushalte einen Einfluss auf die Wahl der Substitute haben würde (geringere versus höhere Kosten bei der Beschaffung dieser Substitute). Zweitens verglichen wir die Substitutionsmuster zwischen den fünf großen ethnischen Gruppen des Untersuchungsgebietes (Fulani, Bariba, Ditammarie, Kabiyé und Yom). Die Wahl der Substitute unterschied sich signifikant zwischen den drei Einkommensgruppen, wobei die ärmsten Haushalte die höchste Vulnerabilität aufweisen: Bis zu 30% der in die Stichprobe einbezogenen Haushalte gaben an, dass ihnen ein angemessener Ersatz für die betreffenden NTFP fehle. Darüber hinaus zeigte die ethnische Zugehörigkeit einen erheblichen Einfluss auf die bevorzugten Alternativprodukte, der auf die unterschiedlichen kulturellen Traditionen bei der Nutzung der NTFPs zurückzuführen ist. Mit Blick auf die Sicherung der Beiträge von *V. paradoxa*, *P. biglobosa* und *A. digitata* zur lokalen Ernährung bzw. deren Verbesserung, sollte lokale Landnutzungspolitik die ethnisch bedingten Unterschiede in der Nutzung der NTFPs sowie die besonderen Bedürfnisse der unteren Einkommensgruppen stärker berücksichtigen.

Schlagworte: Nicht-Holz-Waldprodukte, NTFPs, ländliche Einkommen, Wald als Lebensgrundlage, Westafrika, Savanne, ländliche Entwicklung

1 INTRODUCTION

Non-timber Forest Products (NTFPs), i.e. products from wild plant and animal species, are inherent to the social-cultural traditions and livelihoods of rural African communities (CAVENDISH 2000; LYKKE et al. 2004; SHACKLETON et al. 2008; KALABA et al.; 2013a). NTFPs comprise all biological matters except sawn timber but including small wooden poles and stick to be harvested without technological requirements from forests and woodlands (CIFOR, 2011). Fruits, leaves, barks and other vegetable structures, as well as animal products, make important contributions to people's daily diets (ANGELSEN et al., 2014; HEUBACH et al. 2011), are used as firewood (BELCHER 2003; CUNNINGHAM et al. 2002), medicine (e.g., NDAM & MARCELIN 2004; BUNDSCHUH et al. 2011) and construction material (HEUBACH et al. 2013), and play essential roles in indigenous belief systems (CAVENDISH 2002; ANGELSEN & WUNDER 2003; FOPPES & KETPHANH 2004; CIFOR 2015). NTFPs are crucial to the socio-economic viability of households in rural areas worldwide. In unfavorable situations, e.g. famine or financial shocks, they provide a safety-net by filling gaps in consumption or cash income (BABULO et al. 2009; KAMANGA et al. 2009; WORLD AGROFORESTRY CENTER 2013). Globally, 1.6 billion people are considered being highly forest dependent (World Bank 2004, 2008).

In rural sub-Saharan Africa, more than half of the population relies on food harvested from their direct environment (World Resources Institute 2005), next to locally grown crops). A growing body of case studies gives evidence for the particular contribution of NTFPs to the economies of households living in rural agroforestry systems, both in terms of subsistence and cash income. For example, in Malawi, total income shares from fruit tree products only accounted for 15 % of household income (KAMANGA et al. 2009), and in the Republic of Congo wild plant products contributed up to 10 % to local income (DE MERODE et al. 2004). Assessing a larger set of forest products (incl. wooden and selected animal products), a study in Ethiopia found NTFPs to make up 27 % (BABULO et al. 2009), and one in Zimbabwe (including non-renewable NTFPs) even 35 % of rural household income (CAVENDISH 2000). Furthermore, a recent study in Northern Benin revealed wild plants to constitute on average 39 % of household cash and subsistence income (HEUBACH et al. 2011). In most of the studies NTFPs are characterized by open or semi-open access and

their collection does not require special technical equipment or financial means, thus, representing highly beneficial sources for livelihoods particularly for the rural poor (ANGELSEN & WUNDER 2003; VEDEL et al. 2007).

The variety of used species thereby is enormous. Particularly plant species are fundamental ingredients in daily consumption, important for construction and energy supply, and essential for medical treatment – mostly with multiple uses. For example, in the study area located in the south Sudanian zone of Benin more than 90 woody species are locally used, often for multiple uses, such as traditional medicine (61 % of the 90 woody species are used for that), dental care (49 % of the 90 species), firewood (41 % of the 90 species), construction (39 % of the 90 species), and wild foods (32 % of the 90 species) (HEUBACH et al. 2013). Likewise, amongst others, VODOUHÉ (2009) identified more than 70 plant species used daily by people living adjacent to the Pendjari National Park in Northern Benin, and LYKKE et al. (2004) identified 56 woody multi-use species highly valued by rural communities in the Sahel area of Burkina Faso.

However, use preferences for species might differ much within the studied communities. Based on their traditional knowledge and cultural backgrounds, specific social groups show differences in the collection and use of a specific set of plants. According to KEPE (2008) social differentiation is a key factor determining resource use in forest-based communities due to social affiliations to certain groups or networks (e.g., ethnic groups, user groups) and individual characteristics. In this context, recent studies in Benin and Burkina Faso shed light on the role ethnic affiliation plays with regard to plant use. In addition to individual household characteristics, such as e.g. age, gender, location, and access to farmland, ethnicity appeared to be highly influencing use values for woody plant species (CALUWÉ et al. 2009; FANDOHAN et al. 2010; SCHUMANN 2011; GOUWAKINNOU et al. 2011; HEUBACH et al. 2013).

Recently, there is growing concern that the occurrence of NTFP-providing plant species has been continuously negatively impacted by land use change, e.g. through the ongoing conversion of savanna areas into cultivated land (BRINK & EVA 2009), introduction of alien species (SHACKLETON et al. 2007), agricultural intensification (WITTIG et al. 2007), amongst others. Moreover, predicted climatic changes are likely to change future occurrences of plant species (IPCC 2007), including in our study region (WITTIG et

al. 2007). With regard to the three socio-economically most important woody species in Northern Benin – *Vitellaria paradoxa*, *Parkia biglobosa* and *Adansonia digitata* (VODOUHÊ et al. 2009; FANDOHAN et al. 2010; HEUBACH et al. 2013) – HEUBES et al. (2012) predicted a severe decrease in their occurrence in 2050 due to climate and land use change. Thus, it is of interest to assess whether and which alternatives rural communities might draw on to compensate current and possible future outage of those NTFPs they use largely for their daily consumption.

The study at hand investigated the general, current substitution patterns of households in case of temporary shortages for the three socio-economically most important woody species in the region (and in other areas of the Sudanian zone: see e.g. LESSMEISTER et al. 2015) *Vitellaria paradoxa*, *Parkia biglobosa*, and *Adansonia digitata* (VODOUHÊ et al. 2009; FANDOHAN et al. 2010; HEUBACH et al. 2013). Short-term NTFP shortage might be caused by inter-annual variations in NTFP availabilities, low rainfall and/or depleted stocks before the next harvest season. We explored current substitution patterns among the five major ethnic groups (the Fulani, the Ditammarie, the Kabiyé, the Bariba, and the Yom) in two villages in Northern Benin.

While *V. paradoxa* seeds are a key source for fat (MARANZ et al. 2004), *P. biglobosa* and *A. digitata* seeds provide valuable protein (TEKLEHAIMANOT 2004). Protein contents of the fermented *P. biglobosa* seeds even can exceed that of meat (KRONBORG et al. 2014). Besides, all of them add essential vitamins (TEKLEHAIMANOT 2004) to local diets. Being still available in the dry season (fruits of *P. biglobosa* and *A. digitata*), when fields are already harvested, and being suitable for mid-term storage, these species' seeds are excellent to overcome times of seasonal or financial shortcomings (SCHRECKENBERG et al. 2006; ARNOLD et al. 2011).

Potential sources for substitutes for these three species' seeds may be parts of other wild NTFP-providing species found in the adjacent savanna area, or of cultivated or purchased plants, animal products, or other marketed natural or manufactured goods. The choice of the replacement might, firstly, depend on their socio-economic status, i.e. their financial means allowing for more or less costly options. Secondly, as elaborated on above, ethnicity might play a major role in choosing substitutes, since ethnic affiliation comes along with particular knowledge on and traditions of plant and other product use. Thirdly, the choice of the substitute might also account for its potential to adequately complement for the nutritional values of the replaced NTFP.

Our study, thus, identifies households' current choice of substitutes for seeds of *V. paradoxa*, *P. biglobosa* and *A. digitata*, comparing i) three income groups, and ii) five ethnic groups. Additionally, we reflect on whether the substitutes meet nutritional values equaling those of the investigated NTFPs (based on existing figures from the literature), and draft options for adaptive measures to possible changes in NTFP supply.

2 STUDY CONTEXT

2.1 Characteristics of the study area

2.1.1 Socio-economic setting of studied villages

We conducted our study in two villages in Northern Benin, Papatia and Chabi-Couma (30 km apart), in the Department of Atakora (Fig. 1) approximately 35 km from the northern economic urban center Natitingou. In 2008, of the Department population 62.3 % lived in rural areas and 70.3 % were considered poor.

We considered two villages to obtain a replication. Thus, our selection was based on the similarity of the two villages in terms of their socio-economic profile. Both are endowed with piped water, an own small local market, and a primary school. They are located in a similar distance from the urban center and the main road, i.e. have similar access to urban facilities and products. Both have only rudimentary access to electricity, and households' energy demands are primarily met by firewood collected in the adjacent savanna areas. Major ethnic groups located in the area are spread evenly in both villages.

Residents of these villages are mainly engaged in rain-fed crop production in agroforestry systems, small livestock husbandry and NTFP collection in the adjacent savanna areas. Off-farm income (e.g. local trading, tailor, motorbike taxi driver, employment in administrative and educational activities) is very rare. The importance of NTFP collection was conformed and underlined by SIEGLSTETTER et al. (2011), who found that 96 % of the 129 woody species existing in a neighbouring area were used.

2.1.2 Biophysical environment

Belonging to the southern Sudanian zone with tropical climate and a rainy season from May to November, the savanna ecosystems in the study region are covered by tree and shrub savanna (MAYAUX & BARTHOLOMÉ 2003). As a result of the traditional small holder system of slash-and-burn agriculture in shifting cultivation, the agroforestry parklands show a pattern of old and young fields and fallows with selected multi-use trees spared from chopping.

2.1.3 Ethnic groups

The five major ethnicities domiciled in the studied villages are the four tiller societies Bariba (autochthon, i.e. the original settlers in the region), Ditammarie, Kabiyé (both migrated from Togo) and Yom (originally from the Department of Bassila, south of the study area), as well as the pastoralist Fulani (from Kouandé, east of the Atakora chain) who settled in the region due to severe drought events (DE BRUIJN & DIJK 1994; BOLWIG & PAARUP-LAURSEN 1999). All ethnic groups are similar in terms of household size, age and education of head, with insignificant differences with regard to total household income and distribution into income groups (Table 1) (HEUBACH et al. 2011). Access to the savanna areas is traditionally semi-open. While within the village area particular sectors for harvesting NTFPs are exclusively assigned to the different local ethnic groups, access to

Table 1: Comparison of socio-economic characteristics of investigated ethnic groups in Papatia and Chabi-Couma (N = 227 households; modified after HEUBACH et al., 2011). / Comparaison des caractéristiques socio-économiques des groupes ethniques étudiés à Papatia et Chabi-Couma (N = 227 ménages, modifiés après HEUBACH et al. 2011).

N = 227	Bariba	Ditammarie	Kabiyé	Yom	Fulani
Main employment: tiller (%)	98	96	100	100	93
Main employment: livestock breeder (%)	-	-	-	-	5
Total household income (in Euro, per aeu* and year)	731	694	644	690	704
Very low income group (%)	28	35	28	39	37
Medium income group (%)	43	29	30	34	33
Above medium income group (%)	28	35	42	27	30

*aeu = adult equivalent units (DEATON, 1982), i.e. mean income displays the adjusted income per person in the respective household

savanna resources beyond village level is unrestricted. Harvest of trees on farmland remains restricted to the farmland owners. Migrants who have borrowed land don't have rights to the products of the trees on these lands.

2.2 Investigated NTFP species

The selection of the NTFP-providing species to study here is based on the findings of HEUBACH et al. (2013) who found *V. paradoxa*, *P. biglobosa* and *A. digitata* to be the three woody species valued the most by rural communities in the region. They contribute to daily dietary needs in terms of fat, protein, and vitamins contained in their seeds, and present a large share to total household income (Table 2).

3 METHODS

3.1 Study design, data collection and data analysis

The data used in this analysis is part of a household survey on NTFP collection, use and socio-economic characteristics that was conducted with 227 randomly selected households in two villages (Chabi-Couma and Papatia) in Northern Benin, West Africa in 2009. The households were stratified according to their ethnic affiliation to one of the five major ethnic groups in the region, i.e. the Bariba, the Kabiyé, the Fulani, the Ditammarie and the Yom (45, 45, 45, 46, and 46 interviews, respectively).

Being the main collectors of NTFPs, women were asked to report substitutes used in diets when seeds of *Vitellaria paradoxa*, *Parkia biglobosa* and *Adansonia digitata* are not available due to temporal and/or seasonal shortage, e.g. when stocks are depleted before the next harvest. We did not

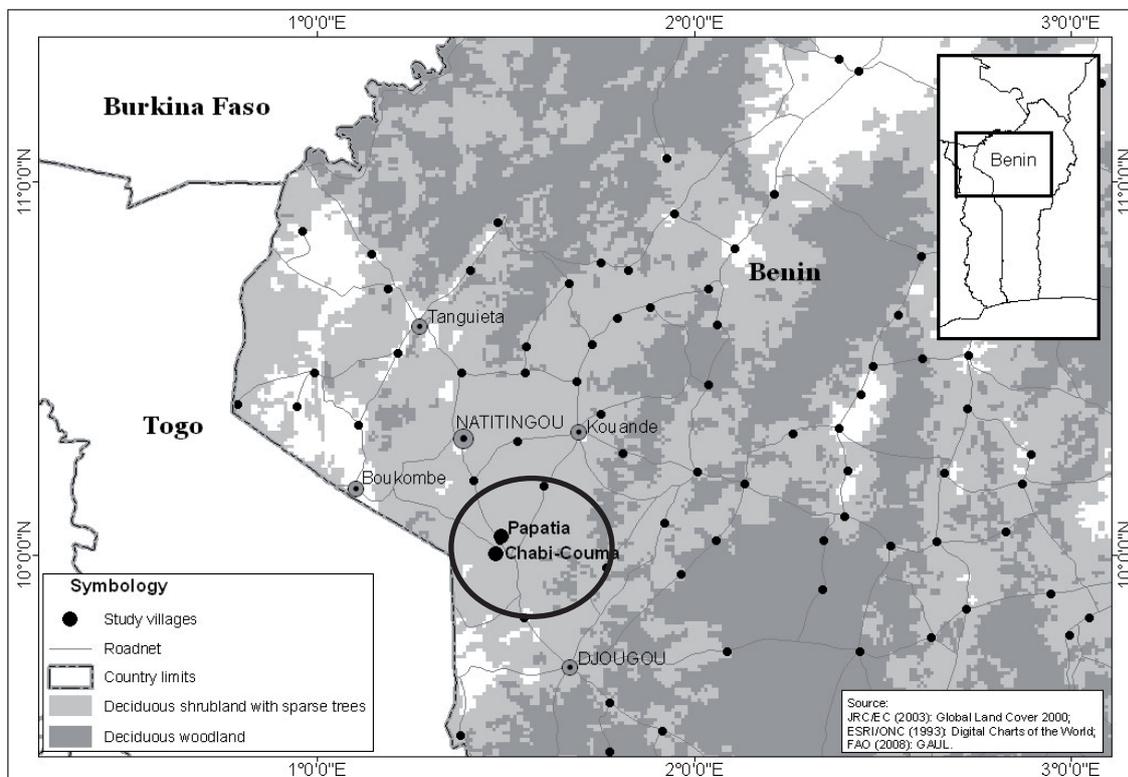


Fig. 1 : Map of the study area (Department of Atakora) with the two studied villages Papatia and Chabi-Couma. Large black dots (labelled) represent the two study villages; other smaller black dots (unlabelled) are displayed in order to represent the density of villages located within the savannah ecosystem. / Carte de la zone d'étude (Département d'Atakora) avec les deux villages étudiés Papatia et Chabi-Couma. De grands points noirs (étiquetés) représentent les deux villages étudiés; d'autres points plus petits (non étiquetés) sont affichés pour montrer la densité des villages situés dans l'écosystème de la savane.

Table 2: Contributions by the three target species *Vitellaria paradoxa*, *Parkia biglobosa* and *Adansonia digitata* to local dietary needs, and related consumption and market patterns. / Contributions des trois espèces cibles *Vitellaria paradoxa*, *Parkia biglobosa* et *Adansonia digitata* aux besoins alimentaires locaux, ainsi que des modèles de consommation et de commerce respectifs.

Species	Product and contribution to local diet	Consumption and market pattern
<i>Vitellaria paradoxa</i> (subspecies <i>paradoxa</i> , Shea Tree, local French name: Karité)	Shea nuts (kernels): contain up to 50 % fatty acids (TEKLEHAIMANOT 2004); processed into shea butter ('beurre du Karité') used as cooking oil and for skin care Fruit pulp: excellent source of protein, calcium and sugar (MARANZ et al. 2004)	Average annual consumption of Shea butter in sub-Saharan countries ranges between 7.3 up to 10 kg per person (BOFFA 1999; DAH-DOVOVON 2006) In 2009, the average share of income from <i>V. paradoxa</i> in total household income in the study area was 13 %, and 89 % of collected shea nuts were sold on local markets (HEUBACH et al. 2013)
<i>Parkia biglobosa</i> (African Locust Bean Tree or Néré)	Seeds: protein-rich with multiple essential amino acids (NORDEIDE et al. 1996); fermented and processed as local ingredient in sauces ('moutarde'); protein content is equal to or even higher than that of various kinds of meat (KRONBORG et al. 2014) Seeds: also rich in fat (TEKLEHAIMANOT 2004)	Highly valued as staple food throughout West Africa (MERTZ et al., 2001) In 2009, the average share of income from <i>P. biglobosa</i> in total household income in the study area was 10 %, and 88 % of collected seeds were sold on local markets (HEUBACH et al. 2013)
<i>Adansonia digitata</i> (African Baobab)	Seeds: rich in protein and fat (DE CALUWÉ et al. 2009); roasted seeds used as ingredient in sauces and as snack food; also as alternative to coffee; by pounding or boiling, the seed's oil can be extracted	In 2009, the average share of income from <i>A. digitata</i> in total household income in the study area was 2 %, and 73 % of collected seeds were sold on local markets (HEUBACH et al. 2013)

ask about changes in the availability of the three NTFPs or whether their reliance on them had increased.

On basis of the income data collected through the questionnaire, we calculated total household income. In accordance with CAVENDISH (2002), we defined a household's total income as the sum of cash income generated from various activities (e.g. crop and livestock production, collection of wild foods, small-scale activities) and the monetary equivalent of a household's subsistence use of the output of these activities. Total household income is accounted on annual basis. It reflects the net income generated by the population sample under investigation, i.e. the total value of output deducted by the total value of input (e.g. fertilizer for agricultural production, veterinary supplies) during the accounted period. Note that net income includes own-labor costs due to absent or thin labor markets in rural African settlements. To calculate income, we used means of local market prices (observed monthly at the two markets of Papatia and Chabi-Couma during the study period) and households' own-reported revenues from selling their products (in local units of measure – 'aguwe'). Both market prices and own-reported revenues were found to be strongly consistent for both agricultural and woodland products. In order to account for the varying compositions (number and sex of adults and children) of the studied households, we applied a combination of the OECD-modified equivalence scale due to type of household member (HAGENAARS et al. 1994) and used an economy-of-scale coefficient resulting in household size as the determinant of needs suggested by DEATON (1982). The adjusted income (all income sources) then equals income per adult equivalent units (aeu).

In order to compare NTFP substitution between income groups, we split the sample into income terciles: "very low income group" (N = 73), "medium income group" (N = 73) and "above medium income group" (N = 72). Mean annual total income per aeu (adult equivalent unit, i.e. adjusted income, according to DEATON (1982)), between income groups was significantly different (406 €, 669 €, and 1017 €, respectively; ANOVA $p < 0.001$).

The substitutes reported in the interviews were grouped into three categories reflecting their origin: i) product of a culti-

vated/purchased plant, ii) product of other wild plant species, and iii) purchased animal or other product. Chi-square test was used to compare the counts of the three categories between income groups, ethnicities and villages. Chi-square tests were performed using IBM SPSS Statistics 22 (IBM 2013).

4 RESULTS

4.1 Substitutes for seeds of *Vitellaria paradoxa*, *Parkia biglobosa* and *Adansonia digitata*

Table 3 shows the results of the survey on NTFP substitutes. Asked for possibilities to substitute the seeds of *V. paradoxa*, women reported three possibilities, of which two are cultivated/purchased plants. More than half of the respondents declared that shea butter could be replaced by palm oil derived from the palm tree *Elaeis guineensis*, and one third mentioned to preferably substitute it by peanut oil. Only a negligible proportion of respondents mentioned to replace *V. paradoxa* seeds by butter from cow milk.

For *P. biglobosa* seeds, in total 12 substitutes were reported. They comprise eight products from cultivated/purchased plants (in decreasing importance: peanuts, chilies, onions, sesame, beans, *Blighia sapida*, soybeans), three purchased animal/ other products (in decreasing importance: fish, MAGGI cubes – product by Nestlé, salt), and one alternative wild plant species (*Ceiba pentandra*). The most quoted products were fish, MAGGI cubes (food flavoring product by Nestlé, main ingredient: salt, frequently used), peanut, and chilies.

The seeds of *A. digitata* can be substituted by five cultivated/purchased plants (in decreasing importance: sesame, peanuts, *B. sapida*, lady's fingers, tomato and two other wild plant species (*Vitex doniana*, *Parinari curatellifolia*). However, only three cultivated plants - sesame, peanut, and the seeds of *B. sapida* - were frequently quoted, while the other products were mentioned by very few respondents.

In general, cultivated/purchased plants were the predominant cited substitute category for all three studied species.

Table 3: Substitutes for seeds of *Vitellaria paradoxa*, *Parkia biglobosa*, and *Adansonia digitata*. The assignment of each substitute to one of the three categories is also presented. / Substituts aux graines de *Vitellaria paradoxa*, *Parkia biglobosa* et *Adansonia digitata*. Le classement de chaque substitut dans une des trois catégories est également présenté.

Substitute	Plant part	% of respondents	Product of a cultivated or purchased plant species	Product of a wild plant species	Purchased animal or other products
<i>Vitellaria paradoxa</i>					
Oil of <i>Elaeis guineensis</i>	fruits	57.9	x		
Oil of <i>Arachis hypogaea</i> (peanut)	fruits	29.8	x		
Butter made from cow milk		0.4			x
no substitutes		11.8			
<i>Parkia biglobosa</i>					
Fish, smoked		28.1			x
MAGGI cubes (Nestlé)		20.8			x
<i>Arachis hypogaea</i> (peanut)	seeds	13.9	x		
<i>Capsicum spec.</i> (chilies)	fruits	4.8	x		
<i>Ceiba pentandra</i>	seeds	3.5		x	
<i>Allium cepa</i> (onion)	bulb (dried)	3.0	x		
<i>Sesamum indica</i> (sesame)	seeds	2.6	x		
Salt		1.7			x
<i>Phaseolus vulgaris</i> (beans)	seeds (dried)	1.7	x		
<i>Blighia sapida</i>	seeds (aril)	1.3	x		
<i>Glycine max</i> (soybeans)	seeds	0.9	x		
<i>Hibiscus sabdariffa</i>	Seeds (fermented)	0.9	x		
no substitutes		16.5			
<i>Adansonia digitata</i>					
<i>Sesamum indica</i> (sesame)	seeds	41.0	x		
<i>Arachis hypogaea</i> (peanut)	seeds	15.4	x		
<i>Blighia sapida</i>	seeds (aril)	14.1	x		
<i>Abelmoschus esculentus</i> (lady's fingers)	seeds	1.3	x		
<i>Vitex doniana</i>	leaves	0.9		x	
<i>Lycopersicon esculentum</i> (tomato)	fruits, powder	0.4	x		
<i>Parinari curatellifolia</i>	seeds	0.4		x	
no substitutes		26.4			

For *P. biglobosa* and *V. paradoxa* seeds, animal and other products were the second most important category of substitutes, while for *A. digitata* seeds of other wild plant species were the second most frequently cited surrogates.

Peanuts were reported as a substitute for the seeds of all three studied species. In addition, the seeds of sesame and *B. sapida* were likewise mentioned as substitutes for the seeds of *A. digitata* and *P. biglobosa*.

Substitutes for seeds of *P. biglobosa* (12 substitutes) are nearly twice as many as for *A. digitata* (7 substitutes), and even four times higher than for *V. paradoxa* (3 substitutes). Furthermore, almost 30 % of respondents stated that they have no substitution for the seeds of *A. digitata*, and 10-20 % of respondents lack replacements for the seeds of *P. biglobosa* and *V. paradoxa*. Interestingly, the three studied NTFP species were not mentioned as substitutes for each other.

4.2 Differences in substitution patterns between income groups

For all income groups, products from cultivated/purchased plants account for the primary source for substitution (63.6 % to 76.5 %), followed by animal/ other products (17.6 %

to 18.8 %) and other wild plant species (5.9 % to 18.2 %). Whilst accounting for a minor share in substitution generally, these alternative local plant species, however, are of high importance to the very low (18.2 %) and medium (12.5 %) income groups.

For *P. biglobosa* and *A. digitata*, the choice of substitutes differed significantly between income groups ($\chi^2=19.8$, $p < 0.01$; $\chi^2=15.4$, $p < 0.01$ respectively), while it did not differ significantly for *V. paradoxa* ($\chi^2=4.38$, $p > 0.05$) (Fig. 2).

Furthermore, a higher proportion of the poorer households (= very low income) reported to have no substitutes for the three NTFP species compared to the less poor households (= medium income and above medium income). For *V. paradoxa* seeds, 20 % of the poorest households, and 10 % of the less poor, lack appropriate substitutes. Above all, wild and, thus, free alternatives were not mentioned.

For *P. biglobosa*, even 30 % of the poorest households lack a proper substitution, compared to 10-15% of the less poor households (= medium income and above medium income). Less poor households preferably replace the raw material for moutarde with fish, being the more expensive alternative, while poorer households use the cheaper manufacture produce MAGGI cubes.

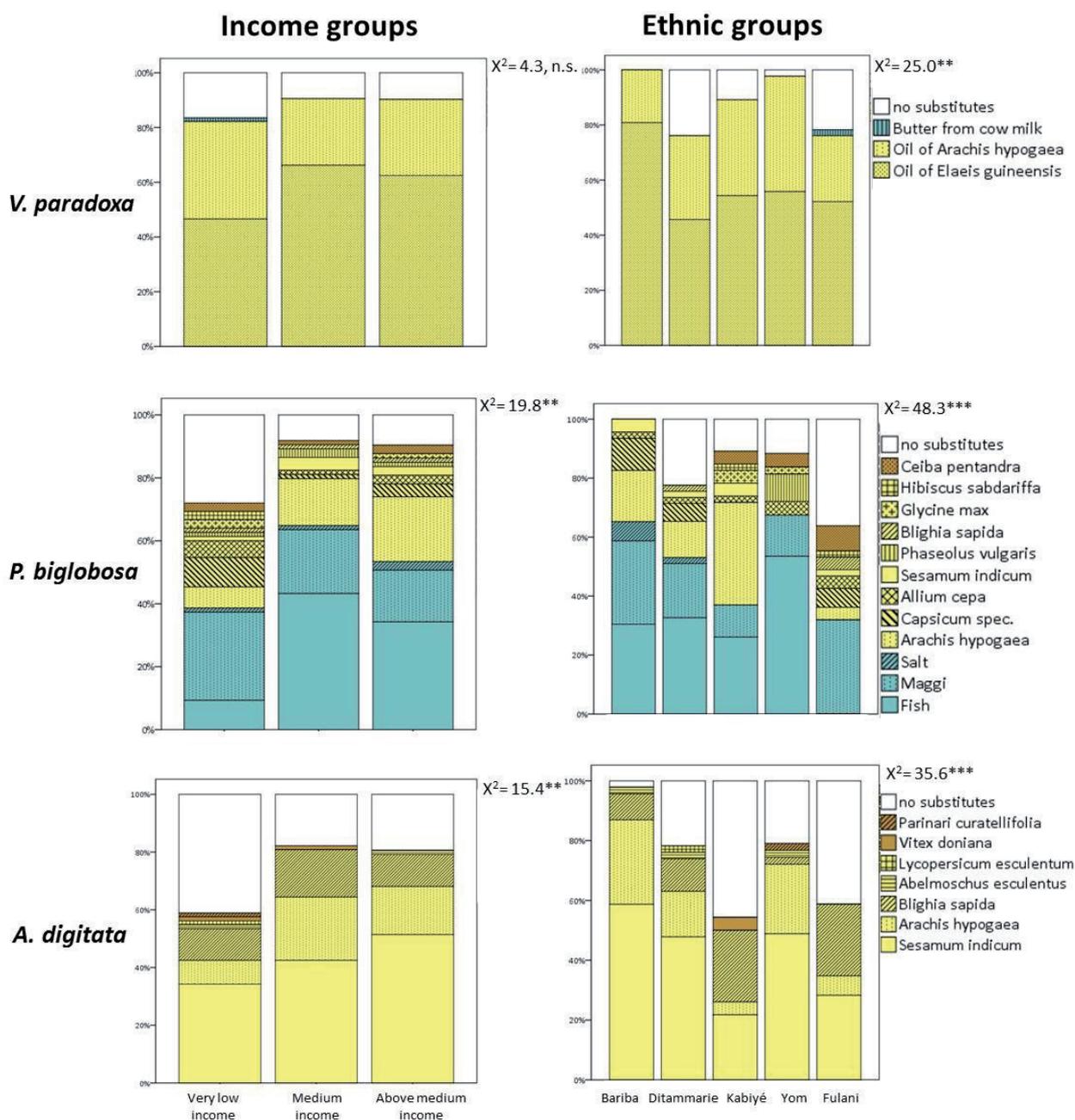


Fig. 2: Differences in substitution patterns of NTFPs between income and ethnic groups. Blue = animal/ other products; yellow = cultivated/purchased plants; brown = other NTFP species. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s. = not significant. / Différences dans les modèles de substitution des PFNL entre groupes économiques (de revenu) et groupes ethniques. Bleu = animal / autres produits; jaune = plantes cultivées / achetées; brun = autres espèces de PFNL. * $P < 0,05$; ** $p < 0,01$; *** $p < 0,001$; N.s. = Pas significatif.

For *A. digitata*, as much as 40 % of the sampled poorest households (and even 30 % and 20 % of the medium and above medium income groups, respectively) stated to have no replacement. Again, less poor households can afford to purchase more costly products (peanuts, sesame, seeds of *B. sapida*) while the poorest ones engage in the collection of the two wild plant species (*V. doniana* and *Parinari curatellifolia*) to use as substitute for sauce ingredient.

4.3 Differences in substitution patterns between ethnicities

For all three species, our analysis revealed significant differences in substitution patterns between ethnic groups (Fig. 2): *A. digitata* ($\chi^2=35.6$, $p < 0.001$), *P. biglobosa* ($\chi^2=48.3$,

$p < 0.001$) and *V. paradoxa* ($\chi^2=25.0$, $p < 0.01$). Albeit resembling regarding the total number of alternatives, they differ significantly especially for *P. biglobosa* (only two matches out of twelve substitutes) and *A. digitata* (only three matches out of seven substitutes).

Due to the very low number of alternatives, replacement of *V. paradoxa* seeds does not show great alterations between groups (except that the Fulani were the only ethnic group that mentioned cow butter as an additional substitute). In contrast, substitution patterns for *P. biglobosa* are highly differentiated between ethnic groups. Fish was mentioned as primary substitute by the four tiller societies Bariba, Ditammarie, Kabiyé and Yom, while the Fulani's first choice is MAGGI cubes when seeds of *P. biglobosa* are unavailable.

Moreover, the Bariba and the Ditammarie only mentioned cultivated and other merchandise as alternatives to *moutarde*, while the Kabiyé, the Yom and the Fulani also count on alternative wild plant species.

For the seeds of *A. digitata*, the Fulani only cited the three most important substitutes regarding the overall sample (sesame, peanuts, and the seeds of *B. sapida*), while the other ethnicities additionally reported other substitutes. For instance, the Ditammarie exclusively cited tomato, the Kabiyé leaves of *V. doniana*, and the Yom seeds of *P. curatellifolia*, with the latter being the only two wild plant species mentioned here.

Overall, about 15% of all substitutes reported by the Kabiyé and Yom were alternative wild plant species (Table 4). In contrast, the Ditammarie never mentioned other wild plant species as substitutes for the three investigated NTFPs.

Interestingly, the autochthon Bariba displayed the lowest proportion of respondents having no substitutes for the three species (Fig. 2), while particularly the Fulani seem to have difficulties to substitute the investigated NTFPs.

5 DISCUSSION

As our analysis shows, rural communities use a wide range of different products to substitute the seeds of the three investigated local NTFP species, *Vitellaria paradoxa*, *Parkia biglobosa* and *Adansonia digitata*. Of the 18 substitutes mentioned in total, 61 % are cultivated/purchased plants, 22 % animal or other products, and 17 % wild plant species collected in the adjacent savanna areas.

However, there are considerable differences in substitution patterns between both income groups and ethnic groups. From our figures, it becomes evident that income has a significant effect on the choice of alternatives, reflecting differences in financial resources to access these substitutes for the NTFPs under investigation. Being the ones with the least range of alternative products and least financial means to engage in pricy products, the poorest households are likely to be the ones most affected by the absence of the in-

vestigated NTFPs. Other wild plant species, thus, are essential to meet basic household needs as they are low cost opportunities with relatively easy access. In contrast, purchased/cultivated products are often pricy and sufficient quantities remain unaffordable for very poor households.

However, there may be justified assumption that a decreasing occurrence of *V. paradoxa*, *P. biglobosa* and *A. digitata* not only will hit the poorest but rather all their beneficiaries. Evidence is presented by a recent study conducted by HEBES et al. (2012) in Northern Benin who showed that the occurrence of the three target species and, subsequently, their contributions to household economies, will be severely affected by predicted land use and climate change until 2050. For *V. paradoxa*, losses of 20 % up to 50 % in 2050 are estimated for the study area. The same holds true for *P. biglobosa* (losses up to 50 %) and *A. digitata* (losses up to 20 %).

Subsequently, the daily supply of fat and protein as provided by these three species and, thus, their contributions to dietary needs, might be threatened in the future. This particularly holds true for shea nuts as there exist only few alternatives for them as our study showed. Even if the fat content of these substitutes is similar to that of shea nuts the fat quality might be lower, and their production costs, however, differ much compared to that of shea butter. While the manufacture of shea butter originally is an individual household-based activity carried out by women using firewood and simple wooden tools, the processing of peanut oil requires mills, i.e. technical equipment which normally is not affordable on a household level. Instead, households would need to pay mill owners. The production process of palm oil (*Elaeis guineense*) is by far the most expensive one, as interviewed women reported, including the harvest of the seeds. The subsequent processing requires larger machines and substantial energy use, which normally is centralized in specialized production sites. In addition, the palm tree is very scarce in the region, making its products far too expensive to be used on a daily basis. Furthermore, alternative products from other NTFP species to substitute *V. paradoxa* were not cited by our interviewees, and the production and use of butter from cow milk remains with merely a couple

Table 4: Total number of substitutes for the three species, separated per income group and ethnicity. / Nombre total de substituts pour les trois espèces, séparés par groupe de revenu et groupe ethnique.

	<i>V. paradoxa</i>	<i>P. biglobosa</i>	<i>A. digitata</i>	Share by category (%)		
				Product of a cultivated or purchased plant species	Product of a wild plant species	Purchased animal or other products
Income groups						
Very low income	3	12	7	63.6	18.2	18.2
Medium income	2	10	4	68.8	12.5	18.8
Above medium income	2	11	4	76.5	5.9	17.6
No. of substitutes overlapping*	2	10	3			
Ethnic groups						
Bariba	2	7	4	78.6	7.1	14.3
Ditammarie	2	8	5	80.0	0.0	20.0
Kabiyé	2	8	4	71.4	14.3	14.3
Yom	2	6	5	69.2	15.4	15.4
Fulani	3	8	3	78.6	7.1	14.3
No. of substitutes overlapping*	2	2	3			

* among all groups

Fulani households owning few cattle. Apart from that, the calcium content of shea butter (340 mg/100 g; DEI 2008) by far exceeds that of peanuts (92 mg/100 g; ATAGA & VAN DER VOSSEN 2007), palm oil seeds (60 mg/100 g; NTARE 2007) and cow milk butter (72 mg/100 g; USDA 2002). This is in line with findings of LEAKEY (1999) who found that the biochemical profiles of native species are often superior to exotic species in terms of essential fat, micronutrients, fiber and protein. In contrast to the case of shea nuts, the options mentioned to replace protein-rich seeds of *P. biglobosa* are not as sufficient in terms of nutritional values (Table 5). Apart from peanuts and the seeds of the local species *Ceiba pentandra*, none of the alternatives cited reaches similar protein contents. Additionally, despite being an adequate nutritional substitute *C. pentandra* is very scarce in the study area – a possible reason for the low mention by respondents (3.5 %). This pattern is reflected for *A. digitata*. None of the seeds of the three cultivated plants reported as replacements equals its protein shares (Table 5), nor does the alternative wild local species *Vitex doniana*. However, being quite abundant in the region, the latter presents at least a low cost alternative.

In addition, those substitutes which compensate best in terms of fat and protein supply are all cultivated species (peanuts, sesame and *B. sapida*), i.e. they require access to farmland. This, however, often is limited for the poorest households as the size of farmland they manage is often insufficient (HEUBACH et al. 2011). Hence, we expected to find a greater proportion of other wild plant species used as substitutes, particularly among the poorer households. However, this is not the case. This might probably due to the low abundance of these species in the area as reported by the interviewees. Native species might also be less interesting if they have comparably lower productivities than e.g. crop species, which can be produced in relatively stable and controllable conditions (NEUFELDT et al. 2012), and generally are located nearby homes.

Beyond socio-economic characteristics, ethnic affiliation seems to play a considerable role in choosing substitutes for the three target species. Overall, in the study region, there is quite a range of species whose products are commonly valued by all investigated ethnic groups, such as the three species investigated here, plus a great range of NTFP species used considerably differently (HEUBACH et al. 2013). This is in line with findings of FANDOHAN et al. (2010) who identified use values for 76 plant species among three ethnic groups (Berba, Gourmantche and Waama) in Northern Benin, also highlighting the influence of gender and market proximity on plant use. Particularly woody species were most commonly used by all respondents, including the target species of the study at hand, while a whole set of other plant species were exclusively used by specific ethnic groups. This pattern is in accordance with other recent studies looking either at a collection of plant species (e.g. LYKKE et al. 2004; VODOUHÉ et al. 2009; PARÉ et al. 2010; SOP et al. 2012) or single species uses such as e.g. *Adansonia digitata* (DE CALUWÉ et al. 2009; SCHUMANN et al. 2011), *Tamarindus indica* (FANDOHAN et al. 2010) or *Sclerocarya birrea* (GOUWAKINNOU et al. 2011).

The reported differences reflect preferences of plant and other product use, often brought along from other regions through migratory activities (four of the five ethnic groups migrated into the study area). Particularly for *P. biglobosa* and *A. digitata*, there is only low intersection of substitutes between the five ethnic groups. Four of five groups engage in both purchasing/cultivating products and NTFP collection – except Ditammarie people. Additionally, the Ditammarie are among the two ethnic groups which frequently mentioned not to have alternatives at all; the other one is the Fulani group. In contrast, a high proportion of alternative NTFP species, as identified with the Kabiyé and Yom, might also indicate low financial means to access marketed products and/or limited access to farmland to cultivate them oneself. However, insights from HEUBACH et al. (2011) suggest that there is no significant difference regarding land holding between groups. To further understand the underlying reasons for the choice of substitutes more research at the household level is needed.

6 CONCLUSION

If the provision of seeds of *Vitellaria paradoxa*, *Parkia biglobosa* and *Adansonia digitata* is limited, rural communities in savanna areas could built on a wide range of cultivated, purchased or wild plant and animal products to substitute for these NTFPs. However, the three species of focus remain superior to all of their substitutes both in terms of their contribution to daily diets and accessibility. They generally exceed their alternatives in terms of protein, fat and micronutrients, and they are semi-open access resources readily available without requiring costly financial means or equipment. Thus, they are most attractive to the rural poor. However, this unique combination of characteristics also reflects the other side of the medal: maintaining the supply of those NTFPs is most crucial for the poorest households and thus will be a major future challenge to secure a healthy, self-sufficient food provision and income sources.

Subsequently, there is concern to maintain the availability of *V. paradoxa*, *P. biglobosa* and *A. digitata* in existing agroforestry systems. To support this, future research should have a closer look at how tree domestication, seed quality and genetic diversity of the three focus species could help to improve yields, and underlying reasons for substitution patterns to help developing appropriate management measures.

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Impact of land use on juvenile densities of woody plants in a West African savanna

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Summary: In West African savannas, human land use affects the density of woody species seedlings and saplings (juveniles) by altering the state of the physical, chemical, and biological characteristics of the land resulting in different land-cover types. We determined juvenile densities of 25 characteristic woody savanna species on non-arable sites, in fallows and in a protected area (in total 39 plots), and analyzed the influence of land use on juvenile densities. We further related the influence of land use on juvenile densities to 23 environmental parameters describing soil properties and vegetation structure. Soil acidity, particle size distribution of the soil, and vegetation structure differed between land-cover types. In terms of human impact, we detected five groups of species responding similarly to land use. Although we detected significant differences in soil properties, their direct effects on juvenile densities are less pronounced than their indirect effects. By altering the availability of resources, soil properties affect height and cover of all plants growing in the surrounding of a young woody plant, increasing the competition for light, water and nutrients during the establishment and initial growth. These effects are intensified by human land use and vary between land-cover types.

Key words: abundance, Benin, human impact, soil conditions, vegetation cover, vegetation height

IMPACT DE L'UTILISATION DES TERRES SUR LES DENSITÉS JUVÉNILES DE PLANTES LIGNEUSES DANS UNE SAVANE D'AFRIQUE DE L'OUEST

Résumé: Dans les savanes de l'Afrique de l'Ouest, l'occupation des sols affecte la densité des semis et des jeunes plants des espèces ligneuses par son influence sur les caractéristiques physiques, chimiques et biologiques des terres, ce qui entraîne de différents types de couvert végétal. Nous avons déterminé la densité juvénile de 25 espèces caractéristiques de savane ligneuse sur des sites non arables, en jachère et dans une aire protégée (au total 39 parcelles), et nous avons analysé l'influence de l'utilisation des terres sur les densités juvéniles. Nous avons également mis en rapport l'influence de l'utilisation des terres sur les densités juvéniles avec 23 paramètres environnementaux décrivant les propriétés du sol et la structure de la végétation. L'acidité du sol, la répartition granulométrique du sol et la structure de la végétation différaient selon les types de couvert végétal. En termes d'impact humain, nous avons détecté cinq groupes d'espèces répondant de manière similaire à l'utilisation des terres. Bien que nous ayons détecté des différences significatives dans les propriétés du sol, leurs effets directs sur les densités juvéniles sont moins prononcés que leurs effets indirects. En modifiant la disponibilité des ressources, les propriétés du sol affectent la hauteur et la couverture de toutes les plantes qui poussent à l'entour d'une jeune plante ligneuse, augmentant la concurrence pour la lumière, l'eau et les nutriments pendant l'établissement et la croissance initiale. Ces effets sont intensifiés par l'utilisation des sols et varient selon les types de couvert végétal.

Mots clés: abondance, Bénin, impact humain, conditions du sol, couverture végétale, hauteur de végétation

AUSWIRKUNGEN DER LANDNUTZUNG AUF DAS VORKOMMEN VON GEHÖLZJUNGWUCHS IN EINER WESTAFRIKANISCHEN SAVANNE

Zusammenfassung: In den westafrikanischen Savannen beeinflusst die Landnutzung die Dichte der Gehölzkeimlinge und Jungpflanzen, indem sie physikalische, chemische und biologische Eigenschaften der Flächen verändert und zu unterschiedlichen Landnutzungstypen führt. Es wurde der Einfluss der Landnutzung auf die Individuendichte von Keimlingen und Jungpflanzen von 25 charakteristischen Savannengehölzarten auf nicht kultivierten Flächen, in Brachen und in einem Schutzgebiet (insgesamt 39 Parzellen) untersucht. Darüber hinaus haben wir den Einfluss der Landnutzung auf die Individuendichte mit 23 Umweltparameter in Beziehung gesetzt, die die Bodeneigenschaften und die Vegetationsstruktur beschreiben. Die Bodensäure, die Korngrößenzusammensetzung des Bodens und die Vegetationsstruktur unterscheiden sich zwischen den Landnutzungstypen. In Bezug auf den menschlichen Einfluss, ließen sich fünf Artengruppen unterscheiden, die jeweils ähnlich auf die Landnutzung reagieren. Obwohl wir signifikante Unterschiede in den Bodeneigenschaften festgestellt haben, sind ihre direkten Auswirkungen auf die Individuendichte der Gehölzkeimlinge und Jungpflanzen weniger ausgeprägt als ihre indirekten Effekte. Die Bodeneigenschaften verändern die Verfügbarkeit von Ressourcen und beeinflussen darüber die Höhe und Bedeckung der Pflanzen, die im Umfeld des Gehölzjungwuchses wachsen. Dadurch erhöht sich die Konkurrenz um Licht, Wasser und Nährstoffe für den Jungwuchs in seiner Etablierungs- und anfänglichen Wachstumsphase. Diese Effekte werden durch die Landnutzung verstärkt und variieren zwischen Landnutzungstypen.

Schlagworte: Abundanz, Benin, menschlicher Einfluss, Bodenbedingungen, Vegetationsbedeckung, Vegetationshöhe

1 INTRODUCTION

The savanna regions of West Africa are frequently affected by human-induced disturbances. Aside from agricultural activities (crop production and animal husbandry), the harvesting of timber and non-timber forest products affects savanna vegetation (see, e.g., WITTIG et al. 2002). During recent decades, social and economic conditions have changed dramatically (DESCROIX et al. 2009, NORRIS et al. 2010, OUEDRAOGO et al. 2010), causing habitat loss, the shortening of fallow periods, over-grazing and the removal and vitality impairment of reproductive individuals of trees and shrubs (e.g. by harvesting of non-timber forest products). JURISCH et al. (2012) showed that the population structure of some woody plant populations, especially tree populations, is strongly affected by human-induced disturbances, while others perform quite well under the current land use system, mainly shrub species. For many tree species, reproductive individuals of the sub-adult and adult stage were missing. This can reduce the availability of their seeds and may thereby lead to a lack of regeneration and a low density of their juveniles (young, immature individuals) (PLUMPTRE 1995, MAKANA & THOMAS 2004, McLAREN et al. 2005). This development becomes more pronounced as due to increased human pressure, habitats suitable for juvenile establishment are becoming fewer. In the long run, the observed results may have implications for local woody species composition.

In particular, the seedling and sapling stages are usually a critical phase in the regeneration of woody species, as for plants at these stages the risk of abiotic stress caused by human-induced disturbances (e.g. fire and livestock grazing) as well as soil conditions and biological interactions (intra- and interspecific plant competition) is very high (ABRAHAMSON 1980, BOND 2008, JURISCH et al. 2012, 2013; PRIOR et al. 2010, ZIDA 2007). Habitats like less disturbed termite mounds show a consistently higher species richness and diversity of juvenile woody plants than their surrounding savannas (ERPENBACH et al. 2014). Consequently, seedlings must quickly develop an effective root system to allocate and store nutrients and to gain access to water, which enhances the individual's ability to tolerate and be resilient to disturbances (GROSSNICKLE 2005, HOFFMAN et al. 2004, WIGLEY et al. 2009). The topsoil properties are important for the establishment of young plants, as most of their root biomass is located close to the surface (JEFFREY 1987, KAONGA & BAYLISS-SMITH 2012, KNOOP & WALKER 1985, WELTZIN & McPHERSON 1997). In situ experimental studies from semi-arid South Africa have revealed that herbaceous competition was intensified under nutrient-rich conditions by enhancing growth rates of grasses. This may lead to a decrease in seedling densities, as well as to changes in growth rates, morphology and resource allocation (BUSH & VAN AUKEN 1995, KRAAIJ et al. 2006, STAVER et al. 2009, VAN AUKEN & BUSH 1997, VAN DER WAAL et al. 2009).

The impact of human land-use on the density of seedlings and saplings of woody plants in West African savannas has been determined so far only for single species in comparative studies between protected and non-protected areas (DJOSSA et al. 2008, PARE et al. 2009, SCHUMANN et al. 2011) and in relation to management practices (DHILLON & GUSTAD 2004, KOUAMI et al. 2009, KY-DEMBELE et al. 2007).

These studies generally report higher seedling and sapling densities in non-protected areas with moderate human disturbance compared to protected sites. Prescribed fire, moderate livestock grazing and selective removal of trees were found to have an indirect positive effect on seedling and sapling densities and growth by reducing vegetation cover and thus, reducing intra- and interspecific plant competition for light, water and nutrients (DHILLON & GUSTAD 2004, DJOSSA et al. 2008, KELLY et al. 2004, WALKER et al. 1981). By contrast, some studies detected that fire and browsing may suppress the recruitment of young plants by removing above-ground plant parts or the entire plant. This is more pronounced in dry climate with low rainfall causing greater water stress and thus, limiting the regeneration potential of plants (FATUBARIN 1987, GIJSBERS et al. 1994, KESSLER & BREMAN 1991, MENAUT 1983, ZIDA et al. 2007, 2008). Aside from the direct damage of the plant, grazing can reduce fire frequency and intensity due to the reduction of the amount of inflammable biomass (WALKER et al. 1981, JEFFREY 1987, ARCHER 1995) and may change the availability of soil nutrients and structural properties of soil by deposition of dung and the impact of trampling (BRESHEARS et al. 1997, DAVENPORT et al. 1998, POSSE et al. 2000, SAVADOGO et al. 2007, VAN DER WAAL 2010). Fires have chemical and physical consequences, such as the mineralization of nutrients stimulating the growth of surviving species, the increase in soil compaction, soil temperature and a decrease in organic material in turn leading to lowered soil-water content (JEFFREY 1987, SNYMAN 1994). All these factors influence growing conditions for plants (MWAVU & WITKOWSKI 2008) and may facilitate or hinder the development of individuals.

Summarizing these studies, one can assume that human land-use may have either positive or negative effects on the density of woody species seedlings and saplings due to the change of the physical and biological characteristics of the land-cover types caused by human impact. Therefore, we expect to observe a significant effect of human land use on the density of seedlings and saplings by affecting population structure of woody plants and altering abiotic and biotic habitat conditions (SWAINE 1996). We further assume that the strength of this effect is related to species' ecological preferences, which refer to the environmental conditions under which the species is most likely to occur. Within this study, we investigated patterns of population densities of a broad set of characteristic savanna species to obtain a better understanding of the influence of land use and related environmental factors on the juvenile stages of woody species. We aim to answer the following questions:

- How are juvenile densities affected by land use?
- Can we identify specific environmental conditions, soil conditions and vegetation structure, determining juvenile densities?
- Does the density of reproductive adults have an effect on juvenile densities?

2 METHODS

2.1. Study site

The study was carried out around Sampeto village (11°40'-12°23' N, 2°04'-3°05' E) located in the northern part of Benin at the periphery of the W Transborder Park (Parc National du W), one of the largest protected areas in West Africa. Sampeto had 3725 inhabitants in 2013 (KNOEMA 2013), although this number has most likely increased since the last census. The area belongs to the North-Sudanian vegetation zone which is characterized by an average annual precipitation of 700-1000 mm and a 6 month lasting rainy season from May to October (BONOU 2008).

All field data were collected in the surroundings of Sampeto (within maximal distance of 10 km). The communal area of the village represents a typical example of a savanna landscape in West Africa with an alternating mosaic of croplands, fallows and non-arable land. The most common agricultural system is shifting cultivation where almost all land is used for agriculture excluding protected areas or areas ill-suited due to their relief conditions or where we find crusted soils or soils containing a high amount of gravel (RUTHENBERG 1980, FAO 1983, OKIGBO 1985, ALEXANDRE & KAÏRÉ 2001). Because the location is at the periphery of a national park (W National Park), we were also able to consider sites which are less altered by human impact – the buffer zone of the national park - and represent semi-natural conditions.

Harvesting of NTFPs for firewood, medical purposes or livestock forage is common in the settlement area, thus fallow areas and non-arable areas are equally exposed to harvesting activities. In the buffer zone, these activities are limited by law, but still some illegal timber extraction occurs. An integral part of land use is extensive livestock breeding of both cattle and small ruminants such as goats and sheep. Mixed livestock in herds of different size are rotationally grazed during the day affecting all land-cover types through grazing and trampling. The buffer zone is mainly grazed by cattle, but generally less altered by livestock grazing activities compared with the communal area. Fires are irregularly set by the farmers once or twice during the dry season in order to support the re-growth of palatable forbs and grasses and for protection against intensive fires at the end of the dry season. In the buffer zone, early fires are set for management purposes at the beginning of the dry season and during a period of about six weeks (from 2004 to 2009, GRÉGOIRE & SIMONETTI 2010). The fire activity tends to increase and clearly indicates an increased overall anthropogenic pressure on the protected areas. The mean fire density was three fires per 1000 ha between 2004 and 2009, and is approximately the same in the buffer zone and the adjacent communal area (SUN 2010, unpubl. data).

Three land-cover types were studied. (1) Tree and shrub savanna on shallow skeletal soils without prior cultivation, but with frequent use of non-timber forest products (NTFPs) and as pasture. This habitat is dominated by the shrub species *Detarium microcarpum* whereas the herbaceous layer is sparsely developed (hereafter referred to as 'non-arable'). (2) Tree and shrub savanna on nutrient poor-to-medium, previously cultivated soils (at least 10 y ago, with differ-

ent crops), frequent use of NTFPs and as pasture. The canopy layer is composed of different woody plants; such as *Piliostigma thonningii*, *Dichrostachys cinerea*, *Terminalia laxiflora* and *Flueggea virosa*. The herb layer is characterized by *Tephrosia pedicellata*, *Spermacoce ruelliae*; *Penisetum polystachion*, *Desmodium velutinum* and *Chasmodium caudatum* (hereafter referred to as 'fallow'). (3) Semi-natural tree and shrub savanna on medium soils covered with tall grasses, such as *Hyparrhenia involucreta* and the perennial species *Andropogon gayanus*, where use of natural resources is limited due to regulation by law (hereafter referred to as 'buffer zone'). The latter is located in the buffer zone of the W National Park, while the first two land-cover types can be found in the communal area. The studied land-cover types were comparable with respect to their adult vegetation composition (Appendix 1). Fallows and non-arable land are exposed to similar disturbance intensities (fire, grazing, harvesting) and are freely accessible. As a result of the stepwise land-use change, the landscape becomes fragmented and consists of patches of more or less native vegetation embedded into a matrix of different land-cover types, including non-arable sites and fallows (STOATE et al. 2001, GREEN et al. 2005, ABDULLAH & NAKAGOSHI 2006).

2.2 Vegetation data

Within each of the three land-cover types we randomly chose plots for vegetation sampling. The minimal distance between chosen plots was 100 m. The woody layer was investigated in 900 m² plots and the herb layer in 100 m² plots. The herb layer plots were randomly located inside the corresponding woody layer plots. Percentage canopy coverage of all vascular plant species, separately for the tree, shrub and herb layer, was estimated visually on each plot (NACOLMA et al. 2011).

To examine the density of juveniles and adults adequately, squared plots of two sizes were established at each study site. Adult individuals were sampled on 1800 m² plots, while juveniles were determined on four sub-plots (each with a size of 6.25 m²) nested in the 1800 m² plots. In total, 39 of these 1800 m² plots were investigated, 12 on non-arable sites, 17 on fallows, and 10 in the buffer zone. On each of the 6.25-m² subplots, numbers of juveniles were counted, comprising all young, immature individuals of the seedling and sapling stage smaller than 1 m. We analyzed trees and shrubs separately. Trees were defined as single-stemmed individuals branched above breast height (130 cm). Shrubs were shorter than 10 m in height and either with several straight stems, visibly connected at ground level or one single trunk with attached branches below breast height (POWELL 2005, NZUNDA et al. 2007). Biometric data for adults with diameter at breast height (dbh) of more than 5 cm were collected, measuring dbh (cm) and height (m). For multi-stemmed individuals, all stems with dbh larger than 5 cm were measured. According to PRETZSCH (2002) we used the equation $\sqrt{\sum d_i^2}$ to reduce multiple diameter of a multi-stemmed individual to a single composite measurement in order to be able to compare it with those of single-stemmed trees.

To account for weather-related annual and seasonal variation, vegetation sampling was repeated five times. Three censuses were conducted at the end of the dry season (May/June 2008, May/June 2009 and May/June 2010), and two were carried out at the end of the rainy season (September/October 2008 and September/October 2009). The plant species nomenclature followed the African Plants Database (<http://www.ville-ge.ch/musinfo/bd/cjb/africa>).

2.3. Environmental data

Environmental conditions were characterised by the vegetation structure and soil analysis. Structural characteristics of the land-cover types were described as cover and height of the tree and shrub layer (on plots of 1800 m²) and the herbaceous layer (on one subplot of 100 m²) in September/October 2007. Measurements were performed for the tree and shrub layer (woody plants > 5 m) and the herbaceous layer (all plants up to 0.5 m in height).

On each of the 1800-m² plots, we took three randomly placed soil samples of the upper 0-20 cm layer in May 2009. These three samples were pooled and subsequently analysed for plant-available phosphorus, potassium, nitrogen, organic and inorganic carbon, cation exchange capacity (CEC, with ion concentrations of sodium, potassium, calcium, and magnesium), particle size distribution (PSD), and pH. Plant-available phosphorus (phosphorus pentoxide, P₂O₅) and potassium (potassium oxide, K₂O) determination was carried out by calcium-acetate-lactate (CAL)-method (SCHÜLLER 1969, 1973); pH was measured in aqueous solution against 0.1 M KCl (MEIWES et al. 1984) and 0.01 M CaCl₂ solution (DIN 19 684, sheet 1 1977). We determined organic carbonate by the wet combustion method (Lichtenfelder (DIN 19 684, sheet 2 1977) and colorimetric detection using spectral photometer Cadas 100 (Lange). Nitrogen was determined quantitatively by the Kjeldahl-titrimetric method modified by BREMMER (1960, 1965). Cation exchange capacity and ion concentrations were determined in BaCl₂ solution buffered with triethanolamine by the Mehlich-extraction method according to DIN 19 684, sheet 8 (1977). PSD for fine soil particles was determined with Köhn-pipette method (DIN 19 683, sheet 1 and 2 1973).

2.4 Differences in environmental factors between land-cover types

We calculated the mean of all environmental parameters per land-cover type and used Tukey's multiple comparison tests to search per environmental parameter for differences between land-cover types. Prior to statistical analysis, numerical variables were normalized by scaling them between zero and one. Such standardization is required to make the explanatory variables that were measured on different scales comparable. Furthermore, all environmental variables were checked for possible inter-correlations. Using a correlation threshold of $r^2 > 0.7$, we found that the amount of potassium and potassium oxide were highly correlated ($r^2 = 0.785$) and consequently removed potassium oxide from the further analyses (for Pearson correlation coefficients see Appendix 2).

2.5 Influence of land use and environment on juvenile densities

Juveniles were recorded individually, so we were able to distinguish between established individuals and new recruits. For our analysis, we only chose individuals that were present at the end of the dry season and at the end of the rainy season in 2009. In total, we considered 16 shrub and seven tree species (for density values see Appendix 3). To analyze if a population has good regeneration relative to the number of adult trees, we determined the mean of the density per hectare of adult individuals (trees: dbh > 15 cm. shrubs: dbh > 12 cm) per species.

The statistical analyses addressed two different issues for each species: (1) to determine the influence of land use on juvenile densities, and (2) to determine which environmental conditions affect juvenile densities additional to the influence of land use.

To answer the first issue, we calculated a linear mixed-effect model (LME) with number of juveniles as response variable and land-cover type (factor) as explanatory variable was calculated. To correct for potential auto-correlation in time, we induced census as random factor. These LMEs were tested for differences between the land-cover types using Tukey's multiple comparison tests. Based on these tests, we merged land-cover types without significant differences, resulting in LMEs showing which land-cover types differ in seedling densities. Using these models, we assigned each tree and shrub species to a particular group. For example, two species that showed no statistical differences in juvenile densities between fallows and non-arable sites but differed from those in the buffer zone were grouped together even though the juvenile density of two species differed.

To address the environmental conditions which alter juvenile densities, in addition to the influence of land use, we searched for environmental parameters significantly related to each species group. Only environmental parameters differing between land-cover types were used. These pre-selected factors were taken as explanatory variables in generalized linear models (GLM using juvenile densities as dependent variable) using the quasi-Poisson model, as this model described the distribution of the residuals for count data, e.g. the juvenile densities, best. We performed a model simplification by omitting non-significant parameters until only significant parameters remained (CRAWLEY 2007).

All statistical analyses were done using the software package R (version 2.13.2) with the additional package *vegan* (version 2.0-5), "lme4" (version 0.999999-0) and "multcomp" (version 1.2-15).

3 RESULTS

3.1. Differences in environmental factors between land-cover types

We found 11 environmental parameters differing significantly between the land-cover types: height of herb layer, cover of tree/shrub and herb layer characterising the vegetation structure and eight soil parameters (Table 1).

Table 1: Mean (\pm SE) of 23 environmental parameters (soil parameters and vegetation structural data) per land-cover type. The samples were taken at 39 plots (12 on non-arable sites, 17 in fallows, 10 in the buffer zone), different letters (a, b and c) indicate significant differences ($P < 0.05$, highlighted with *). BS-value: percentage base saturation, S-value: Quantity of basic interchangeable Ions / Moyenne (\pm SE) de 23 paramètres environnementaux (paramètres du sol et données structurales de la végétation) par type de couvert végétal. Les échantillons ont été prélevés sur 39 parcelles (12 sur les sites non arables, 17 dans les jachères, 10 dans la zone tampon), différentes lettres (a, b et c) indiquent des différences significatives ($P < 0,05$, accentué avec *). Valeur BS: pourcentage de saturation de base, valeur S: Quantité d'ions interchangeables de

Environmental parameter	Non-arable (n = 12)	Fallows (n = 17)	Buffer zone (n = 10)
Cover tree/shrub layer (%)*	29.8 \pm 4.71 a	19.7 \pm 1.29 ab	13.3 \pm 2.1 b
Height herb layer (cm) *	50.2 \pm 12.46 a	42.8 \pm 6.32 a	184 \pm 5.42 b
Cover herb layer (%)*	48.6 \pm 3.68 a	62.4 \pm 4.25 b	71.9 \pm 2.61 b
CECpot (cmolc/kg) *	73.2 \pm 9.12 a	49.5 \pm 4.29 b	38.1 \pm 5.14 b
Medium silt (%)*	9.3 \pm 0.52 a	8.1 \pm 0.3 b	8.6 \pm 0.47 ab
Clay < 2 μ m (%)*	21.1 \pm 1.34 a	18.6 \pm 1.04 a	13.4 \pm 0.6 b
K ₂ O (mg/100g) *	6.0 \pm 0.36 a	8.4 \pm 0.73 b	7.8 \pm 0.77 ab
Coarse silt (%)*	32.4 \pm 1.35 ab	31.2 \pm 1.69 a	38.6 \pm 1.78 b
pH*	4.8 \pm 3.07 a	5.4 \pm 2.83 b	5.6 \pm 3.85 b
K ⁺ (mmolc/kg) *	0.8 \pm 0.05 a	1.1 \pm 0.11 ab	1.4 \pm 0.16 b
BS-value*	34 \pm 3.27 a	48.3 \pm 2.07 b	54.9 \pm 2.78 b
C/N-ratio	20.1 \pm 2.08 a	22 \pm 2.18 a	20.4 \pm 2.51 a
Ca ²⁺ (mmolc/kg)	25.9 \pm 1.17 a	35.4 \pm 3.89 a	34.6 \pm 5.21 a
Coarse sand (%)	7.9 \pm 1.54 a	8.6 \pm 1.89 a	6.4 \pm 2.22 a
C-organic (%)	1.8 \pm 0.16 a	1.7 \pm 0.18 a	1.5 \pm 0.16 a
Fine sand (%)	18.2 \pm 1.2 a	21.4 \pm 1.45 a	22.7 \pm 1.15 a
Fine silt (%)	4.1 \pm 0.22 a	3.8 \pm 0.23 a	3.9 \pm 0.15 a
Medium sand (%)	7.1 \pm 0.61 a	7.9 \pm 0.65 a	6.5 \pm 0.36 a
Mg ²⁺ (mmolc/kg)	7.7 \pm 0.78 a	10.5 \pm 0.85 a	10.7 \pm 1.2 a
Na ⁺ (mmolc/kg)	0.4 \pm 0.07 a	0.3 \pm 0.03 a	0.3 \pm 0.04 a
N-total (%)	0.1 \pm 0.01 a	0.1 \pm 0 a	0.1 \pm 0.01 a
P ₂ O ₅ (mg/100g)	0.3 \pm 0.05 a	0.3 \pm 0.02 a	0.3 \pm 0.03 a
S-value	34.8 \pm 1.36a	47.4 \pm 4.6 a	47 \pm 6.31 a

On non-arable sites, we detected the highest amount of acid exchangeable cations (CECpot), the lowest amount of exchangeable acid cations (BS-value), the lowest pH as well as the lowest percentage cover of the herb layer, which differed significantly from fallows and the buffer zone (Table 1). Site conditions on fallows were intermediate to those conditions on non-arable sites and the buffer zones, as we did not detect any environmental parameter that was significantly higher or lower on fallows compared to the other land-cover-types. The low percentage of clay in the subsurface and the height of the herb layer, were characteristic for the buffer zone and differed significantly from the communal area (non-arable sites and fallows).

3.2 Influence of land use and environment on juvenile densities

The 16 shrub and seven tree species were assigned to five groups (A-E). Each group comprises species responding similar to land use (Table 2). For groups A-D we detected several but different soil parameters as significantly related to juvenile densities, whereas no parameter was found for group E (Table 3).

The tree species *Pterocarpus erinaceus* was the only member of group A where juvenile densities differed between all

land-cover types. Highest juvenile density of this species was found in the buffer zone whereas the highest number of adults was found on fallows. For species of group B (*Annona senegalensis*, *Crossopteryx febrifuga*, *Lannea acida* and *Terminalia avicennioides*) no differences were found between non-arable land and fallows, but they differed from the buffer zone. All species had high juvenile densities in the communal area, especially on fallows: Only *C. febrifuga* showed more juveniles in the buffer zone compared to the communal area. For group A and B, the height of the herb layer was the only significant environmental parameter explaining differences in juvenile densities between all land-cover types and, and in the case of group B, between the communal area (non-arable and fallows) and the buffer zone. Group C was the largest group, comprising seven shrub and two tree species with similar densities on non-arable land and in the buffer zone, which differed from those on fallows. The vegetation structure (height of the herb layer and percentage cover of the tree/shrub layer), the amount of exchangeable acid cations (CECpot) and the percentage of the coarse-grained silt fraction were the parameters determining differences in the density of juveniles between fallows and those on non-arable sites and the buffer zone. Eight shrub and tree species, whose juvenile densities did not differ between fallows and the buffer zone but on non-arable

Table 2: Juvenile densities, sampled on one subplot of 100 m², of the 25 analyzed woody species. Densities are presented per land-cover type (non-arable land: n=12, fallow: n=17 and buffer zone: n=10). Similarity between land-cover types concerning the juvenile densities, calculated by a linear-mixed-effect model and a subsequent Tukey's multiple comparison test, is marked by (&), dissimilarity by (≠). Growth form: S: shrub, T: tree. / Densités juvéniles, échantillonnées sur une sous-parcelle de 100 m², des 25 espèces ligneuses analysées. Les densités sont présentées par type de couvert végétal (terres non arables: n = 12, jachère: n = 17 et zone tampon: n = 10). La similitude entre les types de couverture concernant les densités juvéniles, calculée par un modèle à effet mixte linéaire et un test de comparaison multiple de Tukey subséquent, est indiquée par (&), dissimilarité par (≠). Forme de croissance: S: arbuste, T: arbre.

Species	Family	Land-cover type		
		Non-arable	Fallow	Buffer zone
Group A: non-arable ≠ fallows ≠ buffer zone				
<i>Pterocarpus erinaceus</i> (T)	Fabaceae	23 ± 3.1	10 ± 1.7	38 ± 5.4
Group B: non-arable & fallows ≠ buffer zone				
<i>Annona senegalensis</i> (S)	Annonaceae	43 ± 6.4	62 ± 5.8	0 ± 0.5
<i>Crossopteryx febrifuga</i> (S)	Rubiaceae	15 ± 3.4	10 ± 1.7	23 ± 5.0
<i>Lansea acida</i> (T)	Anacardiaceae	26 ± 4.4	36 ± 4.1	2 ± 1.1
<i>Terminalia avicennioides</i> (T)	Combretaceae	36 ± 6.1	49 ± 5.4	10 ± 3.2
Group C: non-arable & buffer zone ≠ fallows				
<i>Acacia hockii</i> (S)	Mimosaceae	0 ± 0.0	13 ± 3.2	2 ± 1.0
<i>Anogeissus leiocarpa</i> (T)	Combretaceae	27 ± 7.0	79 ± 14.7	12 ± 3.4
<i>Combretum collinum</i> (S)	Combretaceae	45 ± 5.0	133 ± 15.7	31 ± 7.8
<i>Dichrostachys cinerea</i> (S)	Mimosaceae	126 ± 25.8	223 ± 29.6	14 ± 4.6
<i>Diospyros mespiliformis</i> (S)	Ebenaceae	1 ± 0.7	54 ± 11.2	2 ± 1.0
<i>Feretia apodanthera</i> (S)	Rubiaceae	7 ± 1.7	68 ± 11.8	2 ± 1.0
<i>Gardenia ternifolia</i> (S)	Rubiaceae	22 ± 5.4	13 ± 2.0	14 ± 3.7
<i>Ptilostigma thonningii</i> (S)	Caesalpiniaceae	13 ± 2.2	43 ± 4.3	4 ± 1.3
<i>Strychnos spinosa</i> (S)	Strychnaceae	35 ± 5.8	26 ± 3.4	57 ± 7.6
<i>Vitellaria paradoxa</i> (T)	Sapotaceae	40 ± 13.5	85 ± 15.8	14 ± 2.9
Group D: fallows & buffer zone ≠ non-arable				
<i>Combretum glutinosum</i> (S)	Combretaceae	23 ± 4.0	4 ± 1.1	4 ± 1.3
<i>Combretum nigricans</i> (S)	Combretaceae	93 ± 16.1	34 ± 5.5	10 ± 2.3
<i>Detarium microcarpum</i> (S)	Caesalpiniaceae	461 ± 53.7	45 ± 6.7	0 ± 0.0
<i>Isobertinia doka</i> (T)	Caesalpiniaceae	12 ± 2.7	43 ± 4.9	35 ± 6.3
<i>Philenoptera laxiflora</i> (T)	Fabaceae	1 ± 0.6	19 ± 4.8	30 ± 5.2
<i>Pteleopsis suberosa</i> (T)	Combretaceae	222 ± 41.8	71 ± 9.8	2 ± 1.0
<i>Stereospermum kunthianum</i> (T)	Bignoniaceae	95 ± 9.4	44 ± 5.3	30 ± 4.9
Group E: non-arable & fallows & buffer zone				
<i>Bombax costatum</i> (T)	Bombacaceae	7 ± 1.6	9 ± 1.8	8 ± 1.8
<i>Combretum molle</i> (S)	Combretaceae	68 ± 9.6	65 ± 6.7	69 ± 13.4
<i>Gardenia aqualla</i> (S)	Rubiaceae	4 ± 1.8	9 ± 3.0	8 ± 2.3

sites, were assigned to group D. Some species (*Combretum glutinosum*, *Detarium microcarpum*, *Pteleopsis suberosa* and *Stereospermum kunthianum*) had the highest juvenile densities on those non-arable sites where we also found a high number of adult individuals of this species (Table 4). In the case of *Combretum nigricans*, we found the highest recruitment rates on non-arable site but less adult individuals compared to fallows. Differences in the percentage cover of the herb layer, pH, CECpot and the percentage of clay in the top-soil were the most important soil parameters significantly impacting on juvenile densities of species affiliated to group D. Species of group E (*Bombax costatum*, *Combretum molle*, *Gardenia aqualla*) showed no influence of land use on juvenile abundances (Tables 2, 3). For *B. costatum*, juvenile densities were low in all land cover types similar

as the number of adults. The shrub species *C. molle* showed high recruitment rates in all land cover types which corresponded well to similarly high number of adults (Table 4).

4 DISCUSSION

4.1 Differences in environmental facts between land-cover types

The detected differences between different land-cover types due to chemical and physical soil properties as well as characteristics of the vegetation structure were in line with observations by HAHN (1996) that physical soil properties determined the occurrence of vegetation types in West African savannas. However, as also found by ORTHMANN (2005), we

Table 3: Influence of environmental factors on juvenile densities by species affiliation groups A-E. The GLMs (quasi-Poisson model) were fitted using juvenile densities as dependent variable, and environmental variables (numerical) as explanatory variables. / Influence des facteurs environnementaux sur les densités juvéniles selon les groupes d'affiliation des espèces A-E. Les GLM (quasi-Poisson model) ont été ajustés en utilisant la densité juvénile comme variable dépendante et les variables environnementales (numériques) comme variables explicatives.

	Estimate	SE	t value	Pr (> t)
group A: non-arable ≠ fallows ≠ buffer zone				
Intercept	5.63	0.21	26.6	<0.001***
Height herb layer (cm)	0.55	0.17	3.2	0.003**
group B: non-arable & fallows ≠ buffer zone				
Intercept	6.02	0.14	42.9	<0.001***
Height herb layer (cm)	-0.48	0.17	-2.9	0.005**
group C: non-arable & buffer zone ≠ fallows				
Intercept	63.75	0.15	45.9	<0.001***
Height herb layer (cm)	-0.64	0.17	-3.7	<0.001***
Cover tree/shrub layer (%)	0.29	0.13	2.2	0.026*
CECpot (cmolc/kg)	-0.45	0.17	-2.7	0.007**
Medium silt (%)	-0.29	0.13	-2.3	0.023*
group D: non-arable ≠ fallows & buffer zone				
(Intercept)	6.34	0.16	39.4	<0.001***
Cover herb layer (%)	-0.34	0.17	-2.0	0.043*
pH	-0.62	0.23	-2.7	0.007**
CECpot (cmolc/kg)	0.61	0.14	4.3	<0.001***
Clay < 2µm (%)	-0.49	0.14	-3.4	<0.001***
group E: non-arable & fallows & buffer zone				
(Intercept)	6.10	0.20	30.4	<0.001***

additionally detected soil acidity and alkalinity indicated by pH and percentage base saturation (BS-Value) as important factors differing between land-cover types; in our case the values were increased in the communal area (non-arable sites and fallows) compared to the buffer zone.

4.2 Influence of land use and environment on juvenile densities

In general, in grass-dominated savanna ecosystems, juveniles compete during the establishment and initial growth mainly with stand-forming tall grasses. Such grasses as *Andropogon gayanus* and *Hyparrhenia involucrata* can be frequently found in high abundances in the buffer zone. However, we detected a high number of juveniles of *Pterocarpus erinaceus* in the buffer zone; thus, we suppose that other factors besides the competition between young woody plants and grasses are responsible for the contrasting performance pattern. This species is one of the five most important fodder tree species in the study area (L. HOUËSSOU, pers. comm.) and is pruned to provide additional forage for the livestock during the dry season. Higher densities of large reproductive trees were found on fallows compared to the buffer zone as many mature trees are maintained when land is cleared for agriculture due to the immediate value of the foliage for the cattle. This may influence the relative abundance of regeneration detectable on a site (MILTON 1995). Aside from the fact that cutting of large stems and pollarding in the buffer zone is prohibited and can have a significant impact on reproduction and on population viability over the long term (DHILLION & GUSTAD 2004, GAOUË

& TICKTIN 2008, HALL & BAWA 1993, PETERS 1990), high juvenile densities may be due to a reduced grazing intensity in the buffer zone as young leaves of this species are preferably consumed by livestock (BAYER 1990, DUVAL 2008, GLELE KAKAÏ et al. 2009).

The lower juvenile density of *Crossopteryx febrifuga* in the communal area compared to the buffer zone may be linked to the high grazing pressure in the communal area that may reduce the number of young plants. The species re-sprouts early after the dry season and is preferably browsed by cattle as our grazing observations have shown. These observations are supported by our results of a previous study where we detected many reproductive trees in the communal area, especially on non-arable sites (JURISCH et al. 2012). For the buffer zone our results imply that the high amount of silt relates to an increased water-holding capacity compared to non-arable sites and fallows. Thus, coupled with a high percentage base saturation, the soils in the buffer zone provide ideal growing conditions for plants. On sites where nutrient availability and water supply are high, grasses, in particular, can quickly form an almost continuous vegetation cover and may repress juvenile woody plants by competing for light, water and nutrients during their establishment and initial growth phase (HARPER 1977, JURENA & ARCHER 2003, RIGINOS 2009, VANDENBERGHE et al. 2006). This corresponds to the findings from MWAVU et al. (2009) who detected competition by the ground vegetation as the most important factor reducing the survivorship of slower-growing, young woody plants. As detected in this study, the result is a reduced seedling density. Additionally, the tall grasses

Table 4: Mean (\pm S.E.) of the density (ha) of adult individuals per species. For shrubs, adult individuals have a diameter in breast height (dbh) > 12cm and trees: dbh > 15 cm. For group details see Table 1. / Moyenne (\pm S.E.) de la densité (ha) d'individus adultes par espèce. Pour les arbustes, les individus adultes ont un diamètre en hauteur de poitrine (dbh) > 12cm et arbres: dbh > 15 cm. Pour les détails du groupe, voir le tableau 1.

Life form	Species	Adults		
		Non-arable	Fallows	Buffer zone
Group A: non-arable \neq fallows \neq buffer zone				
tree	<i>Pterocarpus erinaceus</i> Poir.	0.2 \pm 0.1	0.5 \pm 0.2	0.2 \pm 0.1
group B: non-arable & fallows \neq buffer zone				
shrub	<i>Annona senegalensis</i> Pers.	1.2 \pm 0.4	0.5 \pm 0.3	0.0 \pm 0.0
shrub	<i>Crossopteryx febrifuga</i> (Afzel. ex G.Don) Benth.	6.6 \pm 1.4	0.9 \pm 0.3	5.0 \pm 1.0
tree	<i>Lannea acida</i> A.Rich.	1.2 \pm 0.3	0.9 \pm 0.2	2.1 \pm 0.5
tree	<i>Terminalia avicennioides</i> Guill. & Perr.	1.2 \pm 0.5	0.4 \pm 0.1	0.3 \pm 0.2
Group C: non-arable & buffer zone \neq fallows				
shrub	<i>Acacia hockii</i> De Wild.	0.0 \pm 0.0	0.1 \pm 0.1	0.0 \pm 0.0
tree	<i>Anogeissus leiocarpa</i> (DC.) Guill. & Perr.	0.1 \pm 0.1	0.8 \pm 0.3	0.8 \pm 0.3
shrub	<i>Combretum collinum</i> Fresen.	0.8 \pm 0.5	1.4 \pm 0.4	0.4 \pm 0.3
shrub	<i>Dichrostachys cinerea</i> (L.) Wight & Arn.	0.0 \pm 0.0	0.1 \pm 0.1	0.0 \pm 0.0
shrub	<i>Diospyros mespiliformis</i> Hochst. ex A.DC.	0.2 \pm 0.2	0.4 \pm 0.3	0.0 \pm 0.0
shrub	<i>Feretia apodanthera</i> Delile	0.3 \pm 0.2	0.3 \pm 0.2	0.4 \pm 0.3
shrub	<i>Piliostigma thonningii</i> (Schumach.) Milne-Redh.	0.3 \pm 0.2	3.0 \pm 0.8	0.4 \pm 0.3
shrub	<i>Strychnos spinosa</i> Lam.	0.6 \pm 0.4	0.1 \pm 0.1	0.4 \pm 0.3
tree	<i>Vitellaria paradoxa</i> C.F.Gaertn.	2.5 \pm 0.5	2.5 \pm 0.5	4.0 \pm 1.1
Group D: non-arable \neq fallows & buffer zone				
shrub	<i>Combretum glutinosum</i> Perr. ex DC.	2.9 \pm 0.7	0.8 \pm 0.3	0.7 \pm 0.4
shrub	<i>Combretum nigricans</i> Lepr. ex Guill. & Perr.	1.2 \pm 0.6	2.0 \pm 0.8	0.0 \pm 0.0
shrub	<i>Detarium microcarpum</i> Guill. & Perr.	14.2 \pm 4.3	0.7 \pm 0.3	1.1 \pm 0.6
shrub	<i>Gardenia ternifolia</i> Schumach. & Thonn.	0.2 \pm 0.2	0.2 \pm 0.2	0.0 \pm 0.0
tree	<i>Isoblerlinia doka</i> Craib & Stapf	1.5 \pm 0.4	2.3 \pm 0.5	4.3 \pm 1.1
tree	<i>Phileoptera laxiflora</i> (Guill. & Perr.) Roberty	0.0 \pm 0.0	0.0 \pm 0.0	0.6 \pm 0.3
shrub	<i>Pteleopsis suberosa</i> Engl. & Diels	1.4 \pm 0.6	0.1 \pm 0.1	0.0 \pm 0.0
tree	<i>Stereospermum kunthianum</i> Cham.	0.1 \pm 0.1	0.0 \pm 0.0	0.0 \pm 0.0
Group E: non-arable & fallows & buffer zone				
tree	<i>Bombax costatum</i> Pellegr. & Vuill.	0.0 \pm 0.0	0.1 \pm 0.1	0.1 \pm 0.1
shrub	<i>Combretum molle</i> R.Br. ex G.Don	2.0 \pm 0.5	3.2 \pm 1.0	2.5 \pm 0.6
shrub	<i>Gardenia aqualla</i> Stapf & Hutch.	0.0 \pm 0.0	0.0 \pm 0.0	0.7 \pm 0.6

increase the fuel load and therefore, the potential for high-intensity fires causing a decrease in juvenile densities due to fire-induced mortality (BATIONO et al. 2001, LUOGA et al. 2004, ZIDA 2007). However, burning may stimulate the growth of surviving species and the colonization of species because of the release of plant nutrients and through a range of indirect effects, e.g. decreased shade, higher soil temperatures and reduced competition affecting the growing performance of young plants ('ash-bed' effect, HARPER 1977, JEFFREY 1987, RIGINOS 2009, VANDENBERGHE et al. 2006).

For species affiliated to group C, beneficial effects through human-induced disturbances positively affect juvenile densities, as their juvenile densities are highest on fallows (but compare *Gardenia ternifolia* and *Strychnos spinosa*). These species are well adapted to the alternating cycles of cultivation and fallows like the shrub *Combretum collinum* (NACOUUMA et al. 2011), and *Piliostigma thonningii* which is known as invasive species on fallows regenerating from the

remaining rootstock left after the field clearing (ARBONNIER 2002, BELLEFONTAINE 2005, NIKIEMA 2005). The competitive strength of these species is expressed by their healthy population structure, showing well-shaped size-class distributions with high numbers of juveniles and a gradual decline with increasing stem diameter (JURISCH et al. 2012). In this study, we also detected a high juvenile density and a large number of adult trees for *P. thonningii*. Human activities can have an indirect positive effect on seedlings and saplings by providing diverse, small-scale habitats that vary in time, such as bare soils on fallows, or by reducing vegetation cover. We found that percentage cover of the tree and shrub layer and the height of the herb layer positively affect juvenile densities on fallows. Such opening of the canopy is beneficial for the germination of seeds; in particular pioneer species like *Anogeissus leiocarpa*, whose seeds primarily germinate on bare soils, are favoured on fallows compared to sites with a dense vegetation cover (BOGNOUNOU et al. 2010, SACANDE & SANOGO 2007). We also suppose

that the facilitation of some species by traditionally managed agroforestry systems can affect woody plant populations by altering the relationship between juveniles and adult trees (JURISCH et al. 2012, PARE et al. 2009). *Vitellaria paradoxa*, the shea tree, has a high socioeconomic importance and in particular, individuals with a high fruit yield are spared when woodland is cleared for agriculture (LOVETT & HAQ 2000). Once the land becomes inadequate for crop production, it is abandoned and a few trees producing high numbers of off-springs are left. This may explain the high number of juveniles for *V. paradoxa* in fallows and a low number of adults compared to the buffer zone, where we found significantly less juveniles.

For species assigned to group D (non-arable sites differed from fallows and the buffer zone), high juvenile densities of some species (*Detarium microcarpum*, *Combretum glutinosum*, *C. nigricans*, *Pteleopsis suberosa* and *Stereospermum kunthianum*) might be related to species' ecological preferences or tolerance to specific soil conditions, such as increased soil acidity. The soils of non-arable sites were more acidic than those on fallows and in the buffer zone (high CECpot and low pH); nevertheless, the soils were only slightly acidic which promotes nutrient availability and plant growth. However, for two species, *Isobertlinia doka* and *Philenoptera laxiflora*, we detected the lowest juvenile density on non-arable sites compared to fallows and the buffer zone. Although ARBONNIER (2002) indicated habitat preferences for *I. doka* to loamy, well-drained soils, we suppose that rather human-induced changes in the population structure affect juvenile densities of this species (JURISCH et al. 2012). Low numbers of juveniles may be due to a low density of mature individuals on non-arable sites, producing less offspring, or in the case of *P. laxiflora*, leaves are preferably browsed or used as fodder for goats (ARBONNIER 2002, L. HOUESSOU, pers. comm.), which may limit the number of juveniles and reduce the population viability as well (DHILLION & GUSTAD 2004, GAOUE & TICKTIN 2008, HALL & BAWA 1993). For *I. doka*, some studies showed that the density of seedlings and saplings was more abundant below mature trees as the main dispersal mode of the species is dropping the seeds from pods under the mother tree and suckering that encourage aggregated distribution (BATIONO et al. 2005, DOURMA et al. 2006). Habitat loss and accelerated mortality of adults may have a great impact on juvenile densities of such species where the larger mother tree shelters the smaller, fire and drought sensitive seedlings. The species *P. laxiflora* mainly reproduces by seeds, thus, low numbers of juveniles may be due to the lack of reproductive individuals. In comparison, for *D. microcarpum*, *C. nigricans*, *P. suberosa* and *S. kunthianum*, the number of mature individuals was highest on non-arable sites compared to fallows and the buffer zone. The ability of vegetative reproduction can also be important for explaining differences between adult and juveniles densities, such as in the case of *S. kunthianum*. For this species, a low number of adults or even the lack of adults, such as in fallows and in the buffer zone, does not necessarily have implications for the number of observed juveniles. For *S. kunthianum* it is known, for example, that once established, juveniles develop extensive and widespread root systems under the soil surface, enabling them to set up offspring through vegetative repro-

duction, building a net of connected juveniles (HOFFMAN et al. 2004; OUEDRAOGO 2006; GROSSNICKLE 2005; WIGLEY et al. 2009).

Juvenile densities of *Combretum molle* were high in all land-cover types what is consistent with findings of a former study, where we detected a similar pattern for sub-adult and adult individuals of *C. molle*, in relation to land use (JURISCH et al. 2012). This species is not site-specific and shows wide ecological amplitudes (ARBONNIER 2002, ORWA et al. 2009). The species-specific characteristics, to reproduce vegetatively and to re-sprout after damaging, enhance its competitive strength and allow its persistence in many habitats (BOND & MIDGLEY 2001, DEVINEAU & FOURNIER 2005, DROBNIK et al. 2011, LAVOREL et al. 1997). However, *Gardenia aqualla* preferably grows in shady depressions or on alluvial terraces and has a scattered distribution by nature (ARBONNIER 2002) which might result in this low number of juveniles in all land-cover types. *Gardenia aqualla* is characteristic for sites with low vegetation cover (SCHMIDT & ZIZKA 2014). The affiliation of *B. costatum* to this group might indicate an overall harvesting pressure across the species in all land-cover types; the wood of this tree species is usable as lumber and its fibers are mainly used for stuffing, especially for mattresses and pillows (ARBONNIER 2002, OYEN 2011). The flowers are the main ingredient for a sauce and were often collected through cutting of the entire branch. As mentioned before, the removal of large reproductive trees and plant parts can reduce the availability of seeds and might reduce the overall density of juveniles in an area if the impact is not compensated by their life histories as is the case for *B. costatum* (GAOUE & TICKTIN 2008, SCHUMANN et al. 2011, TICKTIN 2004). Furthermore, its leaves are highly digestible and eaten by livestock, further reducing the number of young individuals.

5 CONCLUSION

Land use was shown to significantly affect juvenile densities of almost all studied woody species, as demonstrated by a grouping of species according to their observed densities. Almost all species (20 out of 25 species) showed higher juvenile densities in the communal area compared to the buffer zone. For those species, we also expect a positive development of the population in the long-run as many woody species showed high survival and growth rates in the communal area (survival probability $> 1 \cdot 10^{-6}$, JURISCH et al. 2013). We have shown that many species regenerate well despite low numbers of adult individuals. Thus, it seems that dispersal limitation is not the major factor controlling juvenile densities (see also PARE et al. 2009).

We determined that the soil acidity and physical properties of the soil sub-surface horizon and vegetation structure are important factors differing between the land-cover types non-arable, fallows and the buffer zone. Although we detected significant differences in soil properties, their direct effects on juvenile densities are less pronounced than their indirect effects by altering the availability of resources (water and nutrients) for plants. Particularly in the buffer zone, the effect of below- and above-ground competition for space, light, water and nutrients may rather limit esta-

blishment and growth of seedlings and saplings, indicating a strong impact of human activities on plant populations by altering the relative ratio between grasses and woody plants (BOND 2008, SANKARAN et al. 2008, SCHOLLES & ARCHER 1997). We showed that physical soil properties affect growing conditions for juveniles on non-arable sites and on fallows; especially through its effect on the amount of water that can be held and on the distribution of water within the soil. A good water-holding capacity of the soil might extend the growing season for a longer time by preserving soil water into the dry season or between rainfalls (MCNAUGHTON et al. 1983) and thus enhance the establishment of juveniles. For plants growing on non-arable sites, drought resistance as well as early development of an effective root system to gain access to water may be an important feature enhancing the individual's ability to low rainfall.

Due to the ongoing land use changes causing habitat loss, the shortening of fallow periods, and over-grazing, diverse sites for juveniles are becoming diminished. This development becomes more pronounced as the current adult populations are already under high human pressure (e.g. harvesting of non-timber forest products), causing removal and impairment of the vitality of reproductive individuals. This can reduce the availability of seeds and may thereby lead to a lack of regeneration (MAKANA & THOMAS 2006, MCLAREN et al. 2005, PLUMPTRE 1995).

Both processes, loss of established individuals as a potential seed source and lack of regeneration due to high juvenile mortality by environmental factors, may result in a total loss of recruitment in an area. More studies on populations in their natural habitat, specifically in relation to land use and environmental conditions, are required to develop species-specific management strategies for allowing a high amount of natural regeneration to occur. Those studies should also investigate ecological characteristics such as dispersal ability, as the exchange of individuals between suitable habitats becomes important in fragmented landscapes and in areas where domestic animals and humans play a significant role in seed dispersal.

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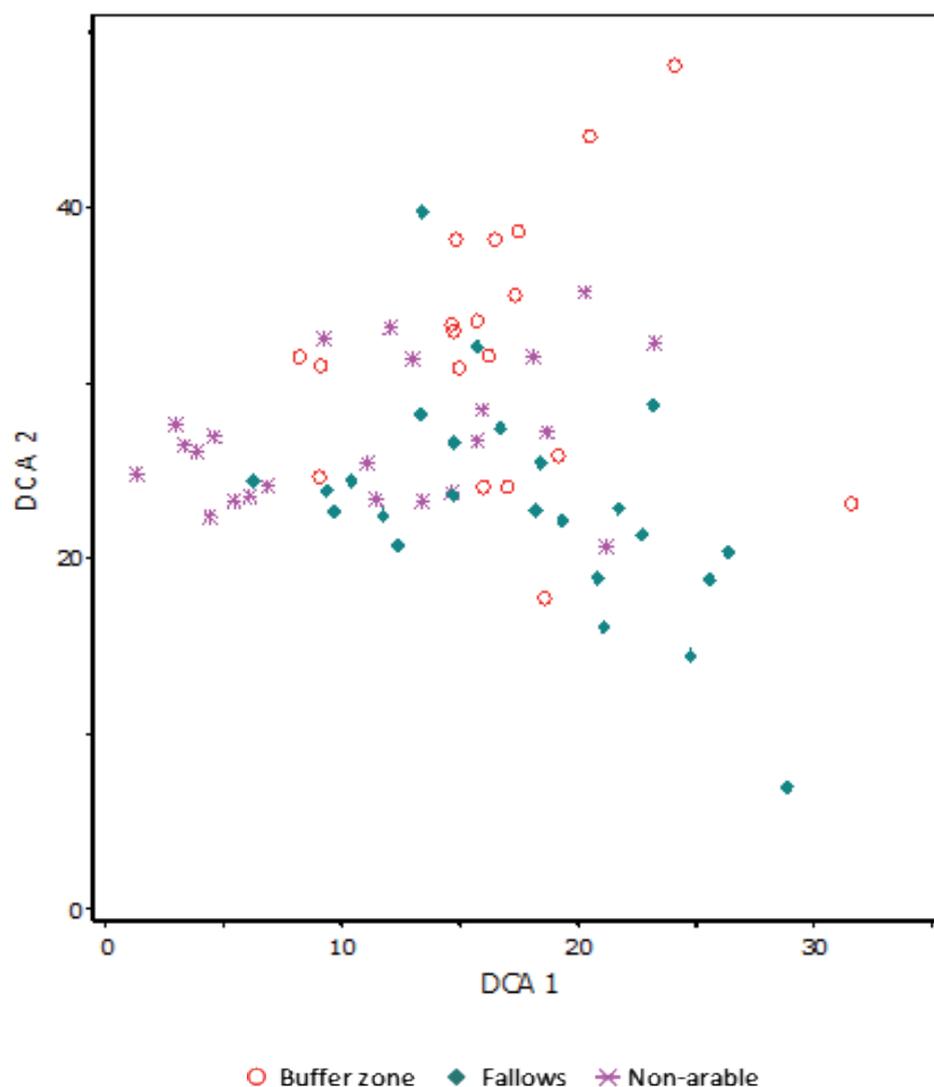
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Appendix



Appendix 1: DCA plot of the vegetation of non-arable sites, fallows and the buffer zone, based on the species cover of woody plants of the woody layers. The ordination was based on 130 species in 66 plots (23 on non-arable sites, 24 in fallows, 19 in the buffer zone), length of first axis 2.5, explained variance: 9.3%, second axis: 6.8% explained variance.

In order to reveal similarities or differences in vegetation composition between the three land-cover types, we used detrended correspondence analysis (DCA), as this technique provides eigenvalues that allow estimation of gradient length as a measure of variation between samples (HILL & GAUCH 1980). Prior to analyses, vegetation data were arcsine-squareroot-transformed. The results of this analysis are presented in Appendix 3 and clearly show that the studied land-cover types were comparable with respect to their vegetation composition. / DCA plot de la végétation des sites non arables, des jachères et la zone tampon, sur la base de la couverture des espèces de plantes ligneuses des couches ligneuses. L'ordination était basée sur 130 espèces réparties sur 66 parcelles (23 sur les terres non arables, 24 sur les jachères, 19 dans la zone tampon), longueur du premier axe 2.5, variance expliquée: 9.3%, deuxième axe: 6.8% de la variance expliquée.

Afin de révéler des similitudes ou des différences de composition végétale entre les trois types de couvert végétal, nous avons utilisé l'analyse de correspondance dérivée (DCA), car cette technique fournit des valeurs propres qui permettent d'estimer la longueur du gradient comme mesure de variation entre les échantillons (HILL ET GAUCH 1980). Avant les analyses, les données sur la végétation étaient transformées en arcsine-squareroot. Les résultats de cette analyse sont présentés dans l'annexe 3 et montrent clairement que les types de couvert végétal étudiés étaient comparables par rapport à leur composition végétale.

Appendix 2: Pearson correlation coefficients (r) between physical and chemical characteristics of soil from 39 study sites, those variables with a strong intercorrelation ($r \geq \pm 0.7$) were highlighted a star. / Coefficients de corrélation de Pearson (r) entre les caractéristiques physiques et chimiques du sol des 39 sites d'étude, les variables ayant une forte corrélation ($r \geq \pm 0,7$) ont été mises en évidence par une étoile.

Parameter 1	Parameter 2	r	F-value	P-value
Height herb layer (cm)	Cover tree/shrub layer (%)	-0.4345	-2.932	0.006
Height herb layer (cm)	Cover herb layer (%)	0.560	4.115	0.000
Height herb layer (cm)	pH	0.382	2.513	0.016
Height herb layer (cm)	K ⁺ (mmolc/kg)	0.433	2.923	0.006
Height herb layer (cm)	CECpot (cmolc/kg)	-0.476	-3.296	0.002
Height herb layer (cm)	BS-value	0.547	3.973	0.000
Height herb layer (cm)	Coarse silt (%)	0.526	3.760	0.000
Height herb layer (cm)	Medium silt (%)	-0.055	-0.337	0.738
Height herb layer (cm)	Clay < 2µm (%)	-0.641	-5.075	1.12*10 ⁻⁵
Height herb layer (cm)	K ₂ O (mg/100g)	0.038	0.231	0.819
Cover tree/shrub layer (%)	Cover herb layer (%)	-0.440	-2.980	0.005
Cover tree/shrub layer (%)	pH	-0.300	-1.904	0.065
Cover tree/shrub layer (%)	K ⁺ (mmolc/kg)	-0.354	-2.303	0.0270
Cover tree/shrub layer (%)	CECpot (cmolc/kg)	0.610	4.682	3.75*10 ⁻⁵
Cover tree/shrub layer (%)	BS-value	-0.549	-3.995	0.000
Cover tree/shrub layer (%)	Coarse silt (%)	-0.329	-2.118	0.041
Cover tree/shrub layer (%)	Medium silt (%)	0.040	0.242	0.810
Cover tree/shrub layer (%)	Clay < 2µm (%)	0.523	3.734	0.000
Cover tree/shrub layer (%)	K ₂ O (mg/100g)	-0.191	-1.181	0.245
Cove herb layer (%)	pH	0.326	2.096	0.043
Cove herb layer (%)	K ⁺ (mmolc/kg)	0.297	1.894	0.066
Cove herb layer (%)	CECpot (cmolc/kg)	-0.637	-5.029	1.29*10 ⁻⁵
Cove herb layer (%)	BS-value	0.598	4.540	5.78*10 ⁻⁵
Cove herb layer (%)	Coarse silt (%)	0.473	3.270	0.002
Cove herb layer (%)	Medium silt (%)	-0.155	-0.957	0.345
Cove herb layer (%)	Clay < 2µm (%)	-0.609	-4.668	3.92*10 ⁻⁵
Cove herb layer (%)	K ₂ O (mg/100g)	0.021	0.130	0.897
pH	K ⁺ (mmolc/kg)	0.536	3.867	0.000
pH	CECpot (cmolc/kg)	-0.208	-1.293	0.204
pH	BS-value	0.610	4.679	3.78*10 ⁻⁵
pH	Coarse silt (%)	-0.128	-0.785	0.438
pH	Medium silt (%)	-0.237	-1.486	0.146
pH	Clay < 2µm (%)	-0.245	-1.539	0.132
pH	K ₂ O (mg/100g)	0.442	2.996	0.005
K ⁺ (mmolc/kg)	CECpot (cmolc/kg)	-0.209	-1.303	0.201
K ⁺ (mmolc/kg)	BS-value	0.559	4.103	0.000
K ⁺ (mmolc/kg)	Coarse silt (%)	-0.182	-1.129	0.266
K ⁺ (mmolc/kg)	Medium silt (%)	-0.139	-0.853	0.399
K ⁺ (mmolc/kg)	Clay < 2µm (%)	-0.0689	-0.413	0.682
K ⁺ (mmolc/kg)*	K ₂ O (mg/100g)	0.785	7.709	3.29*10 ⁻⁹
CECpot (cmolc/kg)*	BS-value	-0.783	-7.663	3.77*10 ⁻⁹
CECpot (cmolc/kg)	Coarse silt (%)	-0.426	-2.861	0.007
CECpot (cmolc/kg)	Medium silt (%)	0.316	2.024	0.050
CECpot (cmolc/kg)	Clay < 2µm (%)	0.574	4.269	0.000
CECpot (cmolc/kg)	K ₂ O (mg/100g)	0.013	0.082	0.935
BS-value	Coarse silt (%)	0.152	0.939	0.354
BS-value	Medium silt (%)	-0.319	-2.045	0.048
BS-value	Clay < 2µm (%)	-0.424	-2.851	0.007
BS-value	K ₂ O (mg/100g)	0.330	2.052	0.047
Coarse silt (%)	Medium silt (%)	0.235	1.468	0.151
Coarse silt (%)	Clay < 2µm (%)	-0.500	-3.509	0.001
Coarse silt (%)	K ₂ O (mg/100g)	-0.415	-2.776	0.009
Medium silt (%)	Clay < 2µm (%)	0.249	1.567	0.126
Medium silt (%)	K ₂ O (mg/100g)	-0.237	-1.486	0.146
Clay < 2µm (%)	Clay < 2µm (%)	0.141	0.868	0.391

Appendix 3: Juvenile densities (100 m²) of the 25 analyzed woody species. Densities are presented according to species group affiliation, land cover type and census (plots sampled on non-arable land: n=12, fallow: n=17 and buffer zone: n=10). Similarity between land-cover types concerning the juvenile densities, calculated by a linear-mixed-effect model and a subsequent Tukey's multiple comparison test, is marked by (&), dissimilarity by (≠). / Densités juvéniles (100 m²) des 25 espèces ligneuses analysées. Les densités sont présentées selon l'appartenance au groupe d'espèces, le type de couverture et le recensement (parcelles échantillonnées sur les terres non arables: n = 12, jachère: n = 17 et zone tampon: n = 10). La similarité entre les types de couvert végétal concernant les densités juvéniles, calculée par un modèle à effet mixte linéaire et un essai de comparaison multiple de Tukey subséquent, est indiquée par (&), dissimilarité par (≠).

Life form	Family	Species	May 2008			Oct 2008		
			non-arable	fallows	buffer zone	non-arable	fallows	buffer zone
Group A: non-arable ≠ fallows ≠ buffer zone								
tree	Fabaceae	<i>Pterocarpus erinaceus</i> .	24	24	32	36	32	60
Group B: non-arable & fallows ≠ buffer zone								
shrub	Annonaceae	<i>Annona senegalensis</i> .	40	148	0	64	160	0
shrub	Rubiaceae	<i>Crossopteryx febrifuga</i>	28	36	40	28	28	40
tree	Anacardiaceae	<i>Lannea acida</i> A.Rich.	24	48	0	24	52	0
tree	Combretaceae	<i>Terminalia avicennioides</i>	28	120	8	52	128	8
Group C: non-arable & buffer zone ≠ fallows								
shrub	Mimosaceae	<i>Acacia hockii</i>	0	36	4	0	36	4
tree	Combretaceae	<i>Anogeissus leiocarpa</i>	8	52	8	8	68	8
shrub	Combretaceae	<i>Combretum collinum</i>	72	360	40	76	376	56
shrub	Mimosaceae	<i>Dichrostachys cinerea</i>	184	696	20	228	732	20
shrub	Ebenaceae	<i>Diospyros mespiliformis</i>	0	124	4	0	132	4
shrub	Rubiaceae	<i>Feretia apodanthera</i>	8	180	4	8	180	4
shrub	Rubiaceae	<i>Gardenia ternifolia</i>	36	44	20	44	36	28
shrub	Caesalpiniaceae	<i>Piliostigma thonningii</i>	16	120	4	20	128	8
shrub	Strychnaceae	<i>Strychnos spinosa</i>	32	38	72	68	80	96
tree	Sapotaceae	<i>Vitellaria paradoxa</i>	56	168	12	62	224	24
Group D: fallows & buffer zone ≠ non-arable								
shrub	Combretaceae	<i>Combretum glutinosum</i>	36	16	4	44	12	4
shrub	Combretaceae	<i>Combretum nigricans</i>	144	92	16	156	84	16
shrub	Caesalpiniaceae	<i>Detarium microcarpum</i>	628	128	0	816	128	0
tree	Caesalpiniaceae	<i>Isoberlinia doka</i>	8	88	32	12	104	60
tree	Fabaceae	<i>Philenoptera laxiflora</i>	4	56	24	0	60	28
shrub	Combretaceae	<i>Pteleopsis suberosa</i>	408	212	0	416	204	4
tree	Bignoniaceae	<i>Stereospermum kunthianum</i>	136	136	20	192	128	52
Group E: non-arable & fallows & buffer zone								
tree	Bombacaceae	<i>Bombax costatum</i>	4	20	12	8	20	12
shrub	Combretaceae	<i>Combretum molle</i>	84	124	76	112	144	92
shrub	Rubiaceae	<i>Gardenia aqualla</i>	8	16	16	4	28	12

Appendix 3 (continued).

Life form	Family	Species	May 2009			Oct 2009			May 2010		
			non-arable	fallows	buffer zone	non-arable	fallows	buffer zone	non-arable	fallows	buffer zone
Group A: non-arable ≠ fallows ≠ buffer zone											
tree	Fabaceae	<i>Pterocarpus erinaceus</i>	44	24	80	52	36	92	52	36	72
group B: non-arable & fallows ≠ buffer zone											
shrub	Annonaceae	<i>Annona senegalensis</i>	68	164	0	84	204	4	140	252	0
shrub	Rubiaceae	<i>Crossopteryx febrifuga</i>	28	28	40	28	28	40	28	24	40
tree	Anacardiaceae	<i>Lannea acida</i> A.Rich.	48	104	8	64	148	0	76	184	8
tree	Combretaceae	<i>Terminalia avicennioides</i>	76	132	20	88	152	28	88	200	28
Group C: non-arable & buffer zone ≠ fallows											
shrub	Mimosaceae	<i>Acacia hockii</i>	0	40	4	0	48	4	0	36	4
tree	Combretaceae	<i>Anogeissus leiocarpa</i>	76	292	20	56	272	36	104	496	36
shrub	Combretaceae	<i>Combretum collinum</i>	72	384	52	92	444	64	104	424	64
shrub	Mimosaceae	<i>Dichrostachys cinerea</i>	240	648	20	256	668	28	252	608	32
shrub	Ebenaceae	<i>Diospyros mespiliformis</i>	4	172	4	4	188	4	4	196	4
shrub	Rubiaceae	<i>Feretia apodanthera</i>	16	216	4	16	228	4	16	220	4
shrub	Rubiaceae	<i>Gardenia ternifolia</i>	36	40	24	44	36	28	44	36	24
shrub	Caesalpinaceae	<i>Piliostigma thonningii</i>	28	112	8	28	132	8	24	148	8
shrub	Strychnaceae	<i>Strychnos spinosa</i>	60	56	96	92	88	120	72	88	120
tree	Sapotaceae	<i>Vitellaria paradoxa</i>	80	268	20	84	82	328	80	292	32
Group D: fallows & buffer zone ≠ non-arable											
shrub	Combretaceae	<i>Combretum glutinosum</i>	40	12	8	48	12	8	44	12	8
shrub	Combretaceae	<i>Combretum nigricans.</i>	164	108	20	192	108	20	204	112	20
shrub	Caesalpinaceae	<i>Detarium microcarpum</i>	824	132	0	1028	136	0	948	152	0
tree	Caesalpinaceae	<i>Isobertinia doka</i>	12	120	64	36	176	96	44	156	56
tree	Fabaceae	<i>Philenoptera laxiflora</i>	0	52	40	4	64	96	0	60	76
shrub	Combretaceae	<i>Pteleopsis suberosa</i>	384	200	4	424	224	4	8	220	8
tree	Bignoniaceae	<i>Stereospermum kunthianum</i>	164	116	48	188	140	76	192	144	68
Group E: non-arable & fallows & buffer zone											
tree	Bombacaceae	<i>Bombax costatum</i>	12	16	8	32	36	24	20	44	12
shrub	Combretaceae	<i>Combretum molle</i>	136	212	88	156	232	136	140	268	212
shrub	Rubiaceae	<i>Gardenia aqualla</i>	8	28	12	8	32	16	8	32	16

Termites and savannas – an overview on history and recent scientific progress with particular respect to West Africa and to the genus *Macrotermes*

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Summary: Particularly in savannas, termites are ecosystem engineers and a keystone group in ecology. For the understanding of the savanna vegetation, mound building termites are of particular interest. Due to their special soil chemistry and physical structure, termite mounds often host other plants than the surrounding savanna. As our knowledge of the specific contribution of mound-building termites to overall savanna diversity and ecosystem dynamics doubtlessly is not complete, this paper summarises the state of the art in order to stimulate further research. According to the research interest of the authors, focus is laid on the West African savanna and on the genus *Macrotermes*.

Key words: ecosystem engineers, *Macrotermes*, savanna, termite biology, termite mounds, vegetation pattern, West Africa

TERMITES ET SAVANES - UNE VUE D'ENSEMBLE DE L'HISTOIRE ET DES PROGRÈS DE LA RECHERCHE AVEC UN ACCENT PARTICULIER SUR L'AFRIQUE DE L'OUEST ET DU GENRE *MACROTERMES*

Résumé: Les termites sont des ingénieurs écosystémiques et un groupe “clé de voûte” en écologie, notamment dans les savanes. Pour comprendre la végétation des savanes, les termites à termitière présentent un intérêt particulier. En effet, de par la spécificité de leurs caractéristiques de sol et de leur structure physique, les termitières hébergent fréquemment une végétation différente de la savane environnante. Cependant, le rôle des termites à termitière dans la diversité [végétale] des savanes et la dynamique de ces écosystèmes n'est que partiellement connu. Cet article propose donc un état des lieux des connaissances et vise à stimuler la recherche sur cette thématique. L'accent est mis sur la savane d'Afrique de l'Ouest et sur le genre *Macrotermes*, qui sont au cœur des travaux de recherche des auteurs.

Mots clés: ingénieurs de l'écosystème, *Macrotermes*, savane, termitières, Afrique de l'Ouest

TERMITEN UND SAVANNEN – EINE ÜBERSICHT ZU GESCHICHTE UND FORTSCHRITTEN DER FORSCHUNG UNTER BESONDERER BERÜCKSICHTIGUNG VON WESTAFRIKA UND DER GATTUNG *MACROTERMES*

Zusammenfassung: Insbesondere in Savannen fungieren Termiten als Ökosystem-Ingenieure und stellen damit eine ökologische Schlüsselgruppe dar. Besonders wichtig für Zusammensetzung und Struktur der Savannenvegetation hügelaufbauende Termiten, denn die Termitenhügel beherbergen aufgrund ihrer besonderen Bodeneigenschaften oft andere Pflanzen als die umgebende Savanne. Trotz einer Vielzahl publizierter Forschungsergebnisse sind die Kenntnisse zweifellos noch nicht ausreichend, um den Beitrag der hügelaufbauenden Termiten zu Diversität und Dynamik von Savannenökosystemen vollständig zu verstehen. Der vorliegende Übersichtsartikel soll als Basis für weitere Untersuchungen dienen. Gemäß den Forschungsinteressen der Autoren wird der Schwerpunkt auf Westafrika und die Gattung *Macrotermes* gelegt.

Schlagworte: Ökosystemingenieure, *Macrotermes*, Savanne, Termitenbiologie, Termitenhügel, Vegetationsmuster, Westafrika

1 INTRODUCTION

Savannas are heterogeneous and species-rich ecosystems that cover a large proportion of the global landmass, characteristically composed of a patch-mosaic landscape of trees and shrubs in a matrix dominated by C4 grasses. Termites, which are particularly abundant in savannas (LEE & WOOD 1971), are ecosystem engineers and a keystone group in savanna ecology (JONES 1990; DANGERFIELD et al. 1998). Even though their mounds cover only a small percentage of the savanna surface, termites and their mounds provide a variety of direct and indirect resources and ecosystem services to various organisms, including plants and animals, but also the local human populations. In addition to influencing key processes such as nutrient flux and carbon cycling, the mound-building activity of certain termite taxa provides a prominent structural feature of savanna landscapes. Termite mounds often support different plants than the surrounding savanna matrix and are explicitly referred to as a specific habitat of many plant taxa in floristic works. Due to their special soil properties, physical structure, and

characteristic vegetation, termite mounds are thus important drivers of environmental heterogeneity, which is considered a major driver of species diversity worldwide (TEWS et al. 2004; STEIN et al. 2014).

Despite the acknowledged importance of termites as ecosystem engineers, doubtlessly our knowledge of the specific contribution of mound-building termites to overall savanna diversity and ecosystem dynamics is not complete. Therefore, in order to stimulate further research, this paper summarises the state of the art.

Literature concerning the influence of termites on ecosystems often integrates results and generalises conclusions across systems (even across biomes), and also across termite species or broader termite groups. As termites are taxonomically and ecologically diverse, we start with a short introduction to termite biology (section 2), then generally treat the influence of termites on savannas (section 3), focus on the influence of *Macrotermes* and the vegetation of the West African savanna (section 4) and summaries some own results concerning the influence of termite-induced heterogeneity on savanna vegetation along a climatic gradient in West Africa (section 5).

2 TERMITE BIOLOGY – A SHORT OVERVIEW

2.1 Research history

Ever since the early naturalists' explorations during the 18th century, termites have occupied a prominent place in writings devoted to tropical environments. The respective scientific literature can be divided into two major branches (DUBOISSET & SEIGNOBOS 2005). One focusses on the short-term consequences of termite activity, which are mostly regarded as detrimental to agriculture, silviculture, and human constructions. This branch, widely concerned with termite control and mitigation of termite damage, produced a large body of publications reaching back to colonial times. More relevant to this paper is the second branch of literature, which focusses on the longer-term perspective of natural history, including the function of termites in tropical ecosystems. While their often destructive impact on human efforts is acknowledged, in this branch of the literature termites are also seen as fascinating study objects. This view already found expression in the first scientific accounts of termites by KÖNIG (1779) and SMEATHMAN (1781), both concerning *Macrotermes*. These ground-breaking publications dealt with the description, classification and systematics of termites, and also delivered vivid and insightful accounts of their natural history, including the intricate construction of termites' nests, and the often complex social organisation of their colonies. The admiration of the early naturalists for termites becomes evident in a comparison of the architectural achievement of erecting large termitaria as surpassing the human effort to build the Great Pyramid of Giza (SMEATHMAN 1781).

SMEATHMAN (1781) also commented on beneficial effects of termites, such as the removal of dead biomass, but these were thereafter mainly ignored or dismissed for a century until DRUMMOND (1886) compared the influence of termites

in the tropics to the beneficial activities of temperate earthworms, inspired by Darwin's work on the latter (DARWIN 1881). Drummond's work, however, was largely ignored and disregarded, besides some rare contributions from the field of vegetation ecology. Nearly six decades later, a review by ADAMSON (1943) called for further research on the question whether termite activity is detrimental or beneficial to the ecosystem on a longer timescale, and addressed open questions. He particularly emphasised the need for research re-evaluating the effects of termites on soil fertility and soil erosion, and he remarked that large abandoned termite mounds may show increased fertility.

With the availability of new analytical methods and their application in the field, numerous studies on the influence of termites on soil have been published since then. In the second half of the 20th century, research articles started to provide pedological data on the composition of termite mound soils (HESSE 1955; NYE 1955; WATSON 1962). These have emphasised the relevance of termites for ecosystem functions, and also confirmed ADAMSON'S (1943) conclusions that different groups of termites may have very different effects on their environment due to their differing ecology and behaviour.

2.2 Termite ecology and classification

2.2.1 Termite diversity

Termites are a group of insects currently comprising approximately 2900 described species (KRISHNA et al. 2013), with an expected 500 to 1000 species remaining to be described (EGGLETON 2011). However, given that a recent study found 20 putative new termite species in Pendjari National Park, West Africa, alone (HAUSBERGER et al. 2011), this estimate is likely conservative. Termites are currently ranked either as infraorder Isoptera or epifamily Termitoidae, but are phylogenetically securely placed within the order Blattodea, more commonly known as cockroaches (BECCALONI & EGGLETON 2013; KRISHNA et al. 2013). The genus *Macrotermes* belongs to the monophyletic Macrotermitinae. However, for our understanding of the impact of termites, and in particular *Macrotermes*, on the savanna ecosystem, the established functional classification is more relevant than the intra-order taxonomy.

2.2.2 Feeding groups

Termites show diverse nesting behaviour and feeding habits. Functionally, they are separated into different feeding guilds. The most recent categorisation, supported by morphological and phylogenetic data (DONOVAN et al. 2001), distinguishes between (phylogenetically) lower-level wood-feeding termites (group I), grass-, wood-, litter-, and lichen-feeding termites (group II, including the fungus-cultivating species), soil/wood-interface-feeding termites (group III) and true soil-feeding termites (group IV). It should be noted that different feeding groups have different impacts on their environment, but also that the vast majority of termites live in the soil environment and provide similar ecosystem services (JOUQUET et al. 2006, 2011; BOTTINELLI et al. 2015). The nutritional habits of termites are probably a major driv-

ing force behind their evolution. Termites have co-evolved with protists, bacteria, and fungi to digest lignocellulose, an extremely abundant biopolymer which very few animals can take advantage of. In cases where both phylogenies are known, the phylogeny of their symbionts matches the termite phylogeny very well (see, e.g., AANEN et al. 2002; ROULAND-LEFEVRE et al. 2002; AANEN & EGGLETON 2005; LO & EGGLETON 2011). *Macrotermes*, like all other Macrotermitinae, are fungus cultivators which co-evolved with the fungus genus *Termitomyces*. The mutualistic symbiosis is obligate for the termites, and *Macrotermes* mounds are an evolutionary result of this symbiosis (AANEN & EGGLETON 2005).

2.2.3 Caste differentiation

In contrast to most other Blattodea, all termites are eusocial insects. They live in nests with communities of up to several million individuals, which are usually all descendants of one founding couple, also called the royal couple, consisting of queen and king. The queen of some species can reach a remarkable age of more than a decade, continuously producing offspring. The vast majority of termite species have castes fulfilling specific tasks in the colony. Different types of workers construct galleries and enlarge the nest, feed the other castes, tend offspring, and, in the case of fungus-cultivating species like *Macrotermes*, tend the fungus. Depending on the species, workers sometimes undergo multiple stages in their lifetime, fulfilling different tasks at different time periods in their development. The reproductive alates are dispersal units, turning into kings and queens when mating to found new colonies. Alates are only produced after the nest has reached a certain size, which makes large investments in the protection of the nest and especially the royal couple adaptive from an evolutionary viewpoint. The soldier caste is concerned with aggressive defence. Soldiers often have enforced head capsules and well-developed mandibles. Some clades have chemical defences instead, with soldiers spraying defensive substances on attackers (PRESTWICH 1984). Interestingly, soldiers show altruistic behaviour, attacking intruders to stall them while workers close off passages into the nest's interior, preventing both intruders and the defending soldiers from entering the nest. Also, in at least one species, senescent workers literally explode to distribute toxic chemicals to stop intruders (ŠOBOTNÍK et al. 2012). While their colonies are thus not completely defenceless, termites are still comparably easy prey. Their main mode of defence is keeping predators out of the nest and ensuring the persistence of the colony by protecting the often completely immobile queen. The nest is therefore an integral part of the termite community, which is especially compelling in case of the mound building genus *Macrotermes*.

2.3 Termite mounds

2.3.1 Nests and mounds

Most, but not all termites construct complicated structures to enclose their nest as *Macrotermes* does. Many species' nests are inconspicuous to the human observer, hidden in

the soil, in living plants, or in dead wood. Some species' nests are as simple as a few tunnels inside a trunk, but others' reach a degree of sophistication and size unrivalled by other constructions in the animal kingdom. Many species reinforce or cover their nests with plant-derived carton, while others use soil cemented by saliva and faeces, or a combination of soil and carton. Nests that are covered by soil and protrude above the soil surface are called termite mounds or termitaria. Several other synonyms exist, especially in older literature (see, e.g., PULLAN 1979). The most imposing mounds are the large termitaria of the savannas, with the largest and most elaborate mounds built by the genus *Macrotermes*, which we focus on in this paper.

2.3.2 Mound functions

It has been argued that termite mounds constitute a part of a colony superorganism in so far as they are a functional unit and no part can survive without the others (EGGLETON 2011). Besides protection against predators, termite mounds protect the colony from direct intrusion of rainwater and flooding, which would otherwise have catastrophic consequences. Damages by, e.g., rain or other organisms, are constantly repaired. The major challenge for a termite colony, however, is minimising variations in temperature and humidity. Especially in the fungus-cultivating genera, the most important function of the mound is creating and maintaining homeostasis for the colony and their symbionts. Termites in this monophyletic group have an obligate mutualistic relationship with basidiomycete fungi of the genus *Termitomyces* (AANEN et al. 2002; AANEN & EGGLETON 2005), cultivating these fungi inside the mound. *Macrotermes* create "fungus combs" with a high surface area out of partly-digested plant material in special fungus chambers of their mounds and inoculate them with fungal spores in a high density. These fungus gardens are then constantly nursed, preventing infection by other biota. While the termite workers already can take advantage of easily digestible parts of the plant material, as e.g. short-chained carbohydrates, the colony depends on the fungus regarding further nutritional needs, especially considering continuous nitrogen supply throughout the year.

Homeostasis of the mound environment might be more important for the fungus than for the termites themselves (KORB 2003; AANEN & EGGLETON 2005), which because of their thin cuticles are very prone to desiccation, but can cope by relocating quickly. In fact, termite workers actively transport water from the groundwater table into the mound, travelling as far as 50 m below ground (LEPAGE et al. 1974); it is however mainly the architecture of the mound which ensures a high and constant air humidity. Two possible and not mutually exclusive hypotheses are that macropores created by termites around the mound increase infiltration and allow percolation of water towards the mound, and that higher clay and silt content in the mound increase the soil water matrix potential to wick up and hold humidity from the surrounding soil (TURNER 2006).

Constant temperature and a continuous gas exchange in the mound are also of particular importance for *Macrotermes*, since *Termitomyces* has a narrow temperature tolerance and

its metabolism is inhibited by CO₂ (KORB 2011). While aeration, gas- and temperature flux within mounds are not yet fully understood, it is clear that the mounds' internal structure of galleries and tunnels is functionally highly adaptive (KORB 2003). Generally, internal and external architecture evolved certain patterns within each species, derived from self-organisation processes. Further self-organisation processes ensure that both internal and external architecture can also be modified in adaptation to environmental conditions, and change over the lifetime of a colony (KORB & LINSENMIR 1998b, 1999; KORB 2011).

In summary, termites are a moderately large but understudied group of social insects. The focus group in the context of this paper, the genus *Macrotermes* in West Africa, constructs large mounds. The main function of *Macrotermes* mounds is to provide a protected and stable environment for the termite nest, including the fungus gardens. Termites transport and modify large amounts of soil over the lifetime of a colony to build and maintain their mounds, continuously engineering the soil environment of savanna landscapes in the process.

2.4 Focus species

2.4.1 Species distribution

This paper focusses on two species of the fungus-cultivating genus *Macrotermes*. *Macrotermes bellicosus* (Smeathman 1781) and *Macrotermes subhyalinus* (Rambur 1842) are widely distributed in West and East Africa. While *M. subhyalinus* occurs through-out West African savannas, *M. bellicosus* seems to reach the northern limit of its distribution within the North Sudanian vegetation zone (sensu WHITE 1983; GUINKO 1984) and only rarely is found in the Sahel vegetation zone.

2.4.2 Variability of mound types

It is difficult to identify termite species in the field, and termite individuals, preferentially from the soldier caste, are needed for species determination. In general, the two *Macrotermes* species present in West Africa build differently shaped mounds. According to KORB (2011), *M. subhyalinus* generally builds mounds featuring openings for ventilation, while *M. bellicosus* always builds completely closed mounds. In our study area, *M. subhyalinus* mostly builds relatively flat hillocks with thick walls, while *M. bellicosus* mounds are more diverse and range from domes to "cathedral" mounds with ridges and turrets, reaching heights of six meters and more.

However, mound architecture of the two species can overlap, as each species shows regional as well as local variability, with mounds being adapted to local environmental conditions (COLLINS 1979; KORB & LINSENMIR 1998b; ABE et al. 2009a). Mounds also can be re-colonised multiple times after the death of a colony, and by different species. Furthermore, the majority of vegetated mounds are uninhabited and heavily eroded. Thus, it is often difficult to identify the species that originally built or at least occupied each mound. Therefore, in the following, we do not differentiate between *M. subhyalinus* and *M. bellicosus*.

2.4.3 Soil composition of *Macrotermes* mounds

While most termite species from all feeding groups manipulate the soil environment, the extent and effects of their actions differ. Between-group differences in effects on the soil environment are generally poorly understood. However, the availability of data for *Macrotermes* is comparably good, and *M. bellicosus* and *M. subhyalinus* in particular are comparably well studied.

One feature generally attributed to *Macrotermes* colonies is an enrichment in nutrients in the mound. *Macrotermes* are one of the few organisms which, with the help of their fungal partners, can completely decompose plant biomass, including the recalcitrant lignocellulose, reportedly leading to nutrient accumulation in mound soil (TILAHUN et al. 2012). Estimates in the literature indicate that termites may process 40 to 100% of dead wood in the ecosystem (KRISHNA et al. 2013), with *Macrotermes* having the greatest impact.

Macrotermes also move large quantities of soil for mound-building and construction of soil sheetings to protect foraging galleries, and therefore contribute to soil turnover. Both sheetings and mound material are enriched in clay (SILESHI et al. 2010), and certain types of clay have shown to be actively selected by termites (JOUQUET et al. 2002a, 2004, 2007). Some evidence even exists that termites may be able to change clay mineralogy, thus changing its swelling and shrinking characteristics (BOYER 1982; JOUQUET et al. 2002b, 2007).

In addition to structural adaptation to local microclimate (KORB & LINSENMIR 1998a,b), recent studies have shown that composition of mound soil varies within populations of *M. bellicosus* according to local topography and hydrology (ABE et al. 2009a,b). Further influence of local geological and pedological conditions on composition of mound soil has been reported for the closely related congeneric species *M. falciger* (Gestäcker 1891) in Central Africa (MUJINYA et al. 2010, 2013, 2014; ERENS et al. 2015a), supporting the idea that the impact of termites on soil turnover and soil composition depends on the surrounding environment.

3 INTERRELATIONSHIP BETWEEN TERMITES AND THE SAVANNA ECOSYSTEM

3.1 Research history

The first descriptions of the association of certain plant species with termite mounds date from the beginning of the 20th century (FILLIPPI 1908; BEQUAERT 1913; FULLER 1915). These works also included speculations that changes in soil conditions due to termite activity were the reason for these associations. The influence of termites and their mounds on the vegetation at a landscape scale was then recognised in an essay by the geographer TROLL (1936). Troll was among the first to describe the influence of Macrotermitinae on the vegetation structure of East African savannas. The importance he attributed to these insects is obvious from the fact that he labelled the corresponding ecosystems "termite savannas". Incidentally, his description of distinct clusters of termite mound vegetation defining the characteristics of a whole landscape predated his seminal coining of

the term "landscape ecology" (TROLL 1939). Further studies of landscape ecology in African savannas in the 1940s (THOMAS 1943; EGGELING 1947; MORISON et al. 1948) explored relationships between soils and vegetation, including the influence of termites. Later detailed studies of savanna vegetation were specifically interested in the synecology of plant communities on termite mounds (WILD 1952; MULLENDERS 1954; SCHMITZ 1963; JACKSON & GARTLAN 1965; FANSHAW 1968). The species lists and community descriptions in these works, as well as occasional remarks like "[growing] on termite mounds" in regional floras provide a baseline for further ecological research. In a parallel branch of investigations, pedological studies analysed chemico-physical composition of termite mound soils (HESSE 1955; NYE 1955; WATSON 1962). Most recently, information from different scientific fields began to get integrated to address the role of termites in the savanna ecosystem (LEE & WOOD 1971; WOOD & SANDS 1978; WOOD 1988; ABE et al. 2000; SILESHI et al. 2010; BIGNELL et al. 2011), and the current scientific debate tries to identify the processes behind patterns in the savanna ecosystem which are caused by termites and their mounds (e.g., DANGERFIELD et al. 1998; LEVICK et al. 2010a; JOUQUET et al. 2011; OKULLO & MOE 2012a,b; BONACHELA et al. 2015). However, even today, termites can be seen as "neglected" soil and ecosystem engineers (JOUQUET et al. 2016).

3.2 Importance of termite mounds for the savanna ecosystem

Termites affect the savanna ecosystem both directly and indirectly. In a direct way, termites influence biomass turnover in the savanna by processing large amounts of organic matter. It is estimated that termites consume and metabolize organic material at the same rate as herbivores of the savanna regions (LEE & WOOD 1971; WOOD & SANDS 1978; ABE et al. 2000), thus contributing greatly to dead biomass removal and biomass mineralisation. Termites also affect the savanna system through their mound-building activity, as their mounds create heterogeneity in availability of water, nutrients and minerals. By transporting and manipulating clay-enriched soil for mound and soil sheeting constructions from the subsoil to the surface, they contribute to soil turnover and mineral redistribution in the savanna. The construction of mounds also can trigger cascades of effects and feedback loops in the soil environment, based on abiotic and biotic environmental processes (JOUQUET et al. 2006; BOTTINELLI et al. 2015). For example, higher air humidity and better aeration changes microbial activity in mounds, affecting nitrogen availability to plants (DUPONNOIS et al. 2006; BRODY et al. 2010). Interactions of other organisms with termite mounds, especially plants, sum up to ecosystem engineering (JONES et al. 1997; DANGERFIELD et al. 1998; JOUQUET et al. 2006, 2016). Plants and animals, including human populations, greatly profit from termites and their mounds, which makes it particularly important to better understand the ecology of mounds systems.

3.2.1 Water availability

Water availability on termite mounds is usually thought to be higher than in the surrounding savanna, as a result of

increased water percolation towards mounds, wick effects, and increased water-holding capacity in mounds due to clay enrichment (TURNER 2006). Soil macropores created by termites can lead to highly increased infiltration rates, but the effect seems to be variable between species and to depend on termite activity patterns (LOBRY DE BRUYN & CONACHER 1990; LÉONARD & RAJOT 2001; LÉONARD et al. 2004; METTROP et al. 2013; KAISER 2014). Despite the known effects of termites on soil moisture, only one study has empirically demonstrated the effect of higher water availability for plants on mounds as compared to the surrounding savanna (KONATÉ et al. 1999). The latter paper, which suggests higher leaf-shedding to be responsible for the higher water availability on mounds is widely cited, but is derived from a very small number of samples: five mounds for leaf-shedding differences and only one mound for water potential measurements.

The mound's pediment, or halo, has been shown to have low infiltrability due to surface sealing by silt and clay eroded from the mound surface, and water transported towards the mound's centre from around and below the mound bypasses the pediment (BONACHELA et al. 2015; TURNER 2006).

3.2.3 Nutrient enrichment

There is much more data on nutrient content of mounds, which is often higher than in the surrounding soils. Termites are generally thought to create nutrient hotspots through accumulation and mineralisation of biomass in their nest and through soil transport (WATSON 1977; SALICK et al. 1983; COVENTRY et al. 1988; WOOD 1988; MILLS et al. 2009; SEMHI et al. 2008; SILESHI et al. 2010). The evidence for enrichment of mound soil with organic matter, nitrogen, and phosphorus is ambiguous (JOUQUET et al. 2004; SILESHI et al. 2010) and varies between species and studies from different localities. Nutrients are slowly released from mounds by leaching and erosion, making termite mounds important for plants both on and off mounds. Some evidence exists that elevated nutrient concentrations, including potassium, in mound soil are of organic origin (SEMHI et al. 2008), or at least subsidised by mineralisation of organic matter. However, like most detailed studies of mound material, the results of SEMHI et al. (2008), that higher potassium content in mounds is due to mineralisation of plant matter by termites, were derived from a small sample size (four mounds), and probably do not reflect broader environmental heterogeneity of termite mounds and their savanna matrix. Other studies assume that nutrients derived from plant material transported to the mound by termites might be retained in the mound centre and thus partly protected from leaching (ERENS et al. 2015a; TILAHUN et al. 2012). However, until recently, it was not yet known whether nutrient input by termites or clay content is more important for soil fertility of termite mounds (SILESHI et al. 2010).

3.2.4 Clay enrichment

An enrichment in clay and silt compared to the surrounding savanna topsoil has been reported by most studies of termite mound soil (HESSE 1955; NYE 1955; WATSON 1962, 1975; WOOD & SANDS 1978; WOOD 1988; SILESHI et al.

2009, 2010), which might strongly influence nutrient availability to plants. Termites select clay and silt particles from the subsoil and transport them to the surface to construct their mounds and foraging gallery sheetings (JOUQUET et al. 2002a; ABE et al. 2009b, 2012), and are probably able to alter clay mineralogy, creating highly expandable clays (BOYER 1982; JOUQUET et al. 2002b). Studies often remark on higher levels of exchangeable bases and higher pH in termite mound soil, which is directly related to cation exchange processes involving high-surface clay particles. Higher clay content may strongly slow leaching of nutrients. Thus, concentration and manipulation of clay particles by termites can influence nutrient availability to plants on mounds. Plants in the surrounding savanna may profit from prolonged leaching as well as from slow and continuous erosion of mound material.

As a combined results of three studies (ERPENBACH et al. 2013, 2014, 2016) described in section 5) clay enrichment can be identified as the most influential factor for the mound–savanna contrast across savanna types. It is, however, important to emphasise that only the interplay of clay with other factors, including the plant macronutrients potassium and phosphorus, was able to explain a large part of the vegetational contrast. Selective transport of subsoil clay particles, mineralization of plant biomass, and possibly also manipulation of clay mineralogy by termites are important for changes in the availability of major and minor cations in termite mound soil. In addition to macronutrients and major cations, plant micronutrients, including trace elements, rare earth elements, and heavy metal elements, have been found in higher concentrations in termite mound soil than in the surrounding topsoil (SEMHI et al. 2008, MILLS et al. 2009, SEYMOUR et al. 2014). Thus, higher cation exchange capacity on mounds is a direct result of termite activity, and increased levels of cations might continue to be available from the mound soil for a prolonged time (ERENS et al. 2015a; MUJINYA et al. 2013).

3.2.5 Soil turnover

For West Africa, the contribution of termite mounds to savanna soil turnover by erosion has been estimated between 0.75 and 1 mm ha⁻¹ mound material per year, equivalent to about 7.5 to 10 m³ha⁻¹ (LEPAGE 1984). Assuming that erosion continues undisturbed, LEPAGE (1984) estimated that it would take 20 to 25 years to completely erode a single large mound of *M. bellicosus*. However, termite mounds can last for several decades, or even centuries (WATSON 1967; SILESHI et al. 2010; ERENS et al. 2015b), depending on recolonisation and local environmental conditions. Besides their contribution to soil turnover by erosion, termites and their mounds can cause larger-scale physical changes to landscape structure.

3.2.6 Ecosystem engineering and effects on vegetation

Termites have been described as ecosystem engineers due to their ability to induce changes in whole landscapes via multiple feedback loops, emphasising plant–soil feedbacks on mounds (JONES et al. 1997; JOUQUET et al. 2006; MCCARTHY et al. 2012). Plant communities on mounds have often

been reported to be different from the surrounding savannas and to show higher diversities on mounds (e.g. MOE et al. 2009), and this is mostly attributed to higher fertility of termite mound soil (SILESHI et al. 2010).

A widely cited paper by DANGERFIELD et al. (1998), the key-stone to a series of studies from the Okavango delta (ELLERY et al. 1993; MCCARTHY et al. 1993, 1998, 2012), showed that the construction of termite mounds leads to the formation of vegetated islands: the combined effects of particular changes to soil composition and vegetation lead to further soil changes due to physico-chemical soil precipitation processes. This, in turn, contributes to enlarging the island and allows further plants to colonise, which further stabilise the emerging microhabitat with their roots, and cause further precipitation processes due to evapotranspiration.

While the local environmental conditions in the Okavango delta are very specific, similar processes seem to take place to a varying degree in other localities as well, and precipitates in termite mound soil have not only been found in the Okavango. Most commonly, studies have reported mounds to contain carbonates, with mounds sometimes developing localised nodules or crusts even in otherwise carbonate-free surroundings (MILNE 1947; HESSE 1955; WATSON 1962, 1974; COLLINS 1979; LIU et al. 2007; MUJINYA et al. 2011). Furthermore, the formation of sesquioxides in mounds has been observed in strongly seasonal localities with a high groundwater table (MUJINYA et al. 2011, 2013, 2014), indicating the influence of local environmental conditions on mound composition.

Very important for the savanna ecosystem are effects of ecosystem engineering related to vegetation. The particular soil conditions of mounds are thought to promote the establishment of specific species and functional groups, such as trees. For example, it has been suggested that termite mounds are focal points of forest species establishment in savanna ecosystems (COLE 1963; TRAORÉ et al. 2008b), and that they offer microhabitats different from the surrounding savanna for plant colonisation (MOE et al. 2009; SILESHI et al. 2010).

In addition to promoting plant establishment, termite mounds are focal sites for woody plant regeneration (TRAORÉ & LEPAGE 2008; TRAORÉ et al. 2008a, 2015) and help plants to survive adverse environmental conditions like fire, drought and inundation (TRAORÉ et al. 2008b). Microclimatic effects like shading and protection from fire and wind by already established vegetation further promote plant survival on mounds (LAWSON & JENIK 1967; OKALI et al. 1973). Termite mounds often harbour succulents, xerophytes and evergreen plant species (e.g., THOMAS 1943; COLONVAL-ELENKOV & MALAISSE 1975; MALAISSE 1975–1976), which are especially sensitive to fire. Succulents are most often found growing in the centre of mound thickets, on top of the mounds (KIRCHMAIR et al. 2012), where they are most protected from fire. Microtopography of mounds and the concretion of the outer soil layer of mounds lead to high runoff rates and low infiltration rates on the mounds themselves, which might be an environmental filter favouring xerophytic adaptations. However, under wetter habitat conditions, microtopographic elevation above the sur-

rounding area and the mounds' internal tunnels and galleries might help plants to escape root asphyxiation in the case of flooding (HUGHES 1988; MCCARTHY et al. 1998). Vegetation can also benefit from higher water availability in mound soil, as foraging tunnels around the mounds lead to higher infiltration and percolation towards the mound, and clay enrichment leads to higher field capacity of mound soil (TURNER 2006). As mentioned in the case of soil precipitation processes, vegetation can cause further feedback loops, for example by acting as collectors of aerosols and enhancing soil structural integrity with their roots (MCCARTHY et al. 2012). Further feedback may happen due to remineralisation of plant biomass contributing to mound soil fertility, which has been reported to be already elevated as compared to the surrounding savanna due to termite activity (JOUQUET et al. 2006, 2011; SILESHI et al. 2010). Termites from the original mound building species as well as other species can be involved in mineralising plant biomass growing on mounds, thus profiting from the effects of ecosystem engineering themselves.

Published germination experiments on mound soil are scarce, but mound topsoil has been shown to have a high mechanical impedance to root penetration (ACKERMAN et al. 2007; ROGERS et al. 1999), hampering seedling establishment. Unfortunately, handling of the soil in experimental studies leads to further soil compaction, sometimes limiting the significance of experimental results for our understanding of the processes involved in seedling establishment under natural conditions (ACKERMAN et al. 2007; GOSLING et al. 2012; GROHMANN 2010; MULLER & WARD 2013). Still, soil compaction on mounds is likely to favour certain plant phenotypes.

Regarding the rhizosphere, it has moreover been reported that *Borassus* palms in West Africa direct their root foraging towards nutrient-rich patches resulting from termite mounds (MORDELET et al. 1996), and that greater rooting depths occur on mounds in Ghana (OKALI et al. 1973). Seedling establishment and survival thus depend both on the soil conditions of mounds and species-specific phenological and morphological traits.

Recent results suggest that disturbances by fire and herbivores interact to maintain community diversity both in the savanna and on mounds, but the differences in community patterns between mounds and the surrounding savannas have been attributed to termite-induced soil changes (OKULLO & MOE 2012a; STØEN et al. 2013; TRAORÉ et al. 2015; SEYMOUR et al. 2016).

3.2.7 Effects on animals and their feedbacks with vegetation

Termite mounds, whether active or vegetated and eroded, are attractive for a wide range of mammals (FLEMING & LOVERIDGE 2003; LOVERIDGE & MOE 2004; OKULLO et al. 2013). Large herbivores have been discussed as maintainers of termite-induced heterogeneity in the savanna as consumers of biomass (OKULLO & MOE 2012a,b; STØEN et al. 2013), but they might also play a considerable role in seed dispersal (ALBERT et al. 2015; DEAN et al. 1999). Also Primates may be important for seed dispersal to mounds, but

there is a lack of systematic observations regarding their utilisation of mounds and mound vegetation. In West African savannas, the genus *Papio* in particular is known to be an effective dispersal agent for a number of species occurring on or even characteristic for termite mounds, like *Diospyros mespiliformis*, several species of *Grewia*, and *Tamarindus indica* (KUNZ & LINSENMAYER 2008; LIEBERMAN et al. 1979). Further ethological as well as ecological studies on primates' relations to termite mounds are needed. Considering small mammals, some studies mention that rodents use abandoned termite mounds for seed hoarding (ALEXANDRE 2002; BATIONO et al. 2002). For *Macrotermes*, the focus genus of this paper, the possible role of termites as dispersal vectors, as suggested by TRAORÉ et al. (2015), can quite safely be dismissed because, unlike many species of ants, *Macrotermes* do not transport and store seeds in their nests.

Termite mounds also affect other animals, both directly and indirectly through effects on the vegetation. Mounds themselves, and the often more dense vegetation on mounds compared to the surrounding savanna, provide food resources and sites for shelter, burrowing, foraging, thermoregulation, roosting, and breeding, as has been found for reptiles (GARDEN et al. 2010), birds (DEAN et al. 1999; JOSEPH et al. 2011), and mammals (FLEMING & LOVERIDGE 2003). Several mammal species feed on termites, and a variety of animal species perch on mounds, take refuge in their cavities, directly exploit the mound material for minerals through geophagy, and prefer browsing or grazing on plants growing on termite mounds (e.g., RUGGIERO & FAY 1994; HOLDO & MCDOWELL 2004; LOVERIDGE & MOE 2004; MOBAEK et al. 2005; GRANT & SCHOLLES 2006; BRODY et al. 2010; LEVICK et al. 2010b; but also see MUVENGWI et al. 2013; O'CONNOR 2013; VAN DER PLAS et al. 2013). The interactions of mounds, plants, and animals are suspected to cause feedback loops, similar to those observed for large trees (DEAN et al. 1999). A summarising conceptual system analysis of this view, focussing on feedbacks creating and maintaining habitat heterogeneity of the savanna landscape, can be found in SILESHI et al. (2010). Thus, both for animals and plants, termite mounds can be described as keystone structures sensu TEWS et al. (2004).

3.2.8 Benefits to humans – the example of West Africa

Several plants used by local communities grow preferentially or exclusively on termite mounds. Some of these plants, and also the mounds themselves, are sometimes of significance in traditional belief systems (SILESHI et al. 2009), while others are harvested for medicinal purposes or as foodstuff. It is also common to harvest termites directly from the mound as poultry fodder, and to capture large amounts of alates on their nuptial flight for animal as well as human consumption, depending on local tradition (SILESHI et al. 2009). Under certain seasonal climatic circumstances, the basidiomycete fungi cultivated by the subfamily Macrotermitinae can produce fruit bodies, which are an important source of protein and are also used in traditional medicine (SILESHI et al. 2009; KONÉ et al. 2011, 2013). Also, in several parts of Africa humans, especially children and pregnant women, are known to consume termite mound soil; this may have medical benefits as a result of its elevated mineral

contents, however research so far is inconclusive (ZIEGLER 1997; WILSON 2003).

Clay-rich termite mound soil is also often used for construction or production of clay bricks throughout Africa, and is also used to amend soils by spreading mound material, which has been reported to increase soil fertility and suppress crop infection with parasitic plants (WATSON 1977; ANDRIANJAKA et al. 2007; SILESHI et al. 2009; TILAHUN et al. 2012). Furthermore, humans can actively promote ecosystem engineering by termites through agricultural practice, and termites have successfully been used in soil restoration, e.g. in case of the traditional Zaï system in Burkina Faso (SAWADOGO et al. 2008; SAWADOGO 2011; KAISER 2014). Termite mounds have also been used for prospecting of gold and other minerals. Already Herodot (2500 BP) relates in his 'History' that according to the Persians most of the gold collected in India would be carried up with sand by 'ants' dwelling under ground. Even though it is doubtful if this description of gold exploitation indeed refers to termites, contemporary research has shown that analysis of termite mound soil can be used to detect gold anomalies (WATSON 1972; PETTS et al. 2009).

Although it is clear that termites provide many benefits to humans, the contribution of termites, termite mounds, and other species depending on termite mounds to household income and human sustenance is yet to be quantified (SILESHI et al. 2009). As far as we are aware, ecological consequences of human utilisation of termites, termite mounds, and their products (including, e.g., NTFPs) have rarely been studied so far. Considering the magnitude and speed of land-use change in most parts of Africa, we suggest that sustainable and locally adapted management of the resources provided by termites would be necessary, and would thus welcome further research informing resource management decisions.

4 TERMITE MOUNDS AND VEGETATION PATTERNS

4.1 Differences between mounds and the surrounding savanna

Most of the differences between the vegetation on mounds and of the surrounding savanna have been mentioned in the frame of treating the interrelationship between termites and the savanna ecosystem (section 3; particularly 3.2.6 and 3.2.7). Some aspects not mentioned above are:

- The majority of characteristic mound species in West Africa is woody, which is in accordance with the notion that termite mounds are focal sites for woody plant regeneration as well as refugia for large trees to reach senescence (JOSEPH et al. 2011, 2013; TRAORÉ et al. 2008b).
- Other characteristic mound species are geophytes, suggesting that water availability on mounds is not uniformly high, especially not in the compact topsoil layer. In addition to having higher water-storage capacity, geophytes in their dormant stage are likely more resistant to cracking/swelling cycles between dry and wet season, which might be another advantage in the

face of higher expansible clay content in mound and pediment soil (JOUQUET et al. 2002a,b, 2004; MUJINYA et al. 2013).

- Studies analyzing the spatial distribution of species on mounds have shown spatial differentiation within mound microhabitats (LAWSON & JENIK 1967; KIRCHMAIR et al. 2012; YAMASHINA 2013), offering soil properties, microclimatic effects and protection from fire as possible explanations for the spatial distribution of species on mounds.
- Up to date, only very few studies (ERPENBACH et al. 2013, DAVIES et al. 2014) have specifically addressed the fact that climatic gradients play a role in the degree of difference between the vegetation of termite mounds and the surrounding savanna. Also, landscape-scale gradients, e.g. based on underlying pedology, hydrology or microclimatic effects have rarely been addressed. Exceptions includes studies on mound composition and structure (KORB & LINSENMAIR 1998a,b; ABE et al. 2009a,b), vegetation composition in relation to soil changes mediated by termites or land use/grazing history (DAVIES et al. 2016; ERPENBACH et al. 2016; LAGENDIJK et al 2016). It is of interest that some of these studies deliver evidence that the notion of termite mounds as being richer in nutrients than the matrix, thus being more densely vegetated by woody plants and more attractive to large herbivores does not hold true in all habitat contexts (MUVENGWI et al. 2013; O'CONNOR 2013; DAVIES et al. 2016; LAGENDIJK et al 2016).

4.2 Creation of vegetation mosaics

Termite mounds have long been suspected to be responsible for various patterns including savanna landscapes dotted with thickets, striped with woody vegetation, or dotted with bare patches, and in some cases research has shown clear causal relationships. Soil heterogeneity introduced by termites in feedback with woody plant growth has been shown to induce the formation of islands in the Okavango delta (DANGERFIELD et al. 1998; MCCARTHY et al. 1998, 2012), leading to a mosaic grassland dotted with vegetated islands. Similar grass-dominated landscapes dotted with thickets were described as "termite savannas" (TROLL 1936), also implying causal relationships. Several studies since have confirmed that termite mounds cause or heavily contribute to the formation of thicket clumps in savannas (e.g., BLÖSCH 2008; HOVESTADT 1997; MOE et al. 2009). In regions of high aridity, savannas often show patterns of dots, bands, or stripes of vegetation, separated by bare areas. These patterns are known collectively as "tigerbush" (CLOS-ARCEDUC 1956; MACFADYEN 1950), and different factors including termite mounds have been hypothesised to be responsible for their creation. Initially, pattern-generation was attributed to low and spatially highly stochastic precipitation and local runoff processes from bare areas, which can, e.g., be initiated by termite mounds (CLOS-ARCEDUC 1956; MACFADYEN 1950; WHITE 1970, 1971). However, spatially explicit modelling studies have shown that vegetation patterns can be self-organising as a result of competition and

facilitation of plants (COUTERON & LEJEUNE 2001; LEFEVER & LEJEUNE 1997; LEJEUNE & TLIDI 1999; THIERY et al. 1995). While these mechanistic modelling approaches did not consider spatial heterogeneity explicitly in modelling banded, striped or dotted patterns, they did not rule out the possibility that termite mounds might have facilitative or inhibitive influences and could be involved in pattern genesis at the landscape scale.

4.3 Desertification

The generation of vegetation patterns by termite mounds has been connected to desertification processes, but recent evidence contradicts this idea. Dotted vegetation patterns have been associated by several authors (e.g., RIETKERK et al. 2004; SCHEFFER et al. 2009) with catastrophic shifts in vegetation cover that lead to desertification of arid environments. This view has been opposed by a recent modelling study (BONACHELA et al. 2015), which demonstrated that ecosystem resilience to drought would be higher and recovery after drought would be faster under local-scale influence of termite mounds. By including only spatial changes in water availability and water use efficiency introduced by regularly spaced mounds in their model, BONACHELA et al. (2015) were able to reproduce vegetation patterns at several spatial scales, both on and off mounds, which matched patterns observed in situ. These results corroborate the hypothesis of JELTSCH et al. (2000) that termite mounds, as ecological buffers, can prevent catastrophic shifts towards either encroachment or desertification, and hence help savanna systems to persist. Termite mounds may therefore play an important role in avoiding desertification in arid areas. The role of termite mounds is particularly important because many regions worldwide are threatened by changes in the amount and temporal distribution of precipitation due to global climate change. However, since the timeframes in regard both to the persistence of termite mounds themselves as well as of colonisation, establishment and senescence of termite mound vegetation are unknown, further research throughout Africa in these regards would be needed when addressing the potential role of termite mounds in the savanna ecosystem under global change.

4.4 Landscape restoration

Besides being important for ecosystem resilience, termites might even be used in landscape restoration after severe droughts. The ecosystem engineering effects of termites on environmental heterogeneity and vegetation have already successfully been used to restore degraded and laterite-encrusted sites in West Africa. Landscape restoration has been a subject of considerable interest in the Sahel region. While some regional-scale vegetation models predict a future 'greening' of the Sahel based on precipitation changes, mainly involving herbaceous vegetation (HEUBES et al. 2011, 2013), the same authors emphasise that human impact, in particular deforestation, might trigger landscape degradation and desertification in West Africa. Results from a series of studies in the Sahel suggest that rehabilitation of degraded landscapes can be facilitated by mulching and actively promoting termite activity (MANDO 1997a,b; MANDO & BRUSSAARD 1999; MANDO et al. 1999; MANDO &

MIEDEMA 1997; MANDO & STROOSNIJDER 1999). The techniques used in these rehabilitation studies are adapted from traditional farming, like the traditional Zaï system, and have been shown to be highly effective (SAWADOGO et al. 2008; SAWADOGO 2011, KAISER 2014, KAISER et al. 2016). In line with findings of improved resilience to drought (BONACHELA et al. 2015), the cited rehabilitation studies have shown that termites indeed play the role of an ecological buffer in a dynamic savanna landscape. Furthermore, long-term management experience in promoting termite activity in a Zaï system in Burkina Faso has shown that termites enable even the formation of a closed-canopy forest on formerly highly degraded land under the current precipitation regime (KAISER 2014, KAISER et al. 2017).

In summary, evidence from multiple sub-disciplines of ecology indicates that termite mounds are important elements of the savanna system across scales, ranging from local scale facilitation/inhibition processes to landscape-scale patch dynamics, pattern generation and ecological buffering mechanisms, to regional - or even continental - scale dynamics of tree-grass coexistence, forest-savanna boundaries, and desertification. Active promotion of termite activity has been successfully used for ecosystem restoration, and it has been shown that termite mounds can enhance ecosystem resilience in the savanna system. However, little progress has been made so far to integrate the effects of termite mounds across scales. In our own projects, shortly presented in the following section, which described and analysed community and diversity patterns, and their drivers from local to regional scales, we tried to deliver a starting point to close this gap.

5 VEGETATION OF TERMITE MOUNDS ACROSS DIFFERENT SCALES AND ALONG A CLIMATIC GRADIENT – THE WEST AFRICAN EXAMPLE

With respect to the effects of termite mound on various ecological parameters, in particular on soil characteristics, it is suggestive to think of "termite mound vegetation" as similar across large areas of a continent, as similar observations regarding soil modification by termites and the prevalence of woody plant thickets on mounds (as compared to the surrounding savanna matrix) have been made in many different locations. However, most of the studies mentioned above have examined termite mound vegetation only at a local scale or even only at a single site, leaving larger-scale patterns largely unknown. In particular, effects of regional and landscape-scale biotic and abiotic environmental variability on termite mound-savanna dynamics have been mostly ignored. Only recently, progress has been made to generalise the effects of termite mounds, at least at the landscape scale, using modern remote sensing and modelling techniques (LEVICK et al. 2010a; BONACHELA et al. 2015; DAVIES et al. 2016). In addition, former studies from Africa have mainly focussed on East African and South African savanna systems. However, our own recent projects (ERPENBACH et al. 2013, 2014, 2016) tried to fill the West African gap. Two of these projects (see 5.1 and 5.2) quantified differences in plant species diversity and community composition between mounds and the surrounding savanna matrix at regional and landscape scales. The third one (5.3) additionally followed

individual seedlings and saplings to address the processes driving the patterns quantified in the first two projects by investigating the influence of termite mounds on colonisation, growth and mortality of plants.

5.1 The influence of termite-induced heterogeneity on savanna vegetation along a climatic gradient in West Africa

5.1.1 Gradient analysis of communities

In a regional study, ranging from the Sahel to the southern limit of the Northern Sudanian vegetation zone, ERPENBACH et al. (2013) showed that termite mound vegetation differs strongly from the surrounding savanna along the entire length of a strong bioclimatic gradient. Interestingly, mound and savanna vegetation pronouncedly changed along the gradient, and with a similar magnitude of change. Thus, mounds do not represent azonal elements in the savanna, but are influenced by climate as strongly as the surrounding savannas. At a regional scale, mean annual precipitation was the most influential factor for differences in vegetation along the transect, both for savannas and for mounds. Differences in plant community composition and plant diversity between mound and savanna vegetation were related to differences in soil composition, particularly in base saturation and cation exchange capacity.

5.1.2 Diversity analysis

The analysed measures of diversity were often, but not consistently higher on mounds than in the surrounding savannas, whether all vegetation layers were considered together or whether woody plants and herbaceous plants were considered separately. Diversity analysis showed a complicated pattern, very likely reflecting variation in local environmental conditions, disturbance regime and protection status of the research sites. The community contrast between mound and savanna quantified using DCA was more pronounced with increasing precipitation. Species accumulation curves showed that species richness generally increased with increasing precipitation. Both a comparison of species accumulation curves and response ratios of diversity measures indicated that the contribution of mounds to local phytodiversity also increased with increasing precipitation. This effect was stronger for woody plants. ERPENBACH et al. (2013) conclude that communities of mounds and savannas are well separated throughout the whole study area and climate and soil help explain the magnitude of this separation.

5.1.3 Indicator species analysis

Several species were identified as characteristic mound species, as they frequently and abundantly occur on termite mounds. Along the entire transect, all in all eleven species were identified as characteristic for termite mounds. According to their position within the transect, the particular plots revealed an increase in the number of characteristic species with increasing precipitation. ERPENBACH et al. (2013) argue that this increase might be related to an overall larger species pool in the more humid areas. Notably, several functional traits reoccurred among characteristic mound

species: all were woody or at least subligneous, several showed scrambling or climbing growth forms, and all, except *Wissadula amplissima* (L.) R.E.Fr. and *Combretum aculeatum* Vent., featured diaspores with adaptations to zoochory. Four species of Malvaceae (*Wissadula amplissima* and three species of *Grewia*) as well as three *Capparaceae* species (*Capparis sepiaria* L., *Cadaba farinosa* Forssk., and *Maerua oblongifolia* (Forssk.) A. Rich.) were among the characteristic species. According to the authors cited above, this might suggest further shared functional traits or preadaptations leading to selection against these species in the surrounding savanna or a competitive advantage of these characteristic species in the mound microhabitat.

5.2 The contribution of *Macrotermes* mounds to landscape-scale variation in vegetation in Pendjari National Park (North Benin)

5.2.1 Soil gradient analysis of communities

In a landscape-scale study in Pendjari National Park (North Benin), strong systematic variation of savanna vegetation was observed (ERPENBACH et al. 2016). In a DCA of termite mound plots, a stronger grouping according to the surrounding savanna types was found than expected. Correlation analysis of DCA results indicated that different soil parameters were related to vegetation differences between savanna plots of different savanna types than to vegetation differences between mound plots of different savanna types. Further correlation analysis of CCA results for each savanna type with soil parameters showed that only some soil parameters (pH, conductivity, available potassium) were correlated with the difference between mound community and savanna community across all savanna types; correlations with further soil parameters differed between savanna types. While mound communities were always distinct from the surrounding savanna, they varied to different extents depending on the surrounding savanna type. In particular, both savanna vegetation and mound vegetation were more variable in areas with moderately deep alluvial soils than in areas with more extreme soil conditions. Results from both correlative analyses combined showed that differences in mound vegetation between savanna types and the contrast between mound and savanna vegetation in each savanna type were influenced by variability in soil parameters. Additional variability in plant communities of mounds and savannas, which differed in extent between savanna types, suggests the importance of further factors, such as local environmental filtering by flooding and available local-scale species pools, for mound and savanna community composition.

5.2.2 Analysis of community distances in response to soil

Clay enrichment and related changes in potential cation exchange capacity, pH, and concentrations of magnesium and calcium explained 22% of the variation in just one latent variable. Concentration of potassium cations was identified to be an important factor for three further latent variables, and additional inclusion of potassium concentration, plant available phosphorus, and sand content increased the variation explained to 62%. These results were interpreted as

confirming the hypothesis that clay enrichment is the most important driving factor for the development of termite mound vegetation, but emphasise the importance of interactions between clay content and plant macronutrients.

5.2.3 Indicator species analysis

ERPENBACH et al. (2016) found ten characteristic species for the termite mound microhabitat. Each of the four sampled savanna types had its own characteristic mound species set. Both *Detarium* and *Crossopteryx* savannas had several indicator species, whereas only one and two characteristic mound species, respectively, were detected for mounds in the temporally waterlogged *Mitragyna* savannas and in *Terminalia* savannas. Characteristic species included six species in the herbaceous layer (i.e., plants below 50 cm height), five of which were geophytes capable of subterranean dormancy. These results were interpreted as support for a hypothesised environmental filtering by protection from fire (TRAORÉ & LEPAGE 2008; TRAORÉ et al. 2008a) and by differences in water availability between mounds and the surrounding savanna.

5.3 Dynamics of juvenile woody plant communities on termite mounds in a West African savanna landscape

5.3.1 Analysis of diversity patterns

In a local-scale monitoring study conducted over the course of two years (ERPENBACH et al. 2014), mound communities were more species rich and more diverse than savanna communities, while savanna communities showed higher species evenness. While the most frequent species occurred both on mounds and in savannas, species that were restricted to one plot type occurred particularly infrequently. Although mound and savanna plots shared nearly half of their species pools, their communities were distinct. In a multivariate analysis of community distances, mound and savanna communities showed a clear separation for both non-woody and juvenile woody plants. Mounds showed a slightly lower within-group β -diversity than savannas for juvenile woody plants, but a slightly higher within-group β -diversity for non-woody plants. Partly in accordance with expectations, the results showed that higher overall diversity on mounds is mainly driven by higher α -diversity, and indicated a trend towards more uniform juvenile woody plant vegetation on mounds than in the surrounding savanna.

5.3.2 Analysis of population dynamics

Basic population metrics of juvenile woody plant community structure (basal area, number of individuals and number of stems) showed significantly higher values on termite mounds than in savannas at each sampling time, and increased over time with one minor exception. Individual turnover between samplings was high, with only about one third of 859 sampled individuals being present at all sampling occasions. No significant differences could be found between mounds and savannas for metrics of juvenile woody plant community dynamics (individual mortality, colonisation and turnover). Further analysis of causal drivers of population dynamics and resulting community pat-

terns was impeded by high turnover and die-back rates of woody juvenile plants, and overall low frequency and abundances of species. Only four woody species were present at more than four sampled plots at all sampling times.

5.3.3 Analysis of soil composition

In the study of ERPENBACH et al. (2014), Termite mound topsoil was significantly different from the surrounding savanna topsoil. On average, mound soil contained more than twice the amount of clay and plant available potassium than the surrounding savanna, and potassium cation concentration was more than four times higher. Base concentration, base saturation, concentrations of magnesium and calcium cations, and pH were also significantly higher on mounds, and the C/N ratio was significantly lower. These results were in accordance with expectations and support the hypothesis that mounds are favourable microhabitats for plant colonisation.

5.3.4 Analysis of plant dispersal modes

A comparison of dispersal modes showed a significantly larger number of zoochorous species within the community of juvenile woody plants on mounds than in the community of juvenile woody plants in the surrounding savanna. Neither anemochorous species nor species with mixed dispersal mode showed differences in frequency of occurrence between mound and savanna. One can conclude that dispersal of zoochorous species is directed towards mounds, which is congruent with the hypothesis that mounds are keystone structures for both animals and plants in the savanna landscape.

In summary, our studies showed that mound communities are more uniform than savanna vegetation on the local scale, but variation of mound vegetation in relation to the surrounding habitat is pronounced at the landscape scale. Furthermore, community composition was related to climatic parameters at the regional scale, where turnover occurred in the same order of magnitude as for the surrounding savannas. Juvenile plant communities on mounds differed in several parameters from juvenile communities in the surrounding savannas, however, individual turnover between seasons is too pronounced to allow final conclusions about colonisation, recruiting and survival processes responsible for the pronounced contrast between termite mound and savanna vegetation. From our findings, and the body of literature discussed above, it can be concluded that termite mounds are an integral part of the savanna ecosystem across scales, and that they are not only of considerable importance for particular characteristic species, but also for maintaining patterns and processes of the savanna over longer time frames.

We suggest that future progress in understanding the role of termite mounds in the savanna ecosystem will depend on an integration of data across scales, while recognising the variability of termite mound vegetation. Currently, much of the actual patterns and processes might still be obscured by unclear definitions of terms, uncertainties in regard to ecological context, and methodological problems regarding comparability of data and suitable analyses. Recent discus-

sions have highlighted several problems to address, e.g. the nutrient status of the matrix soil (MUVENGWI et al. 2013; O'CONNOR 2013), or even the definition of "matrix" including the distance to which mound influence occurs, and may be detected also in regard to statistical tools (SILESHI & ARSHAD 2012, SILESHI 2016). In addition, age and size of termite mounds as well as the identity of their builders are sometimes not well defined in studies (SILESHI 2016).

It is of considerable importance to address such issues before integrating data and aiming at a synthesis. However, it is already clear that termite mounds are an important feature of savanna landscapes throughout Africa, and beyond. The role of termite mounds for savanna vegetation at the landscape scale will likely affect local human population the most, and land use change will certainly affect processes and patterns in regard to termite mounds locally and at the landscape scale. However, the effects of climate change are likely to have an impact on larger-scale patterns, where the role of termite mounds is unclear. Since population dynamics and processes at the local scale are neither fully known nor understood for both termites and termite mound vegetation, further local studies with well-defined protocols regarding species, sizes and possibly ages of mounds could help to inform larger-scale modelling and synthetic approaches.

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