Termite mounds as islands of diversity in West African savanna landscapes

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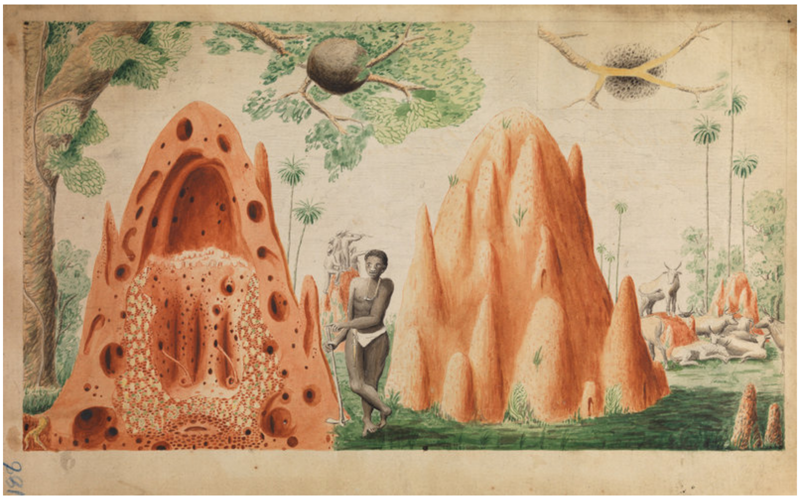

These hills continue quite bare until they are six or eight feet high, but in time the dead barren clay, of which they are composed, becomes fertilised by the genial power of the elements in these prolific climates, and the addition of the vegetable salts and other matters brought by the wind, and in the second or third year, the hillock, if not over-shaded by trees, becomes, like the rest of the earth, almost covered with grass and other plants[.]

Smeathman (1781):

Some Account of the Termites, Which are Found in Africa and Other Hot Climates. In a Letter from Mr. Henry Smeathman, of Clement's Inn, to Sir Joseph Banks, Bart. P. R. S.

Philosophical Transactions of the Royal Society of London 71(2): 139–192 (p.149 & Tab. VII).

Contents

List of tables

List of figures

Summary

Termites are important ecosystem engineers of the savanna biome, with the large mounds of fungus-cultivating termites being sources of habitat heterogeneity and structural complexity in African savanna landscapes. Termite mounds represent microhabitats for various organisms, particularly plants. Studies from different localities throughout Africa have shown that termite mounds harbour a more diverse vegetation than the surrounding matrix, and several plant species, including some of high socio-economic value, are restricted to or primarily found on termite mounds. Differences between mound and savanna vegetation are thought in the literature to result from termite-induced changes in soil composition, in particular higher fertility and higher water availability on mounds, and from protection from fire and the influence of herbivores. However, most research has been conducted only at the local scale, and integrating knowledge across Africa is hampered by different methodology of studies and differing environmental context. Little is known about the variation in vegetation composition on termite mounds compared to the surrounding savanna at the regional scale and at the landscape scale, and the main determinants of plant communities on mounds are yet to be ascertained.

With this thesis I aimed at better understanding the influence of termite mounds on vegetation compared to the surrounding savanna across spatial scales. Specifically, I conducted three research projects analysing vegetation data and soil data from paired mound and savanna plots in West Africa. In project I, I examined the influence of termite-induced heterogeneity on plant diversity and vegetation composition at a regional scale, following a bioclimatic gradient from the Sahel of Burkina Faso to the Sudanian vegetation zone in North Benin. In project II, I analysed variation of vegetation on and off mounds at the landscape scale in Pendjari National Park, North Benin. In project III, I conducted a monitoring study over the course of two years, exploring dynamics of juvenile woody plant communities on mounds and in the surrounding savanna at a local scale. My thesis thus provides the first comparative quantitative analysis of mound and savanna vegetation and the drivers of the mound–savanna difference in vegetation across scales.

I used multivariate statistics to identify groups of plant communities at each scale, and correlative analyses to relate climatic and soil data to variation in vegetation composition. I also conducted pairwise analyses of the differences in diversity and, in the monitoring study, of differences in population metrics between mounds and the surrounding savannas. Moreover, I identified characteristic plant species associated with termite mounds in each study. To determine which soil factors were most important for the mound–savanna contrast in vegetation across different savanna types, I used correlation analysis and projection to latent structures regression (PLSR), which allowed for collinear factors to be included and ranked in the model.

Synthesizing across scales, my results confirm that termite mounds strongly contribute to savanna plant diversity, even though mounds are not generally more species rich than the surrounding savanna. I showed that variation in mound vegetation is much higher along climatic and soil gradients than previously acknowledged. Mound vegetation differed from the surrounding savanna in the whole study area and in each sampled savanna type, with the strongest differences occurring at the most humid study sites. I was able to explain a large proportion of the differences between mound and savanna vegetation with clay enrichment and related soil factors, such as cation concentrations. Plants on mounds thus benefit from favourable soil conditions, including higher fertility and higher water availability, which was also mirrored by the higher abundance and basal area of juvenile woody plants I found on mounds. The variation in mound vegetation I detected between study sites across scales resulted in part from local differences in soil composition and from climatic differences that influence the regional distribution of species. I thus identified different sets of characteristic mound species in each project, and found that specific plant families and traits like succulency, lianescence, and adaptations to zoochory were overrepresented in mound communities.

In addition to my findings in this thesis, remaining parts of the variation in mound vegetation between study sites could likely be explained by investigating further factors. Specifically, mound vegetation depends on habitat context, which includes available species pools, spatial distribution of mounds, biotic interactions with dispersers and herbivores, fire, and also anthropogenic influence. The high proportion of species with adaptations to zoochory I found on mounds, for example, indicates that animal dispersers should be of particular importance for vegetation on termite mounds. Herbivory and fire regime, which are known to contribute to the diversity and community composition of

the mound–savanna system, also show strong local variation, not least because of anthropogenic influence.

In conclusion, I demonstrated that termite mounds play a crucial role in maintaining heterogeneity and plant diversity in the savanna across scales. Ecosystem services provided by termites, especially considering long-term effects on soil fertility and ecosystem resilience, are most likely undervalued. I thus suggest that mounds should be considered in management plans from local to regional, transnational scales as a matter of course, accompanied by further research on the role of termite mounds in savanna ecology on a longer temporal scale. My research presented here thus provides a solid basis for future studies on termite mound vegetation that should specifically consider the biotic and abiotic context of the mound–savanna system.

Zusammenfassung

Termiten sind bedeutende Ökosystem-Ingenieure der Savanne. Die großen Hügel der pilzkultivierenden Arten tragen dabei maßgeblich zur Habitatheterogenität und strukturellen Komplexität afrikanischer Savannenlandschaften bei und stellen Mikrohabitate für zahlreiche Organismen dar, insbesondere für Pflanzen. Studien aus verschiedenen Gebieten Afrikas konnten zeigen, dass Termitenhügel eine vielfältigere Vegetation aufweisen als die sie umgebende Matrix. Darüber hinaus sind einige Pflanzenarten mit zum Teil hohem sozioökonomischen Wert auf Termitenhügel beschränkt oder werden zumindest vorwiegend auf Hügeln vorgefunden.

In der Literatur wird angenommen, dass die Unterschiede zwischen Hügel- und Savannenvegetation auf Änderungen der Bodenzusammensetzung und Bodenbeschaffenheit durch Termiten zurückzuführen sind. Insbesondere eine höhere Bodenfruchtbarkeit und höhere Wasserverfügbarkeit auf Hügeln gelten als Folge der Aktivität ihrer Erbauer. Des Weiteren werden ein möglicher Schutz vor Feuer auf Termitenhügeln und der Einfluss von Herbivoren auf Hügel- und Savannenvegetation in diesem Kontext als bedeutend eingeschätzt. Der Großteil der vorliegenden Literatur besteht allerdings aus Studien auf lokaler Ebene. Eine Integration und Generalisierung ihrer Ergebnisse über den kleinräumigen Maßstab hinaus wird durch die unterschiedliche angewendete Methodik sowie unterschiedliche Rahmenbedingungen der einzelnen Studien erschwert. So ist bisher wenig darüber bekannt, ob und wie die Vegetation auf Termitenhügeln gegenüber der umgebenden Savannenvegetation auf regionaler Skala variiert und welche Bedeutung Termitenhügel für Diversitätsmuster jenseits der lokalen Skala haben. Außerdem besteht Unklarheit darüber, welche Faktoren letztlich entscheidend für Unterschiede zwischen Pflanzengemeinschaften auf Termitenhügeln und den umgebenden Savannen sind.

Das Ziel dieser Dissertation war es, den Einfluss von Termitenhügeln auf Vegetation im Vergleich zur umgebenden Savanne über räumliche Skalen hinweg zu untersuchen und besser zu verstehen. Um dieses Ziel zu erreichen führte ich drei Forschungsprojekte durch, in denen ich Vegetationsdaten und Bodendaten von gepaarten Hügel- und Sa-

vannenplots in Westafrika analysierte. In Projekt I untersuchte ich den Einfluss termiteninduzierter Heterogenität auf die Pflanzendiversität und Vegetationszusammensetzung auf regionaler Skala entlang eines bioklimatischen Gradienten vom Sahel in Burkina Faso bis zum nördlichen Rand der Südsudanzone in Nordbenin. In Projekt II beschäftigte ich mich mit der Variation der Vegetation auf Hügeln und in der Savanne auf der Landschaftsebene im Pendjari Nationalpark in Nordbenin. In Projekt III führte ich eine Monitoringstudie über zwei Jahre durch, in der ich die Dynamik juveniler Gehölzpflanzengemeinschaften auf Hügeln und in der umgebenden Savanne auf lokaler Skala erforschte. Meine Dissertation stellt so die erste vergleichende quantitative Analyse von Hügel- und Savannenvegetation sowie der Ursachen für die Differenzierung zwischen Hügel- und Savannenvegetation über räumliche Skalen hinweg dar.

Um auf jeder einzelnen Skala Gruppen von Pflanzengemeinschaften zu identifizieren, verwendete ich multivariate statistische Methoden. Mittels Korrelationsanalysen untersuchte ich die Beziehung zwischen Variation in der Vegetationszusammensetzung und Klima- sowie Bodenparametern. Des Weiteren untersuchte ich Diversitätsunterschiede und, im Rahmen der Monitoringstudie, auch Unterschiede in Populationsparametern zwischen gepaarten Stichproben von Hügel und Savanne. Darüber hinaus identifizierte ich in jedem Projekt charakteristische Pflanzenarten, die mit Termitenhügeln assoziiert sind. Um festzustellen, welche Bodenfaktoren am wichtigsten für den Vegetationskontrast zwischen Hügeln und Savanne über verschiedene Savannentypen hinweg sind, nutzte ich Korrelationsanalysen und PLSR (Projection to Latent Structures Regression). Letztere ermöglchtes es mir, kollineare Faktoren in mein Modell einzubeziehen und nach ihrer Wichtigkeit einzustufen.

Zusammenfassend über die untersuchten Skalen hinweg bestätigen meine Ergebnisse, dass Termitenhügel stark zur Pflanzendiversität in der Savanne beitragen, auch wenn sie nicht generell und überall artenreicher sind als die umgebende Savanne. Ich konnte zeigen, dass die Variation der Hügelvegetation entlang klimatischer Gradienten und Bodengradienten viel höher ist als bisher angenommen. Hügelvegetation unterschied sich in meinem gesamten Untersuchungsgebiet und in jedem einzelnen untersuchten Savannentyp deutlich in Artzusammensetzung und Abundanzen von der umgebenden Savannenvegetation. Der Kontrast nahm dabei mit steigendem Jahresniederschlag entlang des Transekts zu. Ich konnte in meiner Arbeit klären, dass einen großer Teil der Unterschiede zwischen Hügel- und Savannenvegetation über pedologisch bedingte verschiedene Savannantypen hinweg durch Tonanreicherung in Hügeln und damit zusammenhängende Bodenfaktoren wie höhere Kationenkonzentrationen bedingt wurde. Pflanzen auf Termitenhügeln profitieren von den somit günstigeren Bodeneigenschaften, von denen insbesondere höhere Fruchtbarkeit und Wasserverfügbarkeit wichtig sind. Dies spiegelt sich auch in der höheren Abundanz und Basalfläche von juvenilen Gehölzindividuen wider, die ich in meiner Monitoringstudie zeigen konnte. Die Variation der Hügelvegetation zwischen verschiedenen Lokalitäten ließ sich zum Teil auf lokale Unterschiede in der Bodenzusammensetzung sowie auf großräumigere klimatische Unterschiede zurückführen, welche die regionale Verbreitung von Arten beeinflussen. Ich identifizierte in den Projekten auf unterschiedlichen räumlichen Skalen unterschiedliche charakteristische Hügelarten. In der Hügelvegetation traten bestimmte Pflanzenfamilien sowie Sukkulenz, kletternde Wuchsformen und Anpassungen an Zoochorie vermehrt auf.

Weitere Teile der Variation in der Hügelvegetation zwischen verschiedenen Untersuchungsgebieten können vermutlich durch weitere Faktoren im Habitatkontext erklärt werden. Der vorhandene Artenpool, die räumliche Verteilung der Hügel, biotische Interaktionen mit Ausbreitern und Herbivoren, Feuer sowie anthropogener Einfluss haben wahrscheinlich einen bedeutenden Einfluss. Der hohe Anteil der an Zoochorie angepassten Arten, die ich auf Hügeln feststellte, deutet zum Beispiel darauf hin, dass Tiere als Vektoren von Diasporen sehr wichtig für die Hügelvegetation sind. Des Weiteren ist bekannt, dass Herbivorie und Feuer einen Einfluss auf die Diversität und Zusammensetzung von Hügel- und Savannenvegetation haben. Auch diese beiden Einflussgrößen weisen starke lokale Variation auf, nicht zuletzt durch anthropogenen Einfluss.

Meine Dissertation bietet eine solide Grundlage für zukünftige Studien über Termitenhügelvegetation, die gezielt den biotischen und abiotischen Kontext des Hügel-Savannen-Systems berücksichtigen sollten. Aus meiner Forschung schlussfolgere ich, dass Termitenhügel lokal wie auch großräumig eine entscheidende Rolle in der Aufrechterhaltung von Habitatheterogenität und Pflanzendiversität in der Savanne spielen. Von Termiten zur Verfügung gestellte Ökosystemleistungen, insbesondere in Anbetracht von Langzeiteffekten auf Bodenfruchtbarkeit und Ökosystemresilienz, werden bisher höchst wahrscheinlich unterschätzt.

Auf Grund der hier vorgelegten Ergebnisse sowie der umfangreichen gesichteten Literatur empfehle ich, die Rolle von Termiten und Termitenhügeln grundsätzlich in Management-Plänen von der lokalen bis hin zur regionalen, Länder übergreifenden Skala zu berücksichtigen, begleitet von weiterführender Forschung bezüglich der Rolle von Termitenhügeln in der Savannenökologie über längere zeitliche Skalen.

1

General introduction

1.1 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 C_4 grasses. Termites, which are particularly abundant in savannas (Lee and 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, our knowledge of the specific contribution of mound-building termites to overall savanna diversity and ecosystem dynamics is limited. It is suggestive to think of "termite mound vegetation" as similar across Africa, 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 (e.g., Jackson and Gartlan 1965; Konaté et al. 1999; Blösch 2008; Brody et al. 2010; Seymour et al. 2014). However, most studies 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. In addition, previous studies from Africa have mainly focussed on East African and South African savanna systems; data on West African termite mound vegetation are scarce. The West African knowledge gap is particularly grave because several plant species that are highly sought-after in West Africa frequently occur on and may even be confined to termite mounds. Furthermore, besides harbouring valuable timber and fruit species, termite mounds can be highly important in the context of traditional medicine and belief systems for the local population. A better understanding of mound vegetation composition in West Africa, as well as its variation in space and time, is thus not only of high scientific importance, but also of socio-economic relevance.

The main objective of this thesis is to analyse the vegetation of termite mounds in comparison to the surrounding savanna matrix in West Africa, to gain a better understanding of the influence of mounds on savanna plant diversity and composition. Unlike previous studies, I investigate variation in mound and savanna vegetation from local to regional scales, and cover a range of bioclimatic zones. I identify small- to broad-scale driving factors of variation in plant species diversity and composition. Furthermore, I specifically investigate colonisation and recruitment of plants growing on termite mounds.

I address this research aim with three complementary projects. In project I, I examine the differences between mound and savanna vegetation along a climatic transect with pronounced differences in precipitation to determine if termite mounds constitute extrazonal microhabitats. This research builds on results of previous studies indicating that termite mounds are sites of higher water availability and of higher soil fertility in otherwise nutrient-deficient savannas. In project II, I further compare mound and savanna vegetation in relation to underlying soil characteristics to establish if mound vegetation is a distinct and homogeneously definable unit at a landscape scale. Finally, in project III, I focus on the local dynamics of juvenile woody plants (i.e., colonisation, growth rates, and mortality) on termite mounds compared to the surrounding savanna matrix. I aim to confirm if termite mounds are favourable environments for tree recruitment and regeneration, as is currently argued in the literature because they might provide shelter against fire, drought, and flooding.

In this chapter, I give an introduction to termite biology, followed by a short overview of our current knowledge on the importance of termites for the savanna ecosystems, with a focus on Africa. I continue with a brief geographical and geobotanical description of the study area, and a summary of the study design.

In section 1.2, I outline the aims and scope of this thesis. In addition, for each project, I summarise the key hypotheses and research questions, and briefly describe the methodology used.

Chapter 2, the general discussion, first summarises the main results of the research projects. Following this, I discuss the results in the context of current research on savanna ecology and the role of termite mounds in the African savanna biome. I critically assess both my own results and the prevailing view of termite mound vegetation. Manuscripts detailing the research projects are presented in the appendix, containing a detailed description of materials and methods, results, and a detailed discussion for each project. The appendix furthermore contains supplementary material for each manuscript.

Termite biology

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, I provide an introduction to termite biology in the following, including ecology and classification into different feeding groups and the importance of mounds for the evolution and ecology of mound-building species. My research focusses on the effect of mounds of two species of the fungus-cultivating genus *Macrotermes*, and I thus give more detailed information on the focus species.

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 and 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 thesis 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. Drummond's work was also largely disregarded, besides some rare contributions from the field of vegetation ecology. The topic was ignored until, nearly six decades later, a review by Adamson (1943) addressed open questions and called for further research on the question whether termite activity is detrimental or beneficial to the ecosystem on a longer timescale. Adamson (1943) 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 20$^{\text{th}}$ 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.

Termite ecology and classification

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 and 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.

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 driving 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 and Eggleton 2005; Lo and 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 and Eggleton 2005).

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*.

Termite mounds

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*, the subject of this thesis.

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 homoeostasis 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 and 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.

Homoeostasis of the mound environment might be more important for the fungus than for the termites themselves (Korb 2003; Aanen and Eggleton 2005), which because of their thin cuticles are very prone to dessication, 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 CO_2 (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 and Linsenmair 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 study, 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.

Focus species

Species distribution This thesis focusses on vegetation changes in response to changes of the soil environment induced by 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 throughout, *M. bellicosus* reaches the northern limit of its distribution within the study area.

Variability of mound types It is difficult to distinguish the two species in the field, and termite individuals, preferentially from the solider caste, are needed for species determination. In general, the two species 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 and Linsenmair 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, and because exploratory data analysis did not indicate that the supposed identity of each mound's builders influenced analysis results, I do not consider differences between the two study species in this thesis.

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, 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 and Linsenmair 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)

(Mujinya et al. 2010, 2013, 2014; Erens et al. 2015), supporting the idea that the impact of termites on soil turnover and soil composition depends on the surrounding environment.

Interrelationship between termites and the savanna ecosystem

Research history

The general impact of termites on tropical systems, including the specific functions of termites as detrivores, began to become widely recognised with the dawn of ecology as an integrative scientific field. The importance of termites for soil turnover was first acknowledged in the late 19th century (Drummond 1886). In the following years, with the beginning of modern geobotanical, biogeographical and pedological studies in the tropics, authors began to comment in more detail on the importance of termite activity for savanna vegetation, and particularly on the importance of termite mound building activities for plants growing on mounds. It was noticed that termite mounds often support different plants than the surrounding savanna matrix. 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 and Gartlan 1965; Fanshawe 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 and Wood 1971; Wood and 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 and Moe 2012b; Bonachela et al. 2015)

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 and Wood 1971; Wood and 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). 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.

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 and Conacher 1990; Léonard and 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).

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; 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. It is however not yet known whether nutrient input by termites or clay content is more important for soil fertility of termite mounds (Sileshi et al. 2010).

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 and 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.

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 m^{3}ha^{-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), depending on re-colonisation 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.

Ecosystem engineering 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). For this thesis, ecosystem engineering by termites is considered from the perspective of plant community ecology. 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 keystone 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.

Most important for this thesis 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 also help plants to survive adverse environmental conditions like fire, drought and inundation (Traoré et al. 2008b). Micro-climatic effects like shading and protection from fire and wind by already established vegetation further promote plant survival on mounds (Lawson and Jenik 1967; Okali et al. 1973). Termite mounds often harbour succulents, xerophytes and evergreen plant species (e.g Colonval-Elenkov and Malaisse 1975; Malaisse 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 adaptions. However, under wetter habitat conditions, microtopographic elevation above the surrounding 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 re-mineralisation 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.

Effects on animals 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 and 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 and Fay 1994; Loveridge and Moe 2004; Grant and Scholes 2006; Brody et al. 2010; 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).

Benefits to humans While this thesis does only deal with effects of termite mounds on vegetation, a major motivation for the research presented was the realisation that besides plants and animals, also humans benefit from termite mounds. In 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, 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).

Rationale for this thesis The far-reaching significance of termites for the whole savanna ecosystem is thus evident: as termites process large amounts of biomass and soil, they contribute to local soil changes and landscape-scale soil turnover, having various consequences for plants and animals, including humans. Human populations are likely to grow further and to promote change of savanna ecosystems. For example, land use change and climate change pose a threat to termite populations and the future availability of ecosystem services and goods provided by their mounds. As the exact ways in which termites influence vegetation patterns and processes are so far relatively poorly understood, it is essential to gain a more fundamental understanding of the interplay between termites and the surrounding savanna.

1.2 Aims and scope

The general scope of this thesis is the influence of termite mounds on savanna vegetation in West African landscapes. My aim was to investigate plant communities on termite mounds in comparison to the surrounding savanna matrix at a range of spatial scales, and community structure over time. To this end, this thesis considers the influence of climate, soil, vegetation types, landscape heterogeneity, community differentiation, and individual-based vegetation dynamics and succession on termite mounds. Specifically, I focus on three questions: if and how termite mound vegetation differs along a climatic gradient, if and how termite mound vegetation differs between savanna types in a single landscape, and how juvenile woody plant communities are influenced by termite mounds. These questions are addressed in three research projects:

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

II The contribution of *Macrotermes* mounds to landscape-scale variation in vegetation in a West African national park

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

The first two projects quantify differences in plant species diversity and community composition between mounds and the surrounding savanna matrix at regional and landscape scales. The third project additionally analyses time-series of individual-based data 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 individuals.

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

Termite mounds are thought to support unique vegetation communities, but how these vary at a regional scale is unknown. In multiple studies from different parts of Africa, abandoned termite mounds of the genus *Macrotermes* have been described as harbouring specific plants or even a specific "termite mound vegetation". In addition, regional floristic works often mention termite mounds among the habitats of certain species, and even remark that particular plants are restricted to mounds. Notably woody species, including evergreen forest species and species with delayed leaf shedding, have been noted to prevalently occur on mounds. For instance, adult trees of the socio-economically important species *Tamarindus indica* L., which is otherwise restricted to gallery forests, are also found on termite mounds in West African savannas. However, most studies of termite mound vegetation have a very narrow geographical focus, so that more general conclusions about the dependency of plant species on termite mounds are hampered. It is thus unclear if vegetation on mounds develops similarly under different bioclimatic conditions, and how much variation there is in community composition between vegetation zones. It is furthermore unknown if the differences between mound vegetation and surrounding savanna matrix vegetation are always equally pronounced along regional climatic gradients. The aim of this project, therefore, was to investigate differences between mound and savanna vegetation in different savanna types at the regional scale. The study transect had a length of about 500 km and covered near-natural vegetation from the Sahel area of Burkina Faso to the northern limit of the South Sudanian vegetation zone in Benin.

My predictions were:

I.1 All along a regional climatic gradient, vegetation on mounds should differ from vegetation in the surrounding savanna.

I.2 Diversity on mounds should be higher than in the surrounding savanna, particularly for woody plants, and mound community diversity should increase with increased precipitation along the climatic gradient.

I.3 Characteristic indicator species should be found for termite mound vegetation all along the climatic gradient, with more indicator species in more humid localities.

I.4 Composition of mound soil should differ from the surrounding soil; e.g. nutrient concentration should be elevated on mounds in comparison to the adjacent savanna soil. Differences in soil composition between termite mounds and surrounding savannas should qualitatively and quantitatively be similar all along the study transect.

My sampling across scales covered a range of climatic zones and different vegetation types, to enable a general conclusion about differences in vegetation and soil between *Macrotermes* termite mounds and the surrounding savanna matrix. To the best of my knowledge, no previous research on termite mound vegetation along climatic gradients exists up until this thesis, and no other study addressed regional, landscape-scale, and local variation of termite mound vegetation in contrast to the surrounding savanna. This study therefore provides a framework for a deeper understanding of the role of termite mounds in driving savanna plant diversity and ecosystem functions. It presents the first comparisons of plant diversities, plant communities, and soils of termite mounds across scales, and provides baseline data for more detailed studies of the importance of termite mounds for plant communities and savanna diversity in West Africa.

Project II: The contribution of *Macrotermes* mounds to landscape-scale variation in vegetation in a West African national park

While it is established that termite mound soil affects vegetation on mounds, both the variability of mound soil and the driving factor for differences in vegetation compared to the surrounding savanna are unknown: either nutrient enrichment or clay enrichment in mounds are hypothesised to cause these differences. Therefore, following the regional scale of project I, this project considered termite mound vegetation and soil variation at a landscape scale in Pendjari National Park, North Benin. For plants, termite mounds form a well-defined and sharply delineated micro-habitat that is distinctly different from the surrounding savanna. A large body of literature indicates that termite mounds are comparably rich in plant nutrients, but studies so far have carried out comparisons only within a single locality, or in a small area. Thus, landscape-scale variation in mound and savanna soil properties has been widely ignored, even though it is recognised as a key driving factor of vegetation patterns at this scale. Only very recently, some pedological studies of mound soil under different ecological and geophysical conditions have become available, but none of these studies was related to vegetation on mounds.

This project addresses this research gap by comparing vegetation on and off *Macrotermes* mounds in four different vegetation types occurring on different soils in Pendjari National Park, North Benin. The four savanna types chosen represent the range of conditions found within the national park, from waterlogged habitats to shallow-soiled laterite pans.

My predictions were:

II.1 Composition of termite mound plant communities should differ only moderately between savanna types, while savanna vegetation should vary pronouncedly.

II.2 Termite mounds should have similar soil properties, regardless of vegetation type, with only slight variation resulting from differences in underlying pedology.

II.3 The strong contrast between vegetation on mounds and off mounds should reflect the strength of the contrast between mound and surrounding soil, i.e. should be stronger on waterlogged sites and shallow soils of the laterite hardpans than on alluvial soils moderately enriched in silt and clay.

II.4 Differences in vegetation between mound and the surrounding savanna should reflect differences in soil composition, with either clay content or nutrient content of mounds as the most important factor.

To my knowledge, the variability of mound vegetation at the landscape scale has not been addressed so far. In addition, this study is the first to address the relationship between variations in savanna soil conditions and differences in vegetation between mound and savanna in a consistent analytical framework. This study also demonstrates an approach for identifying the most influential out of a set of collinear drivers of the contrast between vegetation on and off mounds, to identify which variables are driving the general pattern.

Project III: Dynamics of juvenile woody plant communities on termite mounds in a West African savanna landscape

Termite mounds, as *de-novo* microhabitats, are an important source of habitat heterogeneity in savannas, providing unique opportunities and challenges for plant establishment. It has been suggested that mounds enable evergreen forest species to colonise savanna habitats, and that the regeneration of woody plants in general is facilitated by *Macrotermes* mounds. However, the dynamics of juvenile woody plant composition on mounds are unclear, and conclusions about the processes leading to the development of a distinct mound vegetation are prevented by a lack of available data.

The aim of this project was to test the conclusion of Traoré et al. (2008b) that termite mounds are safe sites for woody plant regeneration in the Sudanian savanna vegetation zone, and to provide further data on the succession of woody plants on termite mounds in this region. The study was conducted at the local scale, with an extent of about 2 km^2, in near-homogeneous matrix vegetation. In addition to species diversity and community composition, I analysed basal area gain and population dynamics of juvenile woody plants and non-woody plants on mounds compared to the surrounding savanna.

My predictions were:

III.1 Plant communities of juvenile woody plants should be more diverse on mounds than in the surrounding savanna and, specifically, should show a higher β-diversity.

III.2 Juvenile woody plants should have lower mortality rates, higher colonisation rates, and faster basal area gain on mounds than in the surrounding savannas.

III.3 Overall abundance, density, and biomass of juvenile woody plants should be higher on mounds than in the surrounding savanna.

III.4 Some of the differences between mound and savanna vegetation should be explained by differences in soil composition mediated by termites.

III.5 Directed zoochory towards mounds should also contribute to differences in the plant communities, in that a higher proportion of plants with animal-dispersed diaspores should be present on mounds than in the surrounding savanna.

This project aims to confirm recent results that termite mounds are important sites for woody plant regeneration. Additionally, it presents an effort to collect more data on the composition and dynamics of juvenile woody plant communities on mounds to foster further understanding of colonisation and establishment processes on mounds as compared to the surrounding savanna. Thus, this project contributes to our knowledge of plant succession on termite mounds.

1.3 Study design

Study area

This research was part of the BIOTA Africa project, a research network of large regional biodiversity monitoring transects across the African continent. The BIOTA West Africa subproject collected and analysed data along two major transect routes, the western route reaching from southern Ivory Coast to central Burkina Faso, and the eastern route reaching from northern Burkina Faso to central Benin. In the course of data collection for this project, I followed the eastern BIOTA West Africa transect from northern Burkina Faso to northern Benin, with a north-south spatial extent of approximately 5° latitude or 500 km. West Africa shows a strong bioclimatic gradient from deserts in the north to annual grasslands and savannas to deciduous and evergreen forests in the south. The study transect thus encompassed a strong gradient in the length of the wet season and in mean annual precipitation, which ranges from 360 mm in the north to approximately 1000 mm in the south. Accordingly, the transect comprised several vegetation zones, i.e. the Sahel vegetation zone and the Northern Sudanian vegetation zone *sensu* White (1983) and Guinko (1984). Only savanna was sampled for the research described here; termite mounds in gallery forest, dry forest and agricultural landscapes were not considered.

I selected study landscapes that were least affected by recent land-use, i.e. that were not used for agricultural practices and least impacted by pastoral pressure, timber production and non-timber forest product (NTFP) extraction. Collection of vegetation and soil data thus took place in natural or near-natural sites in five protected areas along the transect (Figure 1.1). The five protected areas will be briefly described in the following, going from north to south.

Sylvo-Pastoral and Partial Faunal Reserve of the Sahel

The northernmost protected area sampled, Réserve Sylvo-Pastorale et Partielle de Faune du Sahel (RPS), is the largest reserve of Burkina Faso, covering an area of approximately 1.6 Mha. It is a habitat management area (category IV) under the IUCN classification, entailing only weak protection. The Sahelian savanna landscapes are largely used as

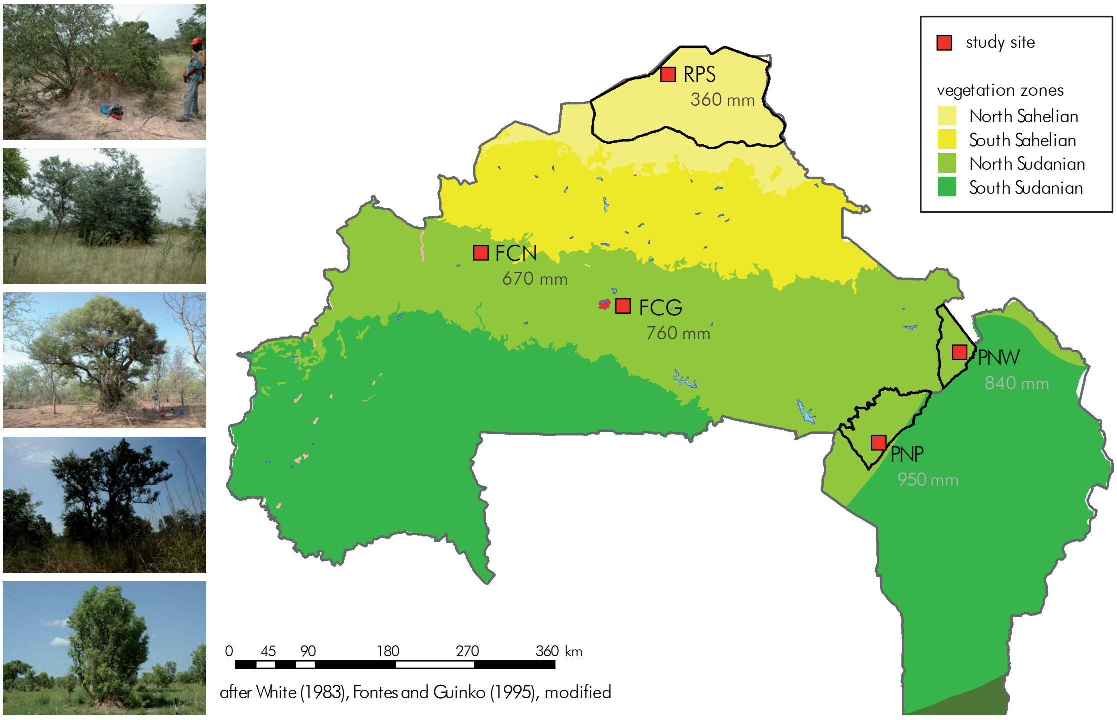

Figure 1.1 Study area covering different vegetation zones in Burkina Faso and Benin, West Africa. Red squares indicate approximate locations of study sites in five protected areas; black lines outline the larger protected areas. Photos show a typical vegetated termite mound from each area. Sites from north to south (and photos from top to bottom): Sahel Partial Reserve (RPS, 360 mm MAP), Niouma Classified Forest (FCN, 670 mm), Gonsé Classified Forest (FCG, 760 mm), W National Park (PNW, 840 mm), and Pendjari National Park (PNP, 950 mm).

pasture rangelands, with a strong impact on the natural vegetation. RPS is the most arid study area I sampled, with only 360 mm mean annual precipitation. The area is characterised by tiger bush, a shrub savanna vegetation dominated by *Pterocarpus lucens* Guill. & Perr. and *Combretum micranthum* G.Don, which form characteristic bands or stripes of vegetation interspersed with areas nearly bare of perennial vegetation. To my knowledge, only *Macrotermes subhyalinus* occurs in RPS.

Niouma classified forest

The second northernmost protected area sampled, Forêt Classée de Niouma (FCN), encompasses only a very small area of 735 ha, a remnant of natural vegetation in an agricultural landscape. FCN was designated as a protected area in 1954. It was extended to include additional, formerly cultivated, lands in 1984, and its weak, merely national protection status allows timber and NTFP extraction under certain conditions. This sub-Sahelic region receives a mean annual precipitation of approximately 670 mm. The vegetation shows intermediate characteristics. I sampled in areas showing banded savanna vegetation patterns which are typically found in the Sahel, dominated by *Pterocarpus lucens* and *Acacia erythrocalyx* Brenan, and other areas dominated by *Terminalia avicennioides* Guill. & Perr. and *Vitellaria paradoxa* C.F.Gaertn., which are more typical for the Sudanian zone. I avoided areas where vegetation was under influence of temporary waterbodies. In FCN, judging from cathedral-shaped mound remnants, with typical ridges and turrets, as well as from reports of local forestry officials, *Macrotermes bellicosus* seems to have occurred recently, but I could only identify living colonies of *M. subhyalinus*.

Gonsé classified forest

Forêt Classée de Gonsé (FCG) encompasses a relatively small area of 6500 ha. Like Niouma classified forest it is only weakly protected, allowing the extraction of firewood and NTFP. Anthropogenic pressure is particularly strong due to its close vicinity to the metropolis of Ouagadougou. In addition, the area suffers from strong erosion and degradation as a consequence of a failed developmental programme involving deforestation for timber production using introduced tree species. Mean annual precipitation in FCG is 760 mm. Two vegetation types were selected for data collection; the first type is a semi-natural savanna habitat dominated by *Terminalia avicennioides*, *Ziziphus mauritiana* Lam. and subdominant *Sclerocarya birrea* (A. Rich.) Hochst. The second, more disturbed, vegetation type is dominated by *Combretum micranthum* and *Guiera senegalensis* J.F.Gmel. and is often accompanied by *Ziziphus mauritiana*. I again excluded areas of temporary waterbodies, and also excluded gallery forest habitats. Living colonies of both *Macrotermes subhyalinus* and *M. bellicosus* were present at the time of data collection.

W National Park

The easternmost protected area, Parc National du W (PNW), is a trans-boundary national park named after a W-shaped bend in the Niger river. PNW includes areas in Burkina Faso, Niger, and Benin, with about 30,000 ha in Burkina Faso, 21,900 ha in Niger, and 50,200 ha in Benin. The park is part of the WAP complex, consisting of PNW, Arli National Park in Burkina Faso, and several adjacent partial reserves and hunting zones. This complex protects the largest remaining continuous savanna area in West Africa, including a variety of vegetation types ranging from arid tiger bush to humid South Sudanian savanna. I collected data and samples in Burkina Faso only, in an area of PNW which receives a mean annual precipitation of 840 mm. Vegetation and soil were sampled in two savanna types that were chosen based on my own data, remote sensing data, and vegetation analysis of adjacent areas (Hahn-Hadjali 1998; Mbayngone et al. 2008; Ouédraogo et al. 2008). The first vegetation type was dominated by *Burkea africana* Hook. and *Terminalia avicennioides*, typical for the northern Sudanian vegetation zone; the second type was dominated by *Isoberlinia doka* Craib & Stapf and *Afzelia africana* Sm. ex Pers., which are more typical for the southern Sudanian vegetation zone. Living colonies of both *Macrotermes subhyalinus* and *M. bellicosus* were present in PNW in high densities at the time of data collection.

Pendjari National Park

The southernmost protected area sampled, Parc National de la Pendjari (PNP), has an area of 27,550 ha. PNP also constitutes part of the WAP complex, and includes a large hunting zone. With 950 mm of mean annual precipitation, PNP is the most humid site in the study transect. In contrast to the other sampling sites, where I avoided strong contrast between sampled savanna types, I aimed to encompass an ecological gradient in my sampling in PNP. I sampled in four vegetation types, which were chosen based on my own data, remote sensing data, and available maps of vegetation and soil conditions (Faure and Viennot 1978; Viennot 1978; Kpadonou et al. 2009). These vegetation types differ in their underlying pedology and "wetness", ranging from seasonally dry shallow soils to deep and seasonally waterlogged soils. The sampled types were *Mitragyna* savanna with *M. inermis* (Willd.) K. Schum. and *Combretum adenogonium* Steud. ex A. Rich. as the dominant species (on temporarily inundated, deep soils); *Terminalia–Burkea* savanna with *T. avicennioides* as the dominant species and *Combretum collinum* Fresen. as subdominant species, accompanied by large individuals of *Burkea africana* (on deep, scelettic soils); *Crossopteryx* savanna with *C. febrifuga* (Afzel. ex G. Don) Benth. as the dominant species, accompanied by *Terminalia avicennioides* (on moderately deep soils of mostly alluvial origin), and *Detarium* savanna with *D. microcarpum* Guill. & Perr. as the dominant species, accompanied by *Combretum adenogonium* (on shallow soils on lateritic crusts). All sampled vegetation types are typical for the northern Sudanian vegetation zone. Living colonies of both *Macrotermes subhyalinus* and *M. bellicosus* were present in PNP at the time of sampling, with very high densities of *M. bellicosus*.

Methods

For this thesis, I sampled vegetation and soil in the same design along the study transect, using plot pairs consisting of a termite mound and a plot of the same size in the surrounding savanna matrix. The study design was stratified by protected areas, savanna types per protected area, and the mound–savanna plot distinction, allowing for comparisons among those categories. Vegetation data was further stratified by vegetation layers.

Savanna type selection

I chose to sample near-natural savanna habitats in protected areas in our study region, because land use is very likely to affect *Macrotermes* populations and their mounds, and also local plant populations. I identified the prevalent savanna types using field prospecting, published and unpublished data from the BIOTA framework (Hahn-Hadjali 1998; Da 2006; Dossou-Yovo 2008; Koadima 2008; Mbayngone et al. 2008; Kaboré 2009; Kpadonou et al. 2009) and LANDSAT images classified with ESRI ArcGIS 9.3. For each study area, I selected the most representative savanna types for the area. I excluded savanna types of extreme environmental conditions, except for lateritic sites with shallow soil and temporarily inundated sites in PNP as an additional stratification to allow for comparison along a gradient of soil "wetness" conditions.

Plot selection

In each savanna type, I sampled at least 12 plot pairs. Selection of mound and savanna plot pairs was randomised. If no road network was available, I chose random GPS locations within the protected area, and from there walked in a random compass bearing for a distance up to 500 m until the preselected savanna type was met. If a road network was available, I haphazardly selected areas where the preselected savanna type occurred within 500 m of the road and walked a random distance between 10 and 500 m in a direction approximately perpendicular to the road. At the end point, I chose the nearest vegetated termite mound in walking direction for vegetation sampling.

Plot design

I measured each mound's longest diameter, and the perpendicular diameter as well as mound circumference and mound height. A paired savanna plot was placed 15 m north of the mound's outer limit (in the literature often named mound pediment, or mound halo), with the south-eastern corner of the square as starting point. The paired savanna plots were matched in size to their paired mound plots. The paired mound's longest diameter was multiplied by its perpendicular diameter. The square root of this value was then used as the length of each side of the savanna plot. In addition to the paired savanna plot, a 30 by 30 m savanna plot encompassing the paired savanna plot and lining up with it at its south-east corner was laid out to characterise woody savanna vegetation. Great care was taken that no other *Macrotermes* mound was within the 30 by 30 m plot, or within 15 m of the limits of the paired savanna sub-plot. If a mound was too near either savanna plot, I rotated the direction for the paired savanna plot counterclockwise away from north in steps of 15 degrees. In cases of high mound density, in which other mounds were unavoidably present within the 30 by 30 m plot, I extended the 30 by 30 m plot side length each by the longest diameter of the included mound, and excluded mound vegetation from savanna sampling. Mound density in each sampled vegetation type in each studied protected area was determined by mapping a haphazardly chosen 1 ha square with a GPS unit.

Vegetation data

For each plot, I sampled three vegetation layers: tree, shrub, and herb layer. In accordance with other projects within the BIOTA framework, the tree layer was defined as woody plants > 5 m, the shrub layer as woody and partly ligneous plants from 0.5 to 5 m, and the herbaceous layer as all plants up to 0.5 m in height. For each layer, I recorded all species present and estimated vegetation cover as percentage. For the third project of this thesis, individual numbers of juvenile woody plants as well as basal diameters of all woody juvenile plant stems were recorded for a subset of twelve plots in PNP at one site, in a *Terminalia–Burkea* savanna.

Climatic data

I obtained climatic data for each study area from the WorldClim dataset (Hijmans et al. 2005), amended with potential evapotranspiration (PET) and aridity index (AI) data from Zomer et al. (2008). Using ESRI ArcGIS 9.3, I extracted values for the plot positions at 30 arc-seconds resolution from the climatic raster files.

Soil data

I sampled mound and savanna soil for laboratory analysis by pooling topsoil samples of approximately 10 cm^3 each from four positions in each plot to account for micro-scale heterogeneity. Mound topsoil was sampled 1 m inwards from the limit of each mound's pediment in each cardinal direction, mixed and air-dried. Savanna topsoil was sampled at four random positions in each savanna plot, and was then mixed and air-dried.

Soil analysis

Soil analysis was performed in the Institute of Physical Geography, University of Frankfurt, Germany. All soil samples were sieved to < 2 mm prior to analysis. To determine pH and conductivity in aquaeus solution, samples were measured against 0.1 M KCl and 0.01 M $CaCl_2$ solution, respectively, using a WTW E56 pH electrode and a WTW 740 conductivity meter. Concentrations of plant-available phosphorus (P_2O_{5av}) and plant-available potassium (K_2O_{av}) were determined in calcium-lactate solution using a Milton Roy 301 spectrometer and an AAS PerkinElmer AAnalyst 300 spectrometer after Schüller (1969). Nitrogen (N) content was determined using the Kjeldahl titrimetry method with a Büchi 430 digester and a Büchi 320 distillation unit (Kjeldahl 1883; Bremner 1960). Content of organic carbon (C_{org}) was determined by the Lichterfelder wet combustion method, using oxidation with chromic-sulphuric acid and a Milton Roy 301 spectrometer, following DIN 19684-2 (Deutsches Institut für Normung 1977a). Total carbon content (C) was determined through dry combustion spectral measurements using LECO RC-412 and LECO EC-12 spectrometers, following DIN/ISO 10694 (Deutsches Institut für Normung 1996). Potential cation exchange capacity (CEC_{pot}) and ion concentrations of magnesium (Mg^{2+}), calcium (Ca^{2+}), sodium (Na^{+}) and potassium (K^{+}) were determined following the Mehlich method in buffered $BaCl_2$ solution using an AAS Perkin Elmer AAnalyst 300 spectrometer, following DIN 19684-8 (Deutsches Institut für Normung 1977b). Particle size distribution was determined using the Köhn pipette method, after destruction of organic matter with H_2O_2, with the sample dispersed in a $Na_4P_2O_7$ solution, following DIN 19683-1 and DIN 19683-2 (Deutsches Institut für Normung 1973a,b)

2

General discussion

2.1 Short summary of main results

Project I

Bioclimatic gradient analysis of communities

In the regional study, ranging from the Sahel to the southern limit of the Northern Sudanian vegetation zone, I showed that in accordance with my expectations, termite mound vegetation differed strongly from the surrounding savanna along the entire length of a strong bioclimatic gradient (Figure I.2 in Appendix I). Interestingly, mound and savanna vegetation both changed pronouncedly along the gradient, and with a similar magnitude of change. Especially for savanna plots, I expected a strong turnover of species to occur along the gradient. Mounds, however, were expected to provide microhabitats for evergreen and xerophytic species, and thus to show a lesser degree of turnover than savanna plots. I concluded that mounds do not represent azonal elements in the savanna, but are as strongly influenced by climate as the surrounding savannas. I further demonstrated that, at a regional scale, mean annual precipitation was the most influential factor for differences in vegetation along the transect (Table I.1, first column), 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 (Table I.1, third column).

Diversity analysis

Contrary to a number of previous studies, I did not observe generally higher plant diversities on mounds. Diversity analysis showed a complicated pattern, very likely reflecting variation in local environmental conditions, disturbance regime and protection status of the research sites (Figure I.4). 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. In accordance with my expectations, the community contrast between mound and savanna that I quantified using DCA was more pronounced with increasing precipitation (Figure I.2). Species accumulation curves (Figure I.3) showed that species richness generally increased with increasing precipitation. Both a comparison of species accumulation curves and response ratios of diversity measures (Figure I.4) indicated that the contribution of mounds to local phytodiversity also increased with increasing precipitation. As anticipated, this effect was stronger for woody plants. The main conclusion regarding my predictions is 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. Future attempts to fully understand patterns of plant diversity and differences in community composition between mounds and surrounding savannas need to consider further biotic and abiotic conditions, spatial configuration of mounds, and anthropogenic influence at the sampling sites.

Indicator species analysis

As predicted based on previous floristic records and anecdotal evidence, several species in my sampling were identified as characteristic mound species, as they frequently and abundantly occurred on termite mounds. Along the entire transect, I identified eleven species as characteristic for termite mounds (Table I.2). I observed an increase in the number of characteristic species with increasing precipitation, which 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 amplissimia* 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. 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.

Project II

Soil gradient analysis of communities

In the landscape-scale study in Pendjari National Park (North Benin), I observed strong systematic variation of savanna vegetation in a DCA (Figure II.1a in Appendix II), in accordance with my expectations. In a DCA of termite mound plots, I found stronger grouping according to the surrounding savanna types than expected (Figure II.1b). Correlation analysis of DCA results indicated that several soil parameters were related to vegetation differences between savanna plots of different savanna types (Tables II.1, II.6); vegetation differences between mound plots in different savanna types also showed correlations with several soil paramters, partly differing from those parameters in the savanna plot analysis (Tables II.1, II.6). 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 (Figure II.2, Tables II.2, II.7). While mound communities were always distinct from the surrounding savanna, they varied to different extents depending on the surrounding savanna type (Figure II.2). 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.

Analysis of community distances in response to soil

I identified the most important soil parameters influencing the differences in vegetation between savanna and mound using projection to latent structures regression (PLSR) (Figures II.3, II.4). PLSR enabled me to analyse the combined influences of all soil parameters, despite their inherent correlation, and rank them according to their influence on the differences in vegetation between savannas and mounds. I found that clay enrichment and related changes in potential cation exchange capacity, pH, and concentrations of magnesium and calcium explained 22% of the variation using just one latent variable, or PLS axis (Tables II.4, II.5). The concentration of potassium cations was identified to be an important factor for three further latent variables (Figure II.3), and additional inclusion of potassium concentration, plant available phosphorus, and sand content increased the variation explained to 62% (Table II.4). I interpret these results as confirming the hypothesis that clay enrichment is the most important driving factor for the formation of termite mound vegetation, but emphasise the importance of interactions between clay content and plant macronutrients.

Indicator species analysis

In Pendjari National Park, I identified ten characteristic species for the termite mound microhabitat (Table II.3). Each of the four sampled savanna types had its own characteristic mound species set. Both *Detarium* and *Crossopteryx* savannas had several indicator species, whereas I only detected one and two characteristic mound species, respectively, 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. I interpret these results as support for the hypothesised environmental filtering by protection from fire and different water availability on mounds than in the surrounding savanna.

Project III

Analysis of diversity patterns

In my local-scale monitoring study conducted over the course of two years, mound communities were more species rich and more diverse than savanna communities, while savanna communities showed higher species evenness (Figures III.1, III.2 and Table III.1 in Appendix III). Most species in my dataset occurred infrequently. While the most frequent species occurred both on mounds and in savannas, species that were restricted to one plot type occurred particularly infrequently (Figure III.3, Table III.6). 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 (Figure III.4). 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 my expectations, my results showed that higher overall diversity on mounds is mainly driven by higher α-diversity, and indicated a trend towards a more uniform juvenile woody plant vegetation on mounds than in the surrounding savanna.

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 (Table III.2). 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, Table III.3). Further analysis of causal drivers of population dynamics and resulting community patterns was impeded by turnover and die-back of woody juvenile plants in combination with overall low frequency and abundances of species. Only four woody species were present at more than four sampled plots at all sampling times. I therefore restricted the analysis to descriptive statistics of soil parameters and dispersal mode on and off mounds, as described in the following.

Analysis of soil composition

I found that termite mound topsoil was significantly different from the surrounding savanna topsoil (Figure III.6, Table III.5). 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 my expectations and support the hypothesis that mounds are favourable microhabitats for plant colonisation.

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 (Figure III.5, Table III.4). Neither anemochorous species nor species with mixed dispersal mode showed differences in frequency of occurrence between mounds and savannas. I 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.

2.2 Discussion of the results across scales

This thesis is a contribution to the ongoing discussion on the importance of termite mounds within the savanna biome, in particular to the questions how and why vegetation on termite mounds differs from the surrounding savannas. In the following, I will link the results of my three projects to research findings from different fields of savanna ecology across spatial scales. The consideration of spatial scale is crucial to our understanding of the determinants of vegetation patterns. It has been suggested that particular sets of parameters are important drivers of patterns at particular scales, with possible overlap of the scales at which they are important (Willis and Whittaker 2002; Pearson and Dawson 2003). Spatial extent and spatial resolution of analysis have to be chosen carefully in relation to analysis aims (Pearson and Dawson 2003; Chase and Myers 2011). In the case of this thesis, taking into account multiple spatial scales in the analysis of termite mound and savanna vegetation allowed me to detect multiple different drivers of variability among sites and between mounds and savannas.

Regional scale

At continental to regional scales, past and current climate are considered strong factors determining not only species richness patterns, but also today's forest–savanna boundary, which has been shown to be driven especially (but not exclusively) by mean annual precipitation (MAP) and precipitation seasonality (Sankaran et al. 2005; Bond 2008; Staver et al. 2011b). The results of project I, that regional variation in savanna vegetation showed the strongest correlation with MAP, are in congruence with the importance of climatic factors for the occurrence of savanna vegetation at a large scale.

Besides a recent paper (Davies et al. 2014), no studies to my knowledge have specifically addressed the influence of climatic gradients on termite mound vegetation. I found that, while showing a clear separation from the savanna matrix, mound vegetation was influenced to the same extent by MAP as the surrounding savannas. Thus, I conclude that mound vegetation is also zonal, and not mainly characterised by broad-leaf forest tree species as suggested by, e.g., Cole (1963). Climate is generally the most important driver of species diversity at broad spatial scales (e.g. Currie 1991; Hawkins et al. 2003; Field et al. 2009), which is in line with the higher overall species richness found at the limit of the South Sudanian Zone in North Benin as compared to the Sahel. Plant diversity in my study area has been shown to be higher in more humid areas (Schmidt et al. 2005, 2013). Notably, in my study, this pattern was especially pronounced for woody plants both on mounds and in savannas. The difference between mound and savanna species richness was more pronounced with increasing mean annual precipitation, particularly for woody plants, so that the contribution of mounds to γ-diversity increases with precipitation. Higher species richness of woody plants on mounds in general is consistent with the notion that mounds are focal sites for tree regeneration (Traoré et al. 2008b, 2015), but an increase in the contrast between mound and savanna woody plant species richness with increasing precipitation has not yet been documented. Besides a possible explanation by the overall higher species pool available, competition by grasses, but also fire impact as well as flooding are likely to act as stronger filters in more humid savannas due to higher standing grass biomass and strong torrential rains during the wet season.

Land use is likely an additional factor influencing species richness on mounds as compared to savannas at a regional scale. In addition to climate, higher woody plant species richness and diversity in W National Park and Pendjari National Park might also be partly attributed to their higher protection status and thereby the restricted land use in these parks. Their more effective protection and larger area with a potentially larger remaining species pool should have an influence on overall richness and potentially the mound–savanna contrast. Land use changes and subsequent land degradation are thought to increase the already prevalent loss of woody cover in West Africa in the long term (Ouedraogo et al. 2010; Nacoulma et al. 2011; Le et al. 2012; Heubes et al. 2013; Houessou et al. 2013), even though the international debate often stresses the increase of woody biomass in savanna ecosystems (compare, e.g., Bond 2008; Heubes et al. 2011). The impact of land use change on termite mound vegetation has not yet been thoroughly investigated, however, land use change might cause an increase in importance of termite mounds for woody vegetation in the future. Termite mounds as focal sites for woody plant regeneration (Traoré and Lepage 2008; Traoré et al. 2008a,b, 2015) should be particularly important in areas where woody plant establishment is hampered by strong anthropogenic pressure in the form of browsing, grazing, and wood extraction. In fact, in Gonsé Classified Forest (FCG), which showed the strongest human influence among all the research sites studied, all characteristic mound indicator species were woody plants, and while mounds showed lower overall plant diversity than the surrounding savanna, this was mainly driven by higher herbaceous plant species richness in the savanna. My findings therefore support the claim that termite mounds are focal sites of woody plant regeneration, although a detailed analysis of anthropogenic influence on mound and savanna vegetation is beyond the scope of this thesis. However, if termite mounds are refugia or at least preferred habitats for some woody species, then the mound microhabitat is likely to be of considerable importance for regional biodiversity and future ecosystem resilience, especially since my data showed strong variability of mound vegetation along the transect. This zonality of termite mound vegetation indicates that termite mounds are sources of heterogeneity and thus are important for landscape-scale processes maintaining savanna diversity. Notwithstanding the need for further studies on the role of termite mounds in determining regional-scale savanna diversity, I suggest that termite mounds and termite mound vegetation should be included in land use management plans at a regional scale, and at finer scales.

Landscape scale

Landscape-scale savanna vegetation composition is thought to be determined mostly by topography, geology, and soil composition (Walter et al. 1971; Higgins et al. 2000; Bond 2008), in interaction with herbivory and fire (Higgins et al. 2000, 2007; Asner et al. 2009; Lehmann et al. 2014). At the landscape scale, savanna vegetation often exhibits a surprising amount of differentiation, considering how little environmental variation is easily visible to the untrained eye. For my study area in West Africa, savanna types have been shown to correlate with underlying soil composition (Hahn-Hadjali 1998).

Landscape-scale heterogeneity in soil fertility and soil water regime, which is increased by termite activity, is thought to drive spatial variation in vegetation composition and species richness (compare Willis and Whittaker 2002; Pearson and Dawson 2003). However, studies on termite mound vegetation rarely address variation in soil composition and often neglect that the surrounding habitat might influence termite mounds and mound vegetation. In project II, I not only confirmed the relation between savanna vegetation and variation in soil composition, but also showed that termite mound vegetation varies at the landscape scale in response to variation in soil composition. Due to the landscape-scale heterogeneity covered in my study, I was able to relate different soil parameters to the variation of vegetation between mounds and savannas in each savanna type.

While several studies have shown that termites locally modify nutrient content and clay content of the soil and also influence water availability on mounds (Konaté et al. 1999;

Turner 2006; Seymour et al. 2014), it has remained unclear until now whether nutrient richness or clay enrichment is more important in driving observed vegetation differences between mound and savannas (Sileshi et al. 2010). I was able to identify clay enrichment 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 contrast. Selective transport of subsoil clay particles, mineralisation 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 (Boyer 1982; Jouquet et al. 2002b; Semhi et al. 2008; Mills et al. 2009). 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 (Mujinya et al. 2013; Erens et al. 2015).

Potassium is likely to be of particular importance in explaining some peculiarities of termite mound vegetation. Potassium is highly important for plant ecology, particularly for water use efficiency, which has recently been re-emphasised in a global context (Sardans and Peñuelas 2015). Potassium is directly involved in regulating water loss in plants via influencing stomatal movements. However, it is lost through leaf-shedding, and is highly leachable from both leaf tissue and soil. Thus, acidic savanna soils are not only often deficient in nitrogen and phosphorus, but also in potassium (Jones and Wild 1975). On termite mounds, leaf-shedding in the dry season is often delayed or even absent, and evergreen species are more frequently found than in the surrounding savannas. While the only experimental study available (Konaté et al. 1999) related delayed leaf-shedding to higher water availability in the upper soil layers of termite mounds, higher potassium content and availability on mounds might be an important factor as well. Furthermore, several studies (including this thesis) have noted succulent plant species growing on mounds, which are also likely to benefit from higher potassium availability on mounds. Especially eye-catching is the case of *Euphorbia candelabrum* Trémaux ex Kotschy, which has often been found to be restricted to *Macrotermes* mounds in East Africa. Thomas (1943) suggested that the occurrence of *E. candelabrum* and species of the Apocynaceae tribus Stapeliae is related to cation exchange capacity, with *E. candelabrum* being confined to base-rich termite mounds in some areas of Uganda.

Clay mineralogy exerts a strong influence on the availability of potassium and other cations. Increasing potassium availability by fertilisation has been shown to exert an influence on the potassium–calcium and potassium–magnesium exchange equilibria in soils dominated by illite and kaolinite clay minerals in Nigeria. These soils preferentially adsorb K^+, releasing magnesium and calcium ions into the soil solution which makes them susceptible to leaching beyond the rooting zone of many plants. In these soils, savanna plant productivity is probably already limited by a lack of magnesium, and thus additional potassium fertilisation is likely to have a negative rather than a positive effect, especially in the long term (Agbenin and Yakubu 2006). This further illustrates the interdependencies between cation exchange processes and how they are modulated by clay content, and specifically clay mineralogy. Soil water retention and swelling/shrinking capacity are also directly related to clay mineralogy. While the analysis of clay mineralogy was beyond the scope of this thesis, the results of soil analyses from all three projects congruently suggest that increased clay content, and thus not nutrient subsidy by termite-processed organic material, is the most important soil parameter for explaining differences between mound and savanna vegetation. My landscape-scale study covers more variability than most other studies and I thus assume that generalisations from my findings are possible. I suggest future experimental studies to investigate the causal effects of clay enrichment on termite mound vegetation, in particular the chemo-physical relation of clay to mineral nutrient availability to plants.

While I identified clay enrichment as the most important driving factor for the vegetational contrast between mounds and savannas, additional nutrient subsidy by termites might still play an important role, especially in the light of the potentially very long lifespans of mounds as a result of re-colonisation. 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. 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 (Tilahun et al. 2012; Erens et al. 2015). I consider it likely that mound vegetation can access nutrients accumulated in mound soil over longer periods after the death of a colony, and that the combined effects of past nutrient input by termites and clay enrichment by termites are thus both important for mound vegetation. 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. Small sampling size is also an issue with the widely cited work of Konaté et al. (1999), who sampled plants on five mounds for leaf-shedding differences, and only one mound for water potential measurements. Remarkably, these measurements are still the only direct evidence available for higher water availability on mounds. Further data from other landscapes or regions would be welcome to confirm these results.

Local scale

At a local scale, communities and species assemblages are thought to be shaped mainly by fine-scale biotic interactions or niche-assembly processes, like competition for resources, facilitation, predation, and parasite-host interactions (Ricklefs 1987; van Dam 2009; Vellend 2010). We are able to observe and analyse results of biological interactions of plants by measuring germination success, establishment, growth and mortality. Thus, monitoring abundances combined with growth parameters like basal area increment often allows the identification of community patterns from a niche-assembly viewpoint.

The higher abundances and basal area of juvenile woody plants on termite mounds I found consistently over time are probably a result of higher nutrient and water availability, and directed dispersal towards mounds. However, in the diverse mound community, stochastic effects are also important to consider when studying niche assembly hypotheses by monitoring. Stochastic changes in species' abundances can change the effect of biotic interactions on community patterns. In small communities, this ecological drift can be considerably more important than competition and facilitation (Vellend 2010). Stochastic effects are a possible explanation for why I could not detect differences in mortality, colonisation, turnover, and diameter gain between mounds and savannas: stochastic elements in the processes of dispersal, germination and death may have outweighed more deterministic effects of competition, facilitation, disturbances and environmental filtering. The observed rates of die-back and turnover within mound and savanna communities were consistent with other findings from the same region (Jurisch et al. 2012, 2013), but together with high community diversity and low frequency of species hampered detailed analysis of species-specific responses to interactions and the mound microhabitat. Notably, the different evolutionary and ecological backgrounds of different species make it difficult to generalise results, as each species responds differently to environmental parameters. Even individuals of the same species sourced from different populations can show variability in traits and responses to influencing factors. I suggest that future studies should thus focus on a selected set of frequent and abundant species for analysis of potential beneficial effects of the mound microhabitat on juvenile woody plant dynamics. However, at the same time, I would caution against very broad generalisations of effects across species, even though environmental filters in the strongly seasonal savanna habitat are likely to affect most species similarly. Still, the consistently higher abundances and basal area on mounds as compared to the savanna confirm the generally positive effect of the mound microhabitat on woody plant regeneration found in other studies (Traoré and Lepage 2008; Traoré et al. 2008a,b, 2015).

In addition to stochastic processes and environmental filtering, niche-assembly theory furthermore assumes that community composition and structure is governed by interspecific facilitation and conspecific density effects (van Dam 2009). The latter include density effects related to the Janzen-Conell hypothesis, which states that seedlings that occur at high density or close to adult conspecifics are more likely to be under strong pressure from pathogens and insect herbivores and should thus show high mortality. I could not test for specific density-dependent effects in my dataset due to low frequency of species, but in a study of woody plant regeneration on termite mounds from my study area, Traoré et al. (2008b) found evidence of density-dependent mortality for *Acacia erythrocalyx*, the only species which was frequent enough in their dataset for this type of analysis. However, a recent study from the area of my monitoring study, Pendjari National Park, could not find support for Janzen-Conell effects, i.e. density-dependent mortality in relation to conspecific adult trees (Azihou et al. 2013). While the study specifically investigated the suitability of the subcanopy for colonisation in the savanna (and not on termite mounds), several species investigated (e.g., *Diospyros mespiliformis* Hochst. ex A. DC.) also frequently occur on termite mounds in the region, and are unlikely to exhibit density-dependent effects on mounds when none were found off mounds.

Disturbances by fire and herbivores can additionally influence community size and species abundances, and both are modulated by termite mounds. While the influence of fire has been shown to be buffered by mounds (Traoré and Lepage 2008; Traoré et al. 2008a), herbivores have been shown to prefer mound vegetation (Holdo and McDowell 2004; Loveridge and Moe 2004; Mobaek et al. 2005). Protection of juvenile woody plants from fire and increased herbivore pressure might balance each other out on short temporal scales, which might explain why I detected similar mortality and turnover rates on mounds and savanna plots. 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 and Moe 2012a; Støen et al. 2013; Traoré et al. 2015). Soil composition of *Macrotermes* mounds was different from the savanna topsoil, and the demonstrated higher clay and nutrient content was consistent with results from both other projects. Physico-chemical characteristics of mound soil may play an important part in the establishment of juvenile plants on mounds of *M. bellicosus* and *M. subhyalinus*, as has been shown for other termite species. Published germination experiments on mound soil are scarce, but mound topsoil has been shown to have a high mechanical impedance to root penetration (Rogers et al. 1999; Ackerman et al. 2007), 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; Grohmann 2010; Gosling et al. 2012; Muller and Ward 2013). Still, soil compaction on mounds is likely to favour certain plant phenotypes. Mechanical impedance is a function of water content, and strong rainfalls in the wet season might lead to a window of opportunity for plant germination and establishment on mounds. Thus, surface hardness of mounds might be a temporary impediment during the long dry season, favouring species fruiting in the late dry season to be dispersed during the wet season. Furthermore, plants adapted to zoochorous dispersal, which often occur on mounds, frequently feature large seeds. In turn, large-seeded plants like *Tamarindus indica* L., *Ziziphus* spp. or *Adansonia digitata* L. are often able to produce strong taproots (Parrota 1990; Van den Bilcke et al. 2013), which could be of advantage on mounds due to their ability to penetrate the outer soil layer. Plants able to penetrate the compacted soil layer might then profit from higher humidity and aeration in the interior of the mounds as well as from higher soil fertility. 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.

Besides this evidence for habitat filtering by the mound microhabitat, mound community composition might also be influenced by dispersal. Dispersal of plant diaspores links local-scale to landscape- and regional-scale species pools, both in a stochastic and in a deterministic way, to explain local species richness and abundance patterns (Tilman et al. 1997; May et al. 2012). Stochasticity of dispersal processes and the influence of ecological drift at the local scale are likely to be more important if the species pool available for colonisation is much higher than the number of species co-occurring at local scale (Chase and Myers 2011). This is the case in Pendjari National Park, as I have shown in project II. However, I hypothesised in project III that directed dispersal towards mounds might explain the higher proportion of animal-dispersed species on mounds, which adds a deterministic component to stochastic dispersal-assembly considerations. The importance of diaspore dispersal for the formation of thicket-clumps in West Africa has been emphasised by Hovestadt (1997), based on studies from a humid savanna in Côte d'Ivoire. Furthermore, recent results from Zimbabwe indicate that termite mounds are especially attractive to birds due to the large and often senescent trees that mounds support (Joseph et al. 2011). Termite mounds, whether active or vegetated and eroded, are also attractive for a wide range of mammals (Fleming and Loveridge 2003; Loveridge and 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 and Moe 2012a,b; Støen et al. 2013), but they might also play a considerable role in seed dispersal (Dean et al. 1999; Albert et al. 2015). Considering small mammals, some studies mention that rodents use abandoned termite mounds for seed hoarding (Alexandre 2002; Bationo et al. 2002). For seeds stored in mounds, surface concretion might be less of an impediment to sprouting than for seeds at the mound surface, and climatic stress might be mitigated by the cooler, more humid and aerated environment, which should promote seed longevity and seedling establishment. Further research is needed to corroborate the so far only anecdotal evidence of seed hoarding in termite mounds. The possibility of termites as dispersal vectors, as suggested by Traoré et al. (2015) for my study species, can quite safely be dismissed because, unlike many species of ants, *Macrotermes* do not transport and store seeds in their nests.

Primates in particular 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 termite mounds, like *Diospyros* *mespiliformis*, several species of *Grewia*, and *Tamarindus indica* (Lieberman et al. 1979; Kunz and Linsenmair 2008), which I identified as characteristic mound species for multiple study sites. My results regarding a prevalence of zoochorous species on mounds suggest that dispersers act as a biotic environmental filter. Considering the surprising lack of information on dispersers in the literature, especially on primates which could act both as primary and as secondary dispersers, more ethological as well as ecological research is urgently needed to evaluate the importance of zoochory for mound vegetation and, in turn, the importance of mound vegetation as a resource to dispersers.

Across scales

Apart from the described patterns and processes occurring at particular spatial scales, termite mounds also affect processes across scales. Diversity patterns caused by mounds at different spatial scales interact to increase γ-diversity: ultimately, high α-diversity on mounds in combination with high β-diversity among different communities leads to high overall landscape and regional diversity, i.e γ-diversity. This is promoted by environmental heterogeneity, which is a major driver of landscape- and regional-scale diversity patterns (Tews et al. 2004; Stein et al. 2014) and can be induced both by termites and by vegetation or caused by abiotic conditions like climate, topography, geology, and soil composition, as shown in this thesis.

The importance of mounds for β- and γ-diversity was mirrored by the fact that I identified different sets of characteristic species in each project. These were species occurring in higher abundance and higher frequency, or in case of my third project, only in higher frequency, on termite mounds, which underlines the importance of mounds as microhabitats for particular plants in the savanna. Scale itself played an important role in identifying characteristic species because mound vegetation showed strong regional and landscape-scale variability. My analysis showed differentiation in characteristic species between study sites and savanna types, and some striking similarities in the traits and taxonomic groups of characteristic species.

The majority of characteristic mound species were 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 (Traoré et al. 2008b; Joseph et al. 2011, 2013). In addition to higher nutrient and water availability on mounds, woody plants may benefit from fire protection on mounds. This compensates for the competitive advantage of grasses in the savanna matrix, which overcome damage through fire by fast resprouting from their subterranean vegetation points. In a feedback loop, out-shading by larger woody plants reduces herbaceous biomass on mounds and thus limits fuel for spreading fires.

The remarkable number of lianas and climbers among characteristic mound species might be related to competition for light in this environment. Higher water availability on mounds might also be an advantage for species with a lianescent growth form, as lianas need to maintain a high stem-specific hydraulic conductivity to be able to ensure the transport of water, nutrients and photosynthates along their long and relatively low-diameter stem (DeWalt et al. 2009; Schnitzer et al. 2015). Furthermore, several of the characteristic species with lianescent growth survive the unfavourable dry period as geophytes, developing large underground storage organs. Other characteristic mound species are also 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. 2002b, 2004; Mujinya et al. 2013).

Several studies have shown spatial differentiation of plant species within mound microhabitats (Lawson and 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. Fire seems an especially compelling factor in the case of perennial succulents like *Sansevieria liberica* Gérôme & Labroy, which in my study region are mostly found on the top part of eroded mounds or in otherwise fire-protected habitats like gallery forest and crevices of rocky outcrops. Interestingly, from my field experience, some geophyte species like the lianescent *Ampelocissus multistriata* (Baker) Planch. and *Asparagus flagellaris* (Kunth) Baker mainly occurred on the mound slope, whereas other geophytes like *Tacca leontopetaloides* (L.) Kuntze and *Stylochaeton hypogaeus* Lepr. seemed to be restricted to the otherwise almost barren mound pediment. 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 (Turner 2006; Bonachela et al. 2015). Water stress near the surface of the pediment might therefore be more pronounced than elsewhere on the mound.

Further data on both species traits and the spatial distribution of individuals on mounds might help to identify which processes are more likely for creating non-random associations between different plant species co-occurring on mounds. My accounts of similarities among characteristic species and their ecological interpretation help to identify potentially meaningful measurable functional traits, like leaf lifespan and specific leaf area, for further analysis. Trait and spatial distribution data on vegetation communities on termite mounds might eventually help to evaluate hypotheses and predictions of niche assembly theory (Ricklefs 1987; Leibold et al. 2004; Vellend 2010) and unified neutral theory of biodiversity (Hubbell 2001; Vellend 2010).

More imminently, however, my identification of different characteristic species for the various study sites indicates that mounds are locally important for plant conservation. As most of these species can also be found in the surrounding savanna, albeit much less frequently and abundantly, mounds can act as refugia and source pools for regeneration of these species in the surrounding area, and I thus suggest consideration of mounds in land use and management plans. The need for a sustainable use of mounds and mound vegetation is necessary not only for conserving savanna diversity, but also to ensure important resources for the local human population as well as lifestock and other animals in the long term.

2.3 Importance of termite mounds for the savanna system from a larger perspective

The primary objective of my research was to investigate patterns of plant communities on and off termite mounds in West Africa, examining the environmental factors underlying these patterns at different spatial scales and along different ecological gradients. In the following, I will further expand the view and argue why termite mounds are of importance from a larger perspective, including current debates on forest–savanna boundary distribution, tree–grass coexistence, bush encroachment, and desertification.

Forest–savanna boundary

In addition to influencing diversity patterns, termite mounds are likely to affect distribution patterns and configuration of savanna vegetation, and the delimitation of savannas from other biomes, i.e. forests and deserts. To explain current and future biome delineations is notoriously difficult, and while forest systems have been found to be limited by a minimum precipitation threshold of 650 mm/year (Sankaran et al. 2005), ingress of savannas into forest systems can occur even at very high precipitation. In fact, an increasing amount of evidence suggests that open-canopy grasslands and closed-canopy forests are two possible stable states of one system, albeit in hysteresis (Sankaran et al. 2005; Staver et al. 2011b; Murphy and Bowman 2012). Modelling studies indicate that disturbance regimes, i.e. the influence of fire and large herbivores, determine the stable state of this system (Bond 2008; Staver et al. 2011a; Lehmann et al. 2014; Moncrieff et al. 2014). While disturbances act at the local scale, they ultimately affect regional- to continental-scale patterns of savanna distribution, which again illustrates the entanglement of scale dependency in savanna ecology. Disturbances by both fire and herbivory are modulated by the existence of termite mounds, which has been confirmed in recent studies, including *in-situ* experiments (e.g. Holdo and McDowell 2004; Loveridge and Moe 2004; Mobaek et al. 2005; Traoré and Lepage 2008; Okullo and Moe 2012b; Traoré et al. 2015). Consequently, I suggest that termites might be of considerable importance for the delineation and stable states of the savanna biome in Africa.

In recent years, an increase in woody plant biomass within savannas has been observed globally (Bond 2008), indicating a potential shift in biome boundaries (Moncrieff et al. 2014). Termite mounds might also contribute to defining savanna boundaries in this respect, although the role of termite mounds in this regard is still unclear and warrants investigation. What is known, however, is that termite mounds have long been discussed as focal sites for forest tree species establishment in the savanna (Cole 1963), indicating their importance for woody plant biomass and diversity in the savanna biome. Even though I could not confirm enhanced colonisation of forest tree species on termite mounds in my study area, high prevalence of tree species on termite mounds was evident across the whole region.

Tree–grass coexistence

To better understand the processes linked to tree species establishment in the savanna, it is helpful to consider the factors determining the coexistence of woody plants and grasses. Historically, tree–grass coexistence has been thought to be governed by bottom-up effects, such as root-competition for water (Walter 1939; Walter et al. 1971; Scholes and Archer 1997; Bond 2008). The Walter hypothesis (see Walter 1939; Walter et al. 1971) suggests that trees are often outcompeted by grasses, as grasses intercept water close to the surface and impede percolation. With increasing precipitation and thereby increasing percolation to lower soil layers, more trees are expected to persist due to their different root system and water-use strategies.

Bond (2008) noted that support for Walter's hypothesis is weak in many savannas and that it is therefore not sufficient as a general explanation for variation of tree cover within savannas. However, it has recently been argued that Walter (1939) only intended the hypothesis for arid (and not for mesic and humid) savannas, and that for arid savannas both experimental evidence and theoretical evidence from modelling studies are congruent with its predictions (Ward et al. 2013). Walter (1939) even excluded savannas where factors other than climate would be primary drivers of the structure of the system, and specifically mentioned termite mounds in this context.

Still, the low cover of grasses compared to woody cover that I found on termite mounds seems compatible with root competition hypotheses, as surface water availability on mounds is very limited due to topsoil concretions on the mound slope, and as percolation of runoff water from the mound surface through macropores at the mound base and subsequent transport towards the mound centre increases water availability for deep-rooting plants, such as trees (Turner 2006).

Overall, tree–grass coexistence and determination of forest–savanna boundaries are likely caused by an interplay of bottom-up effects, including competition for water availability, and top-down effects like the above-mentioned disturbances. I therefore suggest that the interplay of water and resource heterogeneity in space and time introduced to savannas by termite mounds and their modulation of disturbances are an important element to consider when analysing and predicting the effects of global change on forest–savanna boundaries.

Bush encroachment and patch dynamics

The reasons for the bush encroachment observed in the last decades, i.e. the increase in woody plant biomass in the savanna, are still a matter of debate, despite a history of research dating back to the 19th century (Scholes and Archer 1997; Ward 2005; Bond 2008). A relatively recent argument is that bush encroachment is a natural stage in patch dynamics (Ward 2005; Wiegand et al. 2005), and does not indicate a shift in the stability of the ecosystem or even the biome. The patch dynamics concept emphasises the importance of local disturbances and resource heterogeneity for the savanna ecosystem at the landscape scale. Termite mounds have been described as an ecological buffer in this framework, acting by introducing microtopographic and further soil heterogeneity (Jeltsch et al. 2000), and have been shown to modulate disturbance by herbivores (e.g., Brody et al. 2010; Levick et al. 2010b; Okullo and Moe 2012a; Sileshi and Arshad 2012).

Generally speaking, the patch dynamics framework describes a mechanism to maintain mosaic landscapes in accordance with the observations that patches of woody plants in savannas often tend to show similar within-patch population dynamics (Wiegand et al. 2005), and that plants, especially trees, can locally increase soil fertility in savannas and create microhabitats in feedback loops with herbivores and dispersers (Jeltsch et al. 1998; Dean et al. 1999). Patch dynamics assume that positive and negative feedback, in combination with patchy precipitation events and disturbances such as fire, sustain a dynamic savanna–woodland mosaic on a long temporal scale.

The turnover of woody and grassy patches at a landscape scale thus allows for tree–grass coexistence, and bush encroachment is perceived as a stage in this process. Whether or not the savanna represents an equilibrium state (as, e.g., argued in Wiegand et al. 2005) or not (as, e.g., argued in Scholes and Archer 1997) is of little consequence according to Jeltsch et al. (2000), who argue that ecological buffering, e.g. by termite mounds, can prevent catastrophic shifts towards either encroachment or desertification, and hence allows persistence of the savanna system.

Vegetation patterns

In the context of patch-scale dynamics, the influence of termite mounds on the generation of savanna vegetation patterns is important. 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 already described as "termite savannas" early on (Troll 1936), also implying causal relationships. Several studies have since confirmed that termite mounds cause or heavily contribute to the formation of thicket clumps in savannas (e.g., Hovestadt 1997; Blösch 2008; 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 "tiger bush" (MacFadyen 1950; Clos-Arceduc 1956), 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 (MacFadyen 1950; Clos-Arceduc 1956; 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 (Thiery et al. 1995; Lefever and Lejeune 1997; Lejeune and Tlidi 1999; Couteron and Lejeune 2001). 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.

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 with catastrophic shifts in vegetation cover that lead to desertification of arid environments (e.g., Rietkerk et al. 2004; Scheffer et al. 2009). 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.

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 (Mando 1997a; Sawadogo et al. 2008; Jouquet et al. 2014; Kaiser 2014). Landscape restoration has been a subject of considerable interest in the Sahel region, where part of my research was conducted. 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 and Miedema 1997; Mando and Brussaard 1999; Mando and Stroosnijder 1999; Mando et al. 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). 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).

Conclusions

To summarise, 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. While the influence of termite mounds on overall processes and dynamics of the savanna ecosystem are beyond the scope of my thesis, my analysis of community and diversity patterns and their drivers from local to regional scales has brought new and important insights regarding the role of mounds for West African savanna diversity, their importance for particular plant species, and the variability of mound vegetation across scales. My research showed that while mound communities were more uniform than savanna vegetation at the local scale, variation in relation to the surrounding habitat at the landscape scale is pronounced, and community composition turnover related to climatic parameters at the regional scale occurs in the same order of magnitude as for the surrounding savannas. A variety of plants locally profit from mounds and occur in higher frequency and abundance on mounds than in the surrounding savannas. I identified clay enrichment as the most important driver of the mound–savanna vegetation contrast and suggest that related potassium content is highly important for plants on mounds. Moreover, directed dispersal of diaspores by animals towards mounds should be important for mound vegetation, especially for colonisation of mounds. Finally, the influence of fire, drought, inundation, herbivory and land use on mound communities as well as intraspecic and interspecific biotic interactions of plants occurring on mounds are likely to influence community assembly, further contributing to local variation in vegetation.

From these findings, and the body of literature discussed above, I conclude 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 timeframes.

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Appendices

Anlage 1

Erklärung über Anteile der Autoren/Autorinnen an den einzelnen Kapiteln der Promotionsarbeit

Titel der Publikation/ des Manuskripts:

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

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Abstract

Termites are renowned ecosystem engineers. Their mounds have been described as an important element of savanna vegetation dynamics, but little is known about their large-scale impact on vegetation composition. To investigate the influence of termite-induced heterogeneity in savannas along a climatic gradient in West Africa termite mound vegetation was compared with adjacent savanna vegetation using 256 paired plots (size of the termite mound and a corresponding savanna area) in five protected areas from northern Burkina Faso to northern Benin. On each plot vegetation and soil sampling was performed. Additionally bioclimatic variables from the WORLDCLIM database were used. The vegetation on the mounds and the surrounding savanna differed within all study sites (DCA length of gradient 3.85 SD) and showed complete turnover along the climatic gradient (DCA length of gradient 5.99 SD). Differences between mounds and savanna were significantly related to termite-induced changes in soil parameters, specifically clay enrichment and increased cation concentrations (base saturation). On a local scale, termite-induced differences in soil conditions were found to be the most important

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AE conceived this study, and designed it together with KH, AT and RW. AE conducted the fieldwork, analysed and interpreted the data, and wrote the manuscript. MBR and KH contributed to the interpretation of the data, and all authors commented on the manuscript.

factor affecting mound vegetation, while on a regional scale, annual precipitation showed the strongest significant correlations. However, with increasing precipitation, differences between mounds and the surrounding matrix became more pronounced, and the contribution of mounds to local phytodiversity increased. Eleven plant species were identified as characteristic termite mound species. In the more humid parts of the gradient, more characteristic plant species were found that may benefit from favourable soil conditions, good water availability, and a low fire impact in the mound microhabitat.

Introduction

Savanna structure and composition is thought to be mainly subject to the influence of fire and herbivory (Solbrig et al. 1996). However, recent studies suggest that termite activity plays an integral part in generating savanna vegetation patterns and dynamics (Sileshi et al. 2010; Okullo and Moe 2012b), while large herbivores maintain and amplify patterns and processes (Okullo and Moe 2012a). Termites influence patterns of savanna vegetation directly through foraging and indirectly through reallocation of soil, water and nutrients (Wood and Sands 1978; Sileshi et al. 2010). Several species of termite construct above-ground earthmounds that incorporate the colony's nest. Termites, particularly those of the fungus-cultivating genus *Macrotermes*, have been described as ecosystem engineers (Dangerfield et al. 1998; Jouquet et al. 2011) influencing abiotic and biotic properties of savannas. Several authors have outlined similar influences of termite mound building on soils and, hence, on savanna vegetation, proposing that the creation of nutrient hot-spots leads to more heterogeneous ecosystems (Levick et al. 2010; Pringle et al. 2010).

It has been reported that mounds support a greater diversity of plants compared to surrounding areas (Wood and Sands 1978; Moe et al. 2009; Okullo and Moe 2012b). In particular, a greater diversity of woody plant species has been noted on mounds compared to the surrounding savanna. Mounds have been discussed in this context as focal points for tree regeneration within savannas (Cole 1963; Traoré et al. 2008a; Moe et al. 2009).

However, most studies have focused on the local impact of termite mounds on vegetation and have mainly been conducted at a single site. The overarching importance of mounds for savanna vegetation and their dynamics across savanna types and vegetation zones are still unclear. The aim of this study was to investigate differences between termite-mound vegetation and adjacent savanna vegetation both on a local scale and along a regional climatic gradient. We expected the phytodiversity on mounds to be higher than in the surrounding savanna along a climatic gradient, particularly with regard to woody plants. We further hypothesized that the phytodiversity of savanna vegetation and mound vegetation would increase along a climatic gradient from drier to more humid areas. Compared to the surrounding savannas, enrichment of clay and related soil parameters (i.e. increased field moisture capacity and nutrient concentrations) was expected to occur on mounds in similar magnitude along the climatic gradient. Finally, we aimed to reveal whether there were plant species characteristic of termite mounds to improve ecological understanding of the role of termite mounds in creating vegetation heterogeneity.

Methods

Study sites

This study was conducted in five protected areas (PA) in Burkina Faso and Benin, representing a climatic gradient from the Sahel zone to the limit of the southern Sudanian vegetation zone (Figure I.1). Annual precipitation ranges from less than 400 mm in the Sahel to approximately 1000 mm in the Sudanian zone, with a distinct unimodal dry season of 5-7 mo occurring throughout the study area. The study sites were located in the Sahel Partial Reserve (Réserve Sylvo-Pastorale et Partielle de Faune du Sahel, abbreviated as RPS; 14°48′N, 0°42′W), Niouma Classified Forest (Forêt Classée de Niouma, FCN; 12°55′N, 2°41′W), Gonsé Classified Forest (Forêt Classée de Gonsé, FCG; 12°23′N, 1°18′E), W Transborder Park (Parc National du W, PNW; 11°48′N, 2°10′E), and Pendjari National Park (Parc National de la Pendjari, PNP; 11°22′N, 1°33′E). At each study site, we sampled the most abundant savanna types, excluding temporarily waterlogged or seasonally inundated localities, as these represent ecologically extreme situations. Savanna types were identified based on surveys we performed and on vegetation classifications for the respective sites. Supporting Information Table I.3 presents an overview of the sampled savanna types and mean annual precipitation (MAP) at our study sites.

In West Africa, conspicuous thicket clumps can be found on termite mounds, which are usually delimited by a distinct boundary from the adjacent savanna vegetation. Due to erosion, this boundary may be situated several metres from the actual mound slope. This pediment may also consist of areas bare of vegetation, emphasizing the contrast between

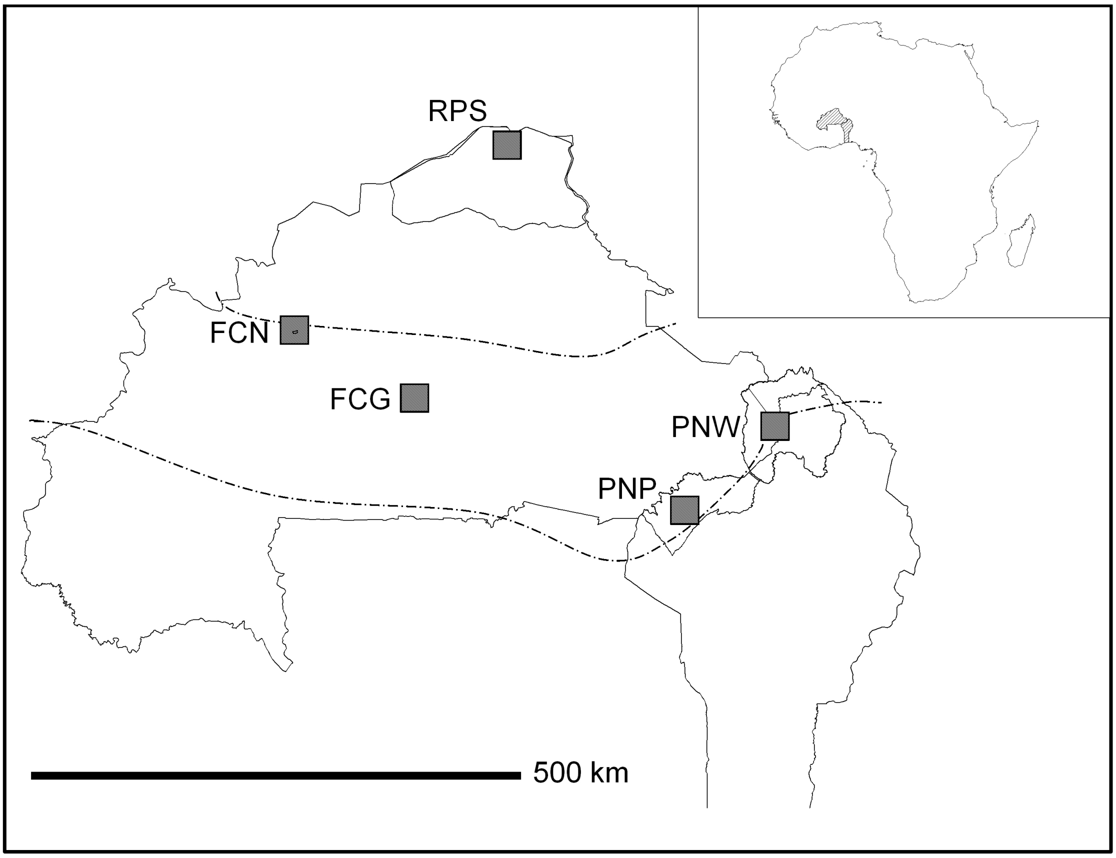

Figure I.1 Study sites in protected areas along a climatic gradient in West Africa (Burkina Faso and northern Benin). Rectangles indicate approximate location of study sites. Sites from north to south: Sahel Partial Reserve (RPS, 360 mm MAP), Niouma Classified Forest (FCN, 670 mm), Gonsé Classified Forest (FCG, 760 mm), W National Park (PNW, 840 mm), and Pendjari National Park (PNP, 950 mm). Broken lines indicate approximate limits of Sahelic and Sudanian vegetation zones.

the mound thicket and savanna. For brevity, we will refer to termite-mound vegetation as mounds.

Survey design

In a paired design, we sampled the vegetation of 128 mounds built by *Macrotermes* colonies and adjacent savanna plots. Within our study area, two *Macrotermes* species build the type of mounds that we studied with respect to architecture and size: *M. subhyalinus* (Rambur) and *M. bellicosus* (Smeathman). Species identification was confirmed by field work carried out in association with termite specialists (J. Korb & collaborators). The two *Macrotermes* species in our study area occur sympatrically, with the northern limit of *M. bellicosus* occurring within our study area (Ruelle 1970). Unfortunately, no detailed data on the distribution of *M. bellicosus* and *M. subhyalinus* in this region are currently available. Mounds containing living colonies of these two species may be identified based on architectural attributes (Korb 2011). In general, eroded and vegetated mounds in our study area do not contain living colonies, but re-colonization, mainly by *Microtermes* and *Ancistrotermes* spp., may occur (J. Korb, pers. comm.). We did not sample mounds where there was visible colonization. Because abandoned, eroded *M. bellicosus* mounds can be confounded with eroded *M. subhyalinus* mounds, we cannot report which *Macrotermes* species built the mounds. However, all of the studied termite mounds were comparable with respect to their structure and were distinguished from mounds built by other Macrotermitinae (e.g. *Odontotermes* spp.).

The topography of the selected savannas is almost flat. When selecting termite mounds, we avoided shallow depressions (bas-fonds) and hillsides. After identifying localities where mounds occur, we randomly selected mounds for vegetation sampling and determined their surface area as the longest diameter of the mound multiplied by its perpendicular diameter. A squared plot of corresponding size was established 15 m north of the limit of the mound to investigate the vegetation of the surrounding savanna. If additional mounds occurred within 15 m of the savanna plot, we rotated the direction from the corresponding mound anticlockwise in steps of 15°.

To avoid interpersonal differences in phytosociological cover estimations, all sampling was done by the first author. Estimations were performed separately for the tree layer (woody plants > 5 m), the shrub layer (woody and partially ligneous plants from 0.5 to 5 m), and the herbaceous layer (all plants up to 0.5 m in height). Vegetation was recorded twice, at the beginning (May—July) and the end of the rainy season (September—November), to account for variation in phenology. For the analysis, we used the maximum cover of each species (expressed in %) from the two samplings. The plant species nomenclature followed the African Plants Database (http://www.ville-ge.ch/musinfo/bd/cjb/africa).

Environmental data

We collected samples of 10 cm^3 from the upper topsoil horizon of mounds and savannas, pooling samples from four directions in each case. Mound soil was collected from the slope of the mound. Savanna soil was sampled at a distance of 15 m from the edge of the mound, and all samples were subsequently sieved and air dried. For each mound and savanna plot, several descriptive soil parameters were used. We determined pH in aqueous suspension and 0.1 m KCl solution. Concentrations of plant-available phosphorus and potassium were determined spectroscopically using the calcium acetate lactate method. Nitrogen was determined using the Kjeldahl method. Organic and inorganic carbon were determined spectroscopically by wet and dry combustion, respectively (DIN ISO 10694), after volumetric determination of carbonates (DIN ISO 10693 1997-05).

Additionally, we selected at least three plot pairs in every savanna type at random, and determined cation exchange capacity (CEC), together with individual ion concentrations of sodium, potassium, calcium and magnesium (DIN ISO 13536:1997-04). For these samples, also particle size distribution (PSD) was determined using the Köhn pipette method in seven grain size fractions.

Moreover, we used a set of 18 bioclimatic variables (Table I.1) from the WORLDCLIM database with a spatial resolution of 30 arc seconds, i.e. approximately 1 km^2 (Hijmans et al. 2005). We added potential evapotranspiration (PET) and the Global Aridity Index (AI) to this dataset (Zomer et al. 2008), which also takes the radiation budget into account.

Statistical analysis

Prior to analyses, vegetation data were arcsine-square-root-transformed. Environmental data were standardized to zero mean unit variance (pH values were previously antilogged). We used detrended correspondence analysis (DCA) to reveal differences in vegetation composition, as this technique provides eigenvalues that allow estimation of gradient length as a measure of variation between samples (Hill and Gauch 1980; Eilertsen et al. 1990). Downweighting of rare species was carried out because 56% of the species in our dataset were recorded in less than five sampling plots. We investigated the influence of climate and soil on vegetation differentiation by calculating Spearman's rank correlation coefficients between environmental data and the DCA scores of the first two axes. We calculated species richness, inverse Simpson's Index of Diversity, and the evenness index E_{var} (Smith and Wilson 1996) separately for the three plant layers. Inverse Simpson's Index is a measure of diversity giving less weight to rare species (Tuomisto 2010). Separate treatment of herbaceous and woody layers is advisable due to their relative phytosociological independence in West African savannas (Hahn-Hadjali 1998), which was especially pronounced in our datasets. To examine species-sampling relations, we calculated species-accumulation curves by permuted random sample addition, with the x axis scaled by plot sampling area. As a net measure of differences in diversity between equal-sized paired mound and savanna plots, we chose the logarithmic response ratio, calculated as the natural logarithm of the quotient of mound and comparison-plot values (Hedges et al. 1999). A positive ratio indicates greater diversity in mound plots, whereas a negative ratio indicates greater diversity in savanna plots. For the woody plant layers, we removed pairs where no woody cover occurred in one of the paired plots. Statistical significance of differences between mounds and adjacent savannas were tested using Welch's two-sample t-test.

We calculated indicator values for each species using the IndVal method (Dufrêne and Legendre 1997), where 0 denoted no indication and 100% denoted perfect indication. We conducted 1000 iterations for each research site independently, using the groups of mound plots and savanna plots set a priori. We used the IndVal procedure to identify species that typically occur on termite mounds. Identification of characteristic species promotes understanding of savanna diversity. This method has the advantage of being based on field data rather than on expert knowledge, which is only partially available via floristic works. Species with significant indicator values greater than 60% (McGeoch et al. 2002) were considered to be characteristic termite-mound species.

All data analyses were performed using R 2.11.1 with the packages vegan 1.17-6 and labdsv 1.4-1.

Results

Gradient analysis

DCA produced eigenvalues of 0.60 and 0.44, and gradient lengths of 5.99 and 3.85 for the first two axes, respectively. The first axis of the DCA showed plots in the latitudinal order of the five research sites from north to south. While the mound and savanna plots followed the first axis in parallel and approximately to the same extent, the second axis showed clear separation between mound and savanna plots (Figure I.2).

The variation in vegetation composition depicted by the first axis was strongly correlated with bioclimatic variables (Table I.1). Mean annual precipitation (MAP) and the Global Aridity Index (AI) correlated strongly with the axis scores (MAP: $\rho^2 = 0.66$, AI: $\rho^2 = 0.65$). The second axis was strongly correlated with soil variables, with the highest correlation occurring with the sum of base concentrations (S-value; $\rho^2 = 0.66$). Other CEC-related variables, such as clay content and the concentrations of K^+, Ca^{2+} and Mg^{2+} ions as well as potential CEC and base saturation (V-value), were also correlated significantly with this axis. Among the set of soil variables available for all plots, pH (ρ^2 = 0.54) and potassium concentration (ρ^2 = 0.43) showed the strongest correlations.

Diversity analysis

Analysis of the mounds' impact on diversity indicated complex patterns. We detected a total of 561 species in our plots, 323 (57.6%) of which occurred in less than five plots. The lowest numbers of species on termite mounds were recorded in the Sahel (RPS, MAP 360 mm), and the highest were recorded in the central part of the north Sudanian vegetation zone (FCG, MAP 760 mm). Considering 30 × 30-m woody-layer savanna plots only, species-accumulation curves exhibited similar patterns with strongly overlapping confidence intervals for all research sites except the Sahel (Figure I.3). Also, curves for woody savanna vegetation showed the strongest notion of saturation. Termite-mound plots showed an overlapping pattern for two groups, with Pendjari National Park (PNP) and RPS both showing low overall species richness compared to the other sites. For adjacent savannas, PNP and RPS also showed congruence, but the species-accumulation curves for the other sites showed distinct differences and little overlap of confidence intervals (Figure I.3). It should be noted that mound size (and, therefore, paired comparison site area) vary strongly between research sites, with smaller mounds in the Sahel. The overall mean species richness did not differ between termite mounds (25.6 ± 11.9) and the adjacent savanna (25.5 ± 15.3, P = 0.84, t-value = 0.19, df = 127). When we partitioned our dataset by research sites (Figure I.4), sites PNW (MAP 840 mm) and PNP (MAP 950 mm) in the south were observed to exhibit significantly higher species richness (SpR) on mounds (PNW SpR: 29.9 ± 5.76, PNP SpR 19.0 ± 5.22) than in savanna plots (PNW SpR: 25.0 ± 4.71, PNP SpR: 13.3 ± 4.98). No significant differences were found in the northern parts of the transect (RPS, MAP 360 mm; FCN, MAP 670 mm). Remarkably, the savanna vegetation at the central north Sudanian site (FCG, MAP 760 mm, SpR in savannas: 43.7 ± 9.12) was found to be significantly more diverse than the mound vegetation (FCG SpR on mounds: 36.2 ± 8.4). This also held true for the inverse Simpson's Index of Diversity (SI), which showed a greater diversity corrected for rare species at FCG (SI in savannas: 13.8 ± 6.35, on mounds: 8.56 ± 4.46), whereas there were no significant differences found for the other research sites.

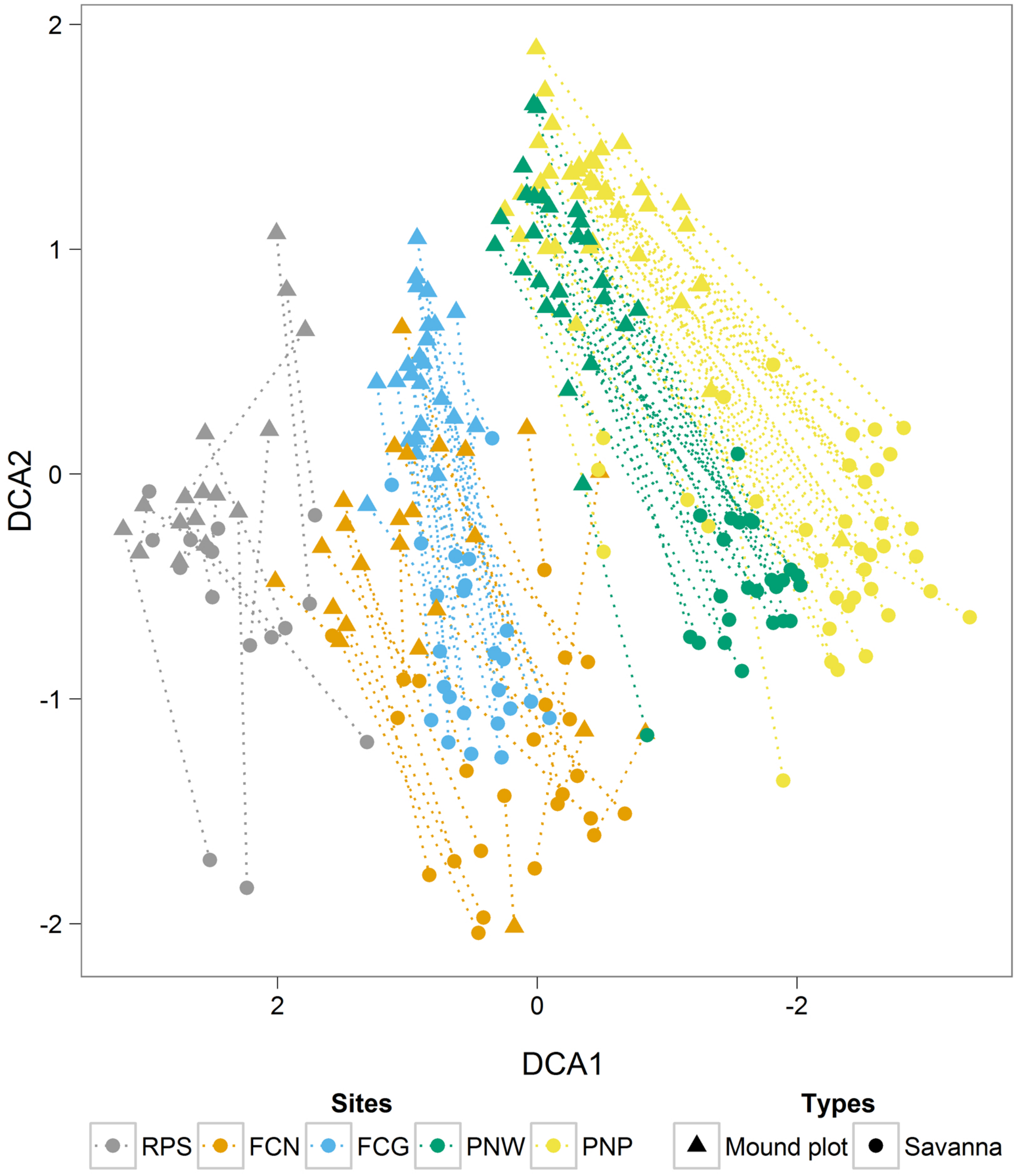

Figure I.2 DCA plot of 128 sample pairs (mounds and adjacent savanna plots) and 561 species along a climatic gradient in West Africa. DCA produced eigenvalues of 0.60 and 0.44, and gradient lengths of 5.99 and 3.85 for the first two axes, respectively. Paired samples are connected by lines. Length of first axis: 6.5 SD units. Symbols indicate the plot type (mound or savanna), colours indicate research sites: Sahel Partial Reserve (RPS), Niouma Classified Forest (FCN), Gonsé Classified Forest (FCG), W National Park (PNW), Pendjari National Park (PNP).

When woody layers were analysed alone, both southern sites showed significantly higher diversities on mounds for both species richness (PNW SpR on mounds: 12.5 ± 4.11, in savannas: 7.54 ± 3.3; PNP SpR on mounds: 9.92 ± 2.98, in savannas: 6.05 ± 2.86) and inverse Simpsons's Index (PNW SI on mounds 12.1 ± 3.93, in savannas: 7.25 ± 3.22; PNP SI on mounds: 9.39 ± 2.73, in savannas: 5.93 ± 2.76), whereas no significant difference was detected at any other sites.

With respect to the herbaceous layer, we found a significantly higher species richness on mounds only at PNP (SpR on mounds: 12.2 ± 5.09, in savannas: 9.26 ± 4.51), whereas savanna herb layers exhibited greater species numbers than mounds at FCG (SpR in savannas: 40 ± 8.71, on mounds: 34.0 ± 8.23). Inverse Simpson's Index for herbaceous layers presented significantly higher values on mounds both at the north (RPS, SI on mounds: 5.04 ± 1.4, in savannas: 3.53 ± 1.85) and the south of the transect (PNW SI on mounds: 12.08 ± 3.93, in savannas: 7.25 ± 3.22; PNP SI on mounds: 9.39 ± 2.73, in savannas: 5.93 ± 2.76), though this was not the case for the central sites on the transect.

The evenness (E_{var}) of all species was significantly higher on mounds only at FCN (E_{var} on mounds: 0.27 ± 0.05, in savannas: 0.22 ± 0.05). Herbaceous evenness was also significantly higher on mounds only at FCN (E_{var} on mounds: 0.32 ± 0.06, in savannas: 0.28 ± 0.04), while evenness for woody species was significantly lower on mounds than in savannas for RPS (E_{var} in savannas: 0.9 ± 0.17, on mounds: 0.7 ± 0.21), FCN (E_{var} in savannas: 0.74 ± 0.22, on mounds: 0.58 ± 0.21), and PNP (E_{var} in savannas: 0.75 ± 0.23, on mounds: 0.61 ± 0.22).

Indicator species analysis

We found a total of eleven species that were characteristic of termite mounds (Table I.2). More characteristic termite-mound species were found at study sites with higher precipitation. At the driest Sahelic site (RPS, MAP 360 mm), we detected no characteristic termite-mound species (only *Boscia angustifolia* presented a significant indicator value, which was 31.3% and therefore below the set threshold). At FCN (MAP 670 mm), several species exhibited significant indicator values, but none exceeded the chosen cut-off value. Among the characteristic species, *Capparis sepiaria* and *Feretia apodanthera* had indicator values higher than 80% and were characteristic mound species for three sites (FCG, PNW and PNP).

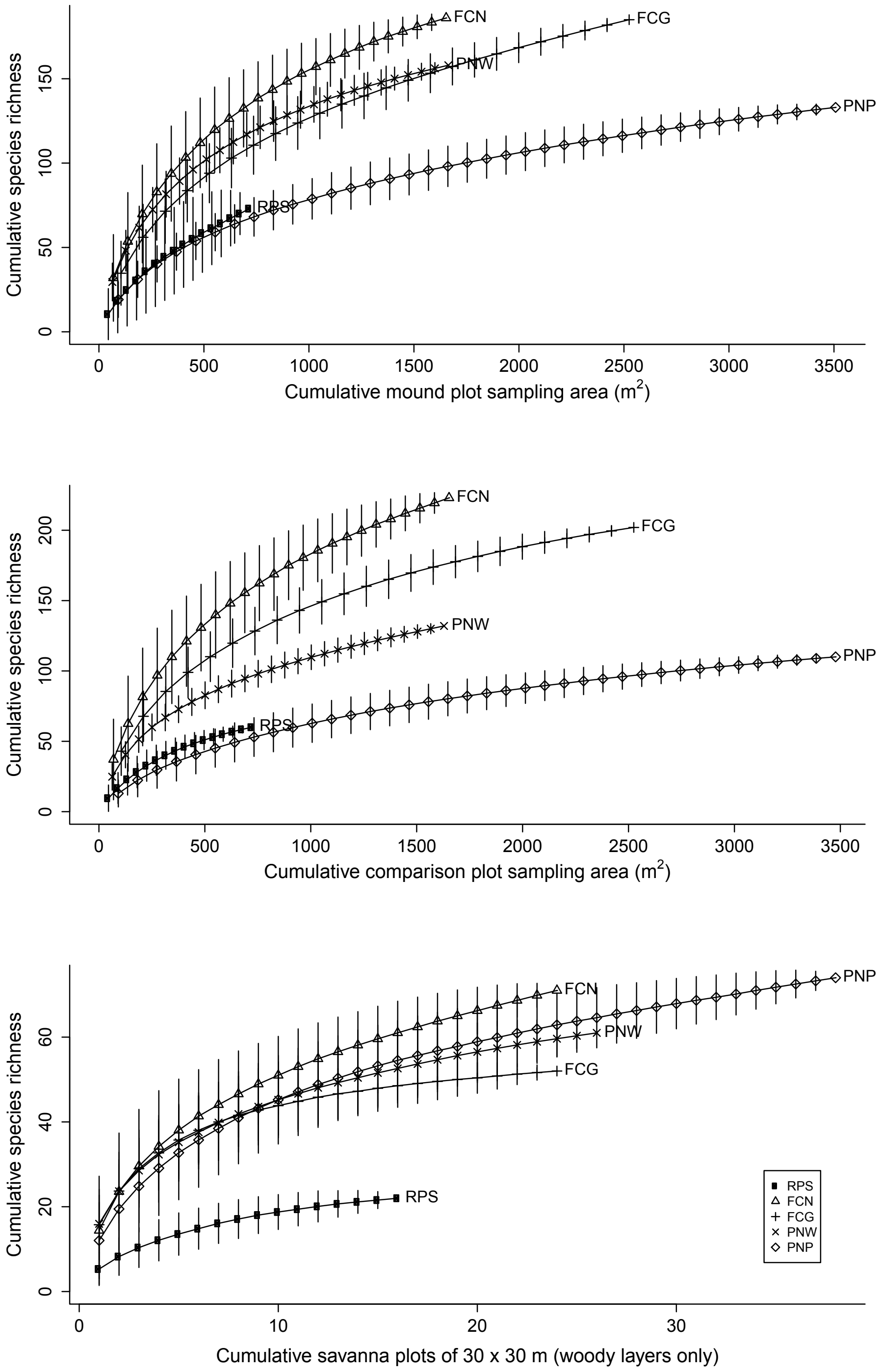

Figure I.3 Plant species-accumulation curves for termite mounds (a), paired adjacent savanna plots (b) and 30 × 30-m woody-plant savanna plots (c) along a climatic gradient in West Africa. Vertical bars indicate confidence intervals after 100 permutations of randomly adding sites. For (a) and (b), x-axes are scaled by sampling plot area. Sites from north to south: Sahel Partial Reserve (RPS), Niouma Classified Forest (FCN), Gonsé Classified Forest (FCG), W National Park (PNW), and Pendjari National Park (PNP).

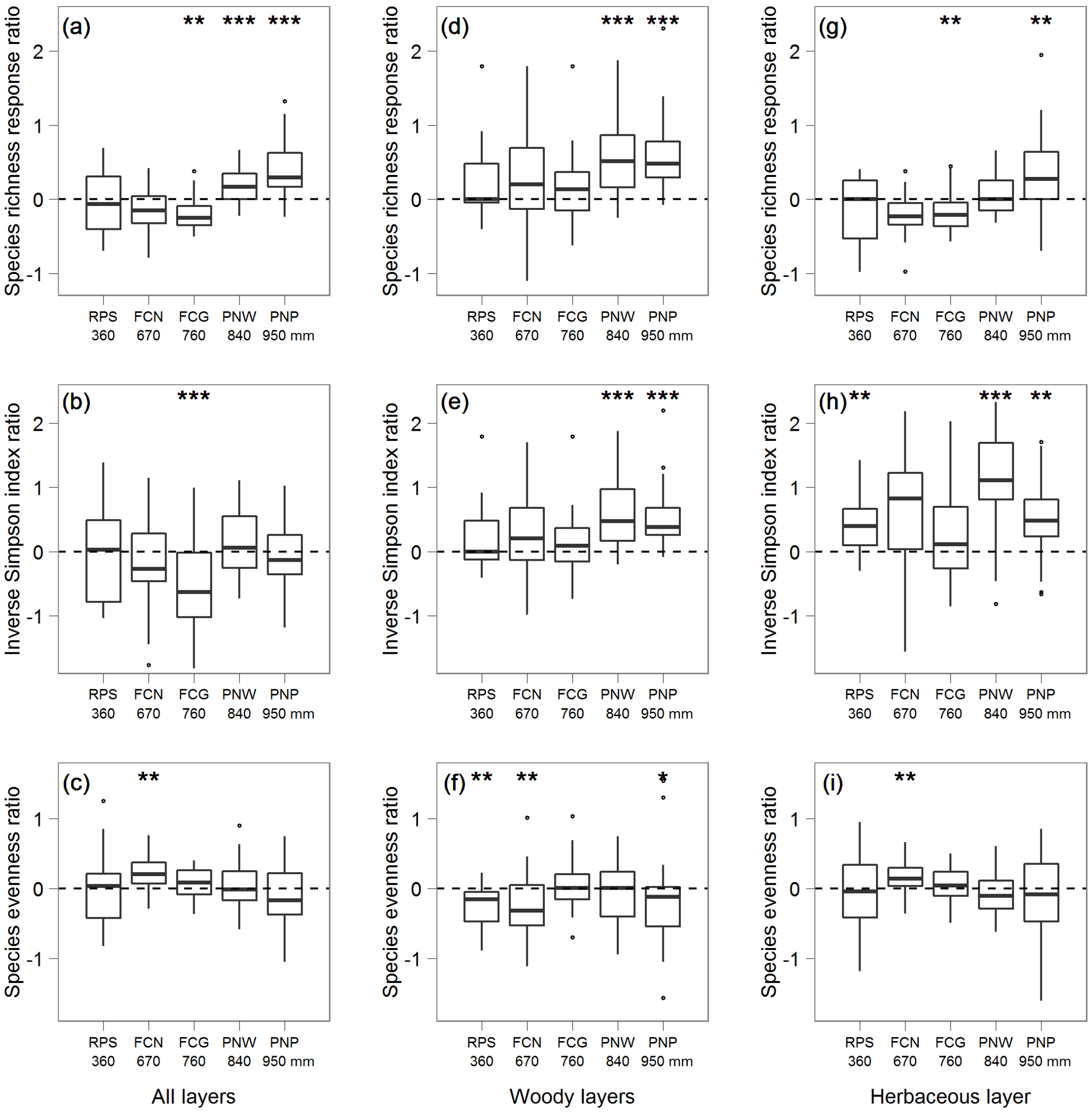

Figure I.4 Log response ratio of plot pairs as measure of net diversity differences between termite-mound microhabitat and adjacent savannas. Boxplots (boxes represent the area between the first and third quartile, the whiskers extend to the most extreme data point which is no more than 1.5 times the length of the box away from the nearest end of the box) for each research site from north to south (RPS: Sahel Partial Reserve, FCN: Niouma Classified Forest, FCG: Gonsé Classified Forest, PNW: W National Park, PNP: Pendjari National Park, each given with MAP). Columns for boxplots of all layers (a-c), woody plant layers (d-f) and herbaceous layers (g-i) are shown separately. Response ratios above the broken line indicate higher values on mounds, while those below the line indicate higher values in corresponding savanna plots. Significant values are indicated by asterisks ($P < 0.05$: *, $P < 0.01$: **, $P < 0.001$: ***)

The characteristic termite-mound species consist of nine shrubs and three ligneous forbs (*Ampelocissus multistriata*, *Asparagus flagellaris* and *Wissadula amplissima*). The last three species and both *Combretum aculeatum* and *Capparis sepiaria* exhibit a scrambling or climbing habit. Notably, at family level, three Capparaceae were found to be characteristic of mounds (*Capparis sepiaria*, *Cadaba farinosa* and *Maerua oblongifolia*).

Discussion

This study provides quantitative evidence of differences between termite-mound vegetation and adjacent savanna vegetation as well as of similar variability between termite-mound vegetation and adjacent savanna vegetation along a climatic gradient. However, mound vegetation was not shown to be more diverse at all of our sites, which we attribute partly to certain traits of the indicator plant species on the termite mounds addressed in this study.

Gradient analysis

We found that the mound and savanna plots formed separate groups along the second DCA axis: mound vegetation differed considerably from the surrounding savanna along the entire climatic gradient. This finding is in accord with those of a wide range of studies reporting mound vegetation to be distinct from savanna vegetation (Schmitz 1963; Fanshawe 1968; Malaisse 1976).

The higher cation concentrations of mound soils compared to the surroundings can be considered an explanation for pronounced differences between mound and savanna vegetation. Nutrient levels and exchangeable cation concentrations have already been described as higher in termite mounds than in surrounding soils (Holt and Lepage 2000; Jouquet et al. 2011). We hypothesize that biopedoturbation, particularly the selection and transport of base-rich soil of the silt and clay fraction from deeper layers to the surface, as described by other authors (Arshad 1982; Abe et al. 2009; Mujinya et al. 2010), is crucial for the specific vegetation on termite mounds and represents a driving factor of general small-scale heterogeneity in African savannas. On a local scale, various studies report lower infiltration rates, but higher water availability on mounds (Dangerfield et al. 1998; Sileshi et al. 2010). It has been suggested that the existence of mounds allows colonization of a savanna by forest species and that the termite-mound vegetation in a particular vegetation zone is adapted to the conditions of a more humid vegetation zone (Cole 1963;

Blösch 2008). However, our regional analysis showed that vegetation differentiation can be attributed mainly to differences in MAP along a climatic gradient. Moreover, the observed changes were as pronounced as in the savanna matrix.

Diversity analysis

Overall species richness did not differ between termite mounds and the adjacent savanna vegetation. However, we found differences in the shape of the species-accumulation curves considering woody species and the vegetation including herbaceous species. High local heterogeneity in herbaceous vegetation of the paired mound and savanna plots leads to lower slopes for these plots. The surprisingly low species richness of the sampling in Pendjari National Park (PNP) might be considered a sampling artefact, as the majority of sites in PNP could not be visited during the wet season due to flooding. Also, local outcompeting of other species by herbaceous plants with higher productivity could be an explanation, which is supported by the species accumulation curve for 30 × 30-m woody-plant savanna plots. However, (also temporally) paired sampling allows for a direct comparison of net compositional differences between mounds and savannas, quite irrespective of differences in sampling time, or differences in the size of different plot-pairs. Net differences of species richness expressed as log response ratio showed no correlation with plot area. In this study, species richness was not found to be significantly higher on mounds when the whole dataset was considered, but even significantly lower on mounds in Gonsé Classified Forest (FCG). Higher plant diversity on mounds than in the surrounding savanna has been reported in several studies, especially for woody plants (Traoré et al. 2008a; Moe et al. 2009). Considering woody layers alone, mound richness in FCG was no longer significantly lower, while both species richness and inverse Simpson's Index were still higher on mounds at W Transborder Park (PNW) and Pendjari National Park. FCG and FCN are considerably smaller than PNP and PNW, and are classified as forest reserves under higher anthropogenic pressure. FCG in particular, which is situated close to the Burkina Faso metropolis of Ouagadougou, is subject to a moderate but ongoing disturbance regime. As synanthropic herbaceous species contributed to the species richness at this site, disturbance might also explain why the overall species richness peaked here, in accordance with the intermediate disturbance hypothesis (Connell 1978; Huston 1979).

The increase in precipitation from north to south leads to an increasing share of phanerophytic life forms in the local flora (Schmidt et al. 2005). Enhanced woody plant establishment rates on mounds (Fleming and Loveridge 2003; Traoré et al. 2008b) could explain the considerably higher species richness and inverse Simpson's Index of Diversity on mounds at higher precipitation. Furthermore, separate treatment of vegetation layers is important, not only due to their phytosociological independence (Hahn-Hadjali 1998), but also because of the influence of canopy density. Shading by species with a long foliage period as well as a pronounced occurrence of climbers characterises mound communities. A single specimen can often present a high cover value on a mound. In our dataset, for instance, single adult tamarind trees exhibited cover values of up to 90% per plot, shading out the herbaceous layer and thus lowering overall diversity.

However, diversity patterns may also be influenced by taxon-specific differences in mound architecture. Within the research area, *Macrotermes subhyalinus* is better able to cope with drier environmental conditions than *M. bellicosus*. Both species are subject to the same environmental constraint regarding homoeostasis of their obligate fungi symbionts, but their mound architecture is different (Korb 2011). Different architecture might fundamentally influence the ability of plants to become established on mounds. The locations and concentrations of nutrients in mounds differ between species and genera of termites (Wood and Sands 1978; Wood 1988), and we can expect that further differences between the two *Macrotermes* species will be detected. However, we could not test this assumption because severely eroded *Macrotermes* mounds could not be attributed to a particular species.

Indicator species analysis

The identified indicator plant species exhibited different functional traits that might be related to their frequent and abundant occurrence on mounds. All species reaching significant indicator values > 60% are ligneous or subligneous perennials. A large proportion presents scrambling or climbing habits, i.e. *Capparis sepiaria*, *Wissadula amplissima*, *Grewia bicolor*, *Ampelocissus multistriata*, *Asparagus flagellaris* and *Combretum aculeatum*. The preference of indicator species for termite-mound microhabitats might be due to several benefits associated with the mounds, e.g. favourable soil conditions, accessible ground water and a certain degree of protection from fire. The higher number of characteristic mound plant species in areas with greater precipitation may be related to increases in overall woody species richness (Schmidt et al. 2005).

Termite mounds have often been recognized as refuges for woody plants within seasonally burned savannas (Troll 1936; Fanshawe 1968; Traoré et al. 2008b; Joseph et al. 2011). Specifically, plants with evergreen leaves (as the Capparaceae indicator species) are sensitive to burning. A previous study (Colonval-Elenkov and Malaisse 1975) specifically described the xerophytic features of termite mound vegetation in a Miombo savanna woodland. However, the sclerophyllous *Capparis sepiaria* exhibited the deepest roots in a study of termite-mound-thicket root distribution in Ghana (Okali et al. 1973), and showed high rates of transpiration in a study of mound microclimate (Lawson and Jenik 1967). We assume that the characteristic Capparaceae species included in our study develop deep roots as well. Dependency on continuous access to ground water can also be assumed for *Feretia apodanthera* (also found in gallery forests and transient watercourses).

Shading and vertical structure provided by woody vegetation could favour lianescent species as well as mesophytic species in the understorey. Lianas are a life-form that is especially adapted to compete for light, and because these plants depend on available water, they develop deep roots (DeWalt et al. 2009). In several instances in the present study, a single shade-tolerant species, such as *Wissadula amplissima*, comprised the herbaceous cover as a result of forming monotypic stands. The mound microhabitats provide a wide range of benefits for other groups of organisms, such as birds (Joseph et al. 2011), large herbivores (Levick et al. 2010; Okullo and Moe 2012a), small vertebrates (Fleming and Loveridge 2003), insects and other invertebrates, and their predators (de Visser et al. 2008; Pringle et al. 2010). The identification of characteristic plant species associated with mounds gives a starting point for subsequent studies of their functional traits and biology, also addressing their role as resources for both the human population and for wildlife in West African savannas. Only recently, a first study from a single reserve in South Africa reported differences in functional traits of plants on and off mounds (van der Plas et al. 2013). Our account of some functional characteristics can be a precursor to similar analyses in West Africa.

Unfortunately, processes of succession in these de novo microhabitats as well as their role in the long-term dynamics of savanna ecosystems remain unclear, as long-term studies are lacking.

Additionally, the population dynamics of mound vegetation in landscapes undergoing rapid land-use changes, as are occurring in West African savannas (Tappan et al. 2004; Reij et al. 2005; Vincke et al. 2010), remain unaddressed. It is likely that the termite abundance, thus the termite-mound abundance outside of protected areas, will further decline. We would like to specifically encourage ongoing research on and the protection of viable mound-building termite populations and vegetation on mounds to elucidate the degree of interdependence of mounds and plants.

Table I.1 Spearman's rank correlation coefficients considering climatic variables and measured soil variables, correlated with DCA axes scores for 256 termite mounds and adjacent savanna plots along a climatic transect in West Africa. Climatic data were extracted from the WORLDCLIM database and the Global Aridity and PET database on a resolution of 30 arc seconds for each mound- and savanna-plot geolocation. Spearman's ρ is given for the correlation between the DCA scores of the first two axes with environmental variables; P-value for rank correlation test.

	Correlations for DCA Axis 1		Correlations for DCA Axis 2	
Environmental variable	ρ	P-value	ρ	P-value
Mean annual temperature	−0.53	<0.01	0.20	<0.01
Mean diurnal temperature range	−0.36	<0.01	0.23	<0.01
Isothermality	0.71	<0.01	−0.21	<0.01
Temperature seasonality	−0.61	<0.01	0.13	0.03
Max. temperature of warmest month	−0.67	<0.01	0.29	<0.01
Min. temperature of coldest month	0.67	<0.01	−0.20	<0.01
Annual temperature range	−0.69	<0.01	0.18	<0.01
Mean temperature of wettest quarter	−0.79	<0.01	0.36	<0.01
Mean temperature of driest quarter	0.67	<0.01	−0.20	<0.01
Mean temperature of warmest quarter	−0.74	<0.01	0.34	<0.01
Mean temperature of coldest quarter	0.34	<0.01	−0.03	0.60
Annual precipitation	0.81	<0.01	−0.41	<0.01
Precipitation of wettest month	0.79	<0.01	−0.40	<0.01
Precipitation of driest month	−0.79	<0.01	0.42	<0.01
Precipitation seasonality	0.81	<0.01	−0.41	<0.01
Precipitation of wettest quarter	0.60	<0.01	−0.12	0.06
Precipitation of driest quarter	0.77	<0.01	−0.26	<0.01
Precipitation of warmest quarter	0.77	<0.01	−0.26	<0.01
Potential evapotranspiration (PET)	−0.40	<0.01	0.22	<0.01
Aridity index (AI)	0.81	<0.01	−0.41	<0.01
pH	−0.13	0.04	0.73	<0.01
P_2O_{5av}	−0.05	0.39	−0.59	<0.01
K_2O_{av}	−0.30	<0.01	−0.65	<0.01
Carbon	0.47	<0.01	−0.48	<0.01
Nitrogen	0.09	0.14	−0.57	<0.01
C/N ratio	0.57	<0.01	0.02	0.72
Carbonates	−0.09	0.17	−0.40	<0.01
Organic substance	0.13	0.23	−0.57	<0.01
Sand	−0.31	<0.01	0.44	<0.01
Silt	0.54	<0.01	−0.15	0.17
Clay	−0.31	<0.01	−0.57	<0.01
Na^+	−0.18	0.10	−0.29	0.01
K^+	−0.25	0.03	−0.55	<0.01
Ca^{2+}	−0.03	0.78	−0.80	<0.01
Mg^{2+}	−0.03	0.82	−0.71	<0.01
CEC_{pot}	0	0.97	−0.72	<0.01
CEC S-value	−0.06	0.57	−0.81	<0.01
CEC V-value	−0.19	0.09	−0.77	<0.01

Table I.2 Characteristic species for 128 termite mounds separated by research sites along a climatic gradient in West Africa derived by the IndVal method. Sites from north to south: Sahel Partial Reserve (RPS, no characteristic species), Niouma Classified Forest (FCN, no characteristic species), Gonsé Classified Forest (FCG, five characteristic species), W National Park (PNW, six characteristic species), and Pendjari National Park (PNP, eight characteristic species). Significant indicator values between 60% and 100% are shown (100%: perfect indicator, $P \leq 0.05$, 1000 iterations). ∗, significant indicator, < 60% IndVal; n.s., present, but not significant; –, absent.

Sites:	RPS	FCN	FCG	PNW	PNP
MAP (mm):	360	670	760	840	950
Feretia apodanthera	–	∗	84.3	92.3	86.1
Capparis sepiaria	–	∗	98.1	80.8	63.0
Cadaba farinosa	–	∗	64.9	80.8	∗
Wissadula amplissima	–	∗	71.3	61.5	∗
Grewia bicolor	n.s.	∗	88.1	∗	–
Grewia lasiodiscus	–	n.s.	–	65.4	65.4
Maerua oblongifolia	–	–	–	76.9	60.5
Ampelocissus multistriata	–	n.s.	–	∗	78.9
Grewia mollis	n.s.	–	n.s.	∗	60.7
Asparagus flagellaris	n.s.	∗	n.s.	∗	62.0
Combretum aculeatum	n.s.	n.s.	n.s.	∗	60.5

Supporting Information

Table I.3 Research sites, mean annual precipitation (MAP) and number of mound/savanna plot pairs for each site per sampled savanna type. Vegetation zones according to White (1983). Tiger bush is a vegetation type composed of alternating, densely vegetated bands and bare areas parallel to the contour.

Vegetation zone	Site	MAP (mm)	Savanna types	Plot pairs
Sahel Zone	RPS	360	Tiger bush dominated by *Pterocarpus lucens* and *Acacia spp.*	16
Sudanian Zone	FCN	670	Tiger bush dominated by *Combretum micranthum* and *Pterocarpus lucens*	12
			Shrub savanna dominated by *Combretum nigricans* with subdominant *Sclerocarya birrea*	12
Sudanian Zone	FCG	760	Shrub savanna dominated by *Combretum micranthum* and *Guiera senegalensis*	12
			Shrub savanna dominated by *Terminalia spp.*, *Ziziphus mauritania* and subdominant *Sclerocarya birrea*	12
Sudanian Zone	PNW	840	Woodland savanna dominated by *Isoberlinia doka* and *Afzelia africana*	13
			Woodland savanna dominated by *Terminalia avicennioides* and *Burkea africana*	13
Sudanian Zone	PNP	950	Shrub savanna dominated by *Crossopteryx febrifuga*	18
			Shrub savanna dominated by *Detarium microcarpum*	16
			Tree savanna dominated by *Terminalia avicennioides* and *Burkea africana*	4

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Anlage 1

Erklärung über Anteile der Autoren/Autorinnen an den einzelnen Kapiteln der Promotionsarbeit

Titel der Publikation/ des Manuskripts:

The contribution of *Macrotermes* mounds to landscape-scale variation in vegetation in a West African national park

Was hat der/die Promovierende bzw. was haben die Co-Autoren/Autorinnen beigetragen[#]	Name des/der jeweiligen Autors/Autoren/Autorin*
(1) Entwicklung und Planung AE (80%) conceived and designed the study together with KH and RW (10% each).	Arne Erpenbach, Karen Hahn, Rüdiger Wittig
(2) Durchführung der einzelnen Untersuchungen/ Experimente AE conducted the fieldwork and experiment.	Arne Erpenbach,
(3) Erstellung der Daten-sammlung und Abbildungen AE processed and analysed the data, and created all figures and tables.	Arne Erpenbach,
(4) Analyse/Interpretation der Daten AE analysed and interpreted the data (80%). MBR and KH contributed to the interpretation of the data (10% each).	Arne Erpenbach, Karen Hahn, Markus Bernhard-Römermann,
(5) übergeordnete Einleitung/ Ergebnisse/Diskussion AE wrote the manuscript (80%). All authors commented equally on the manuscript.	Arne Erpenbach, Karen Hahn, Markus Bernhard-Römermann, Rüdiger Wittig

[#] Bei 2, 3 und 4 bitte kurze inhaltliche Angaben der jeweiligen Anteile, bei 1 und 5 reichen prozentuale Angaben

*Mehrfacheintragungen möglich

Als Autoren/Autorinnen werden solche Personen bezeichnet, die an der Arbeit in Bezug auf die genannten Punkte in einer Weise mitgewirkt haben, dass sie für die ausgewiesenen Passagen (mit) verantwortlich sind. Personen, die an der Arbeit mitgewirkt haben, jedoch nicht in diese Kategorie fallen, sollten in der Danksagung Erwähnung finden.

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II

The contribution of *Macrotermes* mounds to landscape-scale variation in vegetation in a West African national park

Abstract

QUESTIONS: Termite mounds are important sources of local-scale soil heterogeneity and thereby affect savannas vegetation. Studies contrasting mound and savanna vegetation usually neglect variation between savanna types. We aim to answer the following questions: is mound vegetation consistently different from the surrounding savanna vegetation at a landscape scale? Is mound vegetation homogeneous across different savanna types? Are differences between mound and savanna vegetation influenced more by nutrient accumulation or clay enrichment in mounds?
LOCATION: Pendjari National Park, northern Benin.
METHODS: We analyzed the vegetation in 59 pairs of mound and savanna plots in four savanna types. We examined if mounds differed in community composition between savanna types, and from savanna plots using ordinations, and tested for correlations between community composition and soil parameters. We identified characteristic plant species for mounds in each savanna type using the IndVal method. Finally, we evaluated the relative importance of different soil parameters for differences in vegetation between

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AE conceived and designed the study together with KH and RW. AE conducted the fieldwork, analysed and interpreted the data, and wrote the manuscript. MBR and KH contributed to the interpretation of the data, and all authors commented on the manuscript.

mound and savanna plots using projection to latent structures regression (PLSR).
RESULTS: There were clear differences between savanna types for both savanna and mound communities, and in each savanna type, clear differences emerged between mound and savanna vegetation. Community differences correlated with differences in soil parameters in all cases. We identified ten characteristic plant species for mounds, with little overlap between characteristic species from different savanna types. Across savanna types, 63% of the variation in mound—savanna vegetation contrast was explained by variation in nine soil parameters, most importantly clay content.
CONCLUSION: Even at the landscape scale, the influence of mounds on vegetation depends on habitat context. Thus, local mound vegetation patterns can only be understood considering the influence of different soil parameters in each savanna type. However, enrichment of clay and macronutrients together explain the largest part of the differences between mound and savanna vegetation. Further variation in vegetation composition among mounds is likely driven by biotic interactions and spatial distribution of mounds.

Introduction

Termite mounds of fungus-cultivating Macrotermitinae are an important feature of savanna landscapes.As ecosystem engineers (Dangerfield et al. 1998), termites shape their environment and provide important ecosystem functions (Jouquet et al. 2011). Their mounds increase habitat heterogeneity, mostly by re-allocation of nutrients and subsoil particles (Sileshi et al. 2010; Jouquet et al. 2011). Recent reviews have shown that termite mounds affect savanna productivity (Sileshi et al. 2010; Jouquet et al. 2011). Termite mounds, especially when abandoned, provide important microhabitats for plants (Salick et al. 1983; Traoré et al. 2008). Animals also benefit from termite mounds directly and indirectly, for instance birds (Joseph et al. 2011), other small vertebrates (Fleming and Loveridge 2003), and invertebrates (de Visser et al. 2008; Pringle et al. 2010).

Studies from different African savanna landscapes have reported that mounds support distinct vegetation, including specific species, taxonomic groups or lifeforms (Colonval-Elenkov and Malaisse 1975; Malaisse 1976; Moe et al. 2009). Most studies have found a species-enriched flora on mounds (see, e.g., Moe et al. 2009; Sileshi et al. 2010; Okullo and Moe 2012). However, studies so far were usually restricted to one specific savanna vegetation type, and data from a single vegetation type are insufficient to evaluate and generalize the importance of mounds for the heterogeneity and diversity of savanna systems.

Soil is a major factor driving savanna composition (Hahn-Hadjali 1998; Sankaran et al. 2005). Accordingly, differences between mound and savanna vegetation are commonly ascribed to changes in soil composition mediated by termites. Studies from different savannas have reported similar differences in soil composition between mounds and surrounding savanna topsoil (Sileshi et al. 2010; Jouquet et al. 2011), but recent studies have also found differences in soil composition among mounds of different sites based on underlying pedology, geology, and general geography (Abe et al. 2009; Mujinya et al. 2010, 2013). There is a lack of studies comparing mound vegetation and its relation to soil between different savanna types. It is furthermore unclear whether increased soil organic matter content and nutrient input or increased clay content due to termite activity is more important for enriching mound soil, and if either of these factors alone suffices for creating "fertility islands" (Sileshi et al. 2010).

This study tackles these research gaps by addressing the following questions: first, is mound vegetation homogeneous across different savanna types? Second, are differences between mound and savanna vegetation consistent or do they vary across savanna types and their underlying soil conditions? In the latter case, are there different characteristic plant species for mounds in different savanna types? Third, which soil parameters are most important for the differences between mound and savanna vegetation — more specifically, do higher clay or nutrient content cause vegetational differences? We expected moderate variation of species composition among mounds in different savanna types. We also expected mounds in different savanna types to represent similar soil conditions with slight variation based on the surrounding pedology. Therefore, we expected the strength of contrast between soil parameters on and off mounds to be mirrored by vegetation differences, i.e. we expected waterlogged and laterite encrusted sites to show a more pronounced mound vegetation type with a stronger contrast to the surrounding savanna.

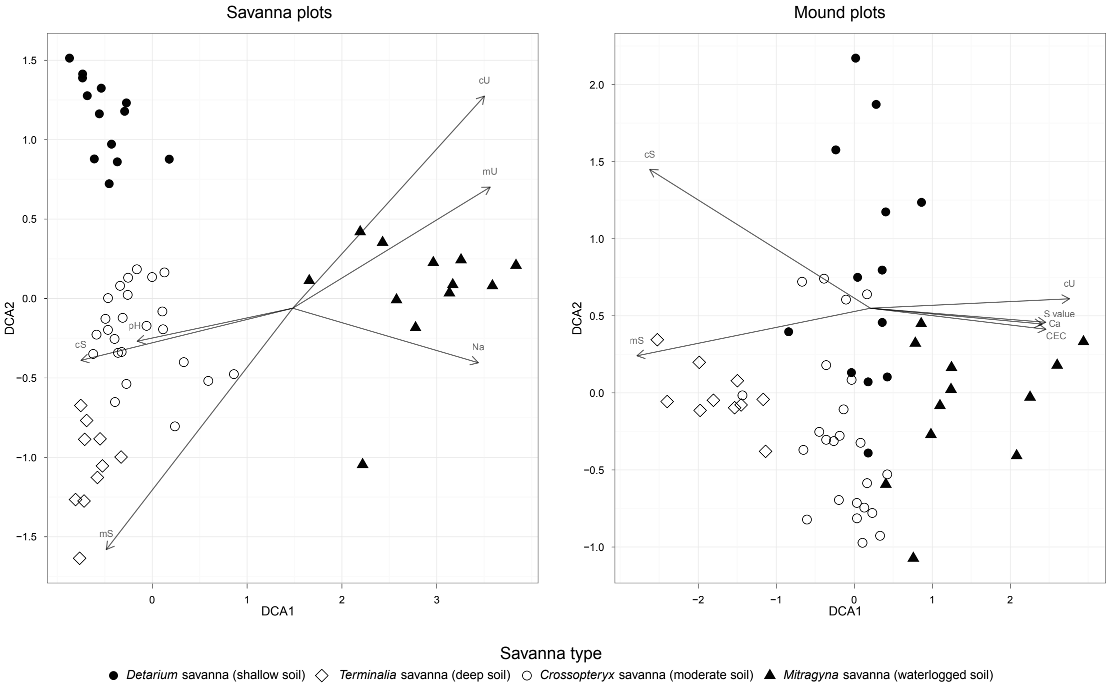

Figure II.1 DCAs of vegetation composition of 59 savanna plots (256 plant spp.), and 59 termite mound plots (266 plant spp.), in Pendjari National Park. Arrows show significant correlations of axis scores with soil environmental parameters. For correlations, see Table II.1 and Supporting Information Table II.6. Correlation labels: pH: pH$_{H_2O}$; Na: Na$^+$[mmol$_c$/kg] ; Ca: Ca^{2+}[mmol$_c$/kg] ; CEC: CEC$_{pot}$[mmol$_c$/kg] ; S value: base concentration [mmol$_c$/kg] ; cS: coarse sand$_{630—2000\mu m}$ [%] ; mS: medium sand$_{200—630\mu m}$ [%] ; cU: coarse silt$_{20—63\mu m}$ [%] ; mS: medium silt$_{6.3—20\mu m}$ [%].

Methods

Study site

Sampling took place in Pendjari National Park (PNP), northern Benin (11°22′N, 1°33′E), at the limit between the Southern and Northern Sudanian vegetation zones (White 1983). Annual precipitation is about 950 mm/a with a pronounced unimodal wet season from May to October.

Survey design

We sampled vegetation and soil on 59 mounds and in 59 paired savanna plots in four savanna types that are abundant in PNP and associated with different soils: *Crossopteryx* savanna on moderately deep soils (24 plot pairs), *Detarium* savanna on shallow laterite encrusted soils (13), *Mitragyna* savanna on temporally waterlogged heavy soils (12), and *Terminalia* savanna on soils with a sceletic base (10). Savanna types were identified based on

Table II.1 Pearson's correlation coefficient *r* between DCA axis scores and measured soil parameters of savanna and mound plots in Pendjari National Park. Parameters shown have at least one significant correlation with $|r| \geq 0.4$ after Bonferroni correction. n.s.: not significant at $P \leq 0.05$.

	Savanna		Mound	
	DCA 1	DCA 2	DCA 1	DCA 2
	r	*r*	*r*	*r*
pH_{H_2O}	-0.498	n.s.	n.s.	n.s.
Na^+[$mmol_c$/kg]	0.594	n.s.	n.s.	n.s.
Ca^{2+}[$mmol_c$/kg]	n.s.	n.s.	0.576	n.s.
CEC_{pot}[$mmol_c$/kg]	n.s.	n.s.	0.588	n.s.
S value [$mmol_c$/kg]	n.s.	n.s.	0.588	n.s.
Coarse $sand_{630—2000\mu m}$[%]	-0.678	n.s.	-0.740	n.s.
Medium $sand_{200—630\mu m}$[%]	-0.597	n.s.	-0.782	n.s.
Coarse $silt_{20—63\mu m}$[%]	0.613	n.s.	0.667	n.s.
Medium $silt_{6.3—20\mu m}$[%]	0.632	n.s.	n.s.	n.s.

our own surveys, landcover (Kpadonou et al. 2009) and pedological data (Faure and Viennot 1978), and vegetation classifications from adjacent areas (Mbayngone et al. 2008; Ouédraogo et al. 2008). We randomly selected eroded, vegetated mounds built by *Macrotermes subhyalinus* (Rambur, 1842) or *M. bellicosus* (Smeathman, 1781).

Each mound, area was approximated by multiplying the longest mound axis by its perpendicular axis. A paired square savanna plot of corresponding size was established 15 m north of the mound's northern limit. Each paired savanna plot constituted the south-eastern corner of a larger, 30 × 30 m savanna plot. To avoid having *Macrotermes* mounds in or near our savanna plots, we rotated the position of the savanna plots relative to the corresponding mound counter-clockwise in steps of 15 degrees until no mounds were within 15 m. Sampling took place in 2008 and 2009, between May and July during the early wet season of each year.

Vegetation data

Vegetation was sampled separately for woody (woody plants > 50 cm) and herb (plants < 50 cm) layers by estimating coverage in percent for each occurring species. In the 30 × 30 m savanna plots, only the woody layer was recorded. Nomenclature followed the African Plants Database (2011).

Environmental data

For every mound and savanna plot, four topsoil subsamples (10 cm^3) were pooled, air-dried, and sieved to < 2 mm. Mound soil was sampled 1 m inwards from the mound plot's northern, eastern, southern, and western limits (pediment). Savanna soil was likewise sampled in four cardinal directions.

Concentrations of plant-available phosphorus (P_2O_5: P_{av}), potassium (K_2O: K_{av}), organic and inorganic carbon, nitrogen, pH, and conductivity were determined for each pooled soil sample. Additionally, we randomly selected plot pairs from each savanna type (*Detarium* savanna: 7 pairs, *Crossopteryx* savanna: 11, *Mitragyna* savanna: 7, *Terminalia* savanna: 10), and determined potential cation exchange capacity (CEC_{pot}, with ion concentrations of sodium, potassium, calcium, and magnesium) and particle size distribution (PSD, in seven fractions).

Statistical Analysis

Vegetation differences between savanna types To test whether mound vegetation was more homogeneous than savanna vegetation across different savanna types, we used detrended correspondence analysis (DCA) with down-weighting of rare species and 26 detrending segments (Hill and Gauch 1980). We calculated Pearson's correlation coefficient r between soil parameters and DCA scores (first two axes) to investigate whether differences in vegetation composition were related to soil conditions. We considered soil parameters with $|r| < 0.4$ to be of minor importance.

Contrast between mounds and savanna To test whether difference between mound and savanna vegetation composition varied between savanna types, we used constrained correspondence analysis (CCA, ter Braak 1986). For each of the four savanna types, we conducted a separate CCA with the first axis constrained by the mound—savanna distinction. We calculated r between soil parameters and CCA scores (first axis) to investigate how much of the vegetation contrast between mound and savanna plots could be related to soil parameters. We considered soil parameters with $|r| < 0.7$ to be of minor importance.

Characteristic mound species We identified characteristic plant species for mounds in each savanna type using the IndVal method (Dufrêne and Legendre 1997; Bakker 2008) stratified for vegetation layers. We defined species with significant indicator values, we defined species with an indicator value of 60% or higher as characteristic species (McGeoch et al. 2002).

Importance of soil parameters To identify the most important soil parameters driving vegetation differences between mounds and savanna, we applied projection to latent structures regression (PLSR, also known as partial least squares regression). We used Bray-Curtis distances as a measure of vegetation differences between plots pairs. Many soil parameters are inherently collinear, posing an analytical problem common in ecological studies (Carrascal et al. 2009). PLSRallowed us to keep collinear soil parameters in the model (Wold et al. 1983) and rank their contribution to the communal explanation of variation using variable loading weights and variable importance in projection index (VIP, Chong and Jun 2005). Soil parameters were represented as projected latent variables (LV) to reduce dimensionality. We used root mean square errors (RMSE) to determine the number of LV included in the model. Parameters with loading weights > 0.05 and VIP values > 1 were considered informative predictors (Carrascal et al. 2009). Predictive power of the PLSR was determined through leave-one-out cross-validation.

Further analysis details Prior to analysis, vegetation data were arcsine-square-root transformed, and soil data were standardized to zero mean, unit variance. In all analyses except PLSR, each PSD fraction was treated as a separate variable to check for correlations with specific particle size classes. In PLSR, PSD was treated as sand, silt, and clay contents, as treating detailed fractions separately provided no additional useful information. In case of multiple testing, Bonferroni correction was applied. Analyses were performed using R 2.15.2 (R Foundation for Statistical Computing, Vienna, AT) with packages vegan 2.0-5, labdsv 1.5-0 and pls 2.3-0.

Results

Vegetation differences between savanna types Vegetation composition of savanna plots clearly differed between the four investigated savanna types, indicating clear grouping of plant communities (Fig. II.1, DCA axis 1 length: 4.7 SD units, eigenvalue: 0.62, axis 2 length: 3.15 SD units, eigenvalue: 0.42). Vegetation composition on mounds also differed between savanna types, but groups were less distinct (Fig. II.1, DCA axis 1 length: 5.46 SD units, eigenvalue: 0.49, axis 2 length: 3.24 SD units, eigenvalue: 0.3).

The differences in vegetation composition between savanna types were linked to several soil parameters. For both savanna and mound plots, we detected significant correlations between the first DCA axis and particle size fractions of sand and silt content (Table II.1 and Supporting Information Table II.6, Fig. II.1). Coarse (cS) and medium sand (mS) content and the proportionally related coarse (cU) and medium silt content (mU, significantly correlated for savanna plots only) were particularly strongly correlated with DCA axis scores.

These correlations were mirrored by differences in soil composition among savanna types: savanna plots in *Detarium* and *Terminalia* savannas had higher cS contents than in the other savanna types (Supporting Information Fig. II.5), with *Terminalia* savannas also showing elevated mS contents. Savanna plots in moist *Mitragyna* savannas had higher silt contents, especially cU and mU, higher sodium levels and lower pH, which was also reflected in correlations with DCA axis scores.

Mound soil composition varied more than expected, particularly between savanna types, but this variation only partly related to vegetation differences. For instance, in *Mitragyna* savannas, sodium content was even higher on mounds than in savanna plots, but was not significantly correlated with DCA axis scores. In contrast, cation exchange capacity (CEC_{pot}), calcium ion content, and overall base concentration (S value) on mounds were correlated with the first DCA axis and were lower in *Terminalia* savannas and higher in *Mitragyna* savannas than in other savanna types. No soil parameters correlated significantly with the second DCA axis for mound or savanna plots.

Contrast between mounds and savanna CCA constrained by plot type (savanna/ mound) revealed different patterns of within-group variation for the four savanna types. In particular, savanna vegetation was less homogeneous in *Crossopteryx* savannas, and mound vegetation was more homogeneous in *Mitragyna* savannas than in the other savanna types.

Differences in vegetation composition between paired mound and savanna plots were related to different soil parameters in each savanna type. Some variables (pH, conductivity, Kav) were higher for mounds in all savanna types, and significantly correlated with CCA axis scores. For other variables (e.g. clay content, CECpot), correlations with vegetational differences between mound and savannas varied strongly between savanna types

(Table II.2 and Supporting Information Table II.7, Fig. II.2 and Supporting Information Fig. II.6).

Table II.2 Pearson's correlation coefficient *r* between CCA axis scores and measured soil parameters for plots in four savanna types in Pendjari National Park. The correlations between soil parameters and CCA scores account for variation of vegetation between savanna and mound plots, as the first axis is constrained by plot type. Parameters shown have at least one significant correlation after Bonferroni correction. ns: not significant at $P \leq 0.05$; –: $|r| < 0.7$.

	Detarium savanna type	*Crossopteryx* savanna type	*Terminalia* savanna type	*Mitragyna* savanna type
	r	*r*	*r*	*r*
pH_{H_2O}	0.746	0.760	0.854	0.707
Conductivity [μS/cm]	0.767	0.729	0.743	0.900
K_{av} [%]	0.723	0.746	0.715	0.842
Carbonates [%]	n.s.	n.s.	0.753	n.s.
K^+[mmol$_c$/kg]	n.s.	0.733	-	0.828
Ca^{2+}[mmol$_c$/kg]	n.s.	0.750	n.s.	0.780
Mg^{2+}[mmol$_c$/kg]	n.s.	0.751	n.s.	n.s.
CEC_{pot}[mmol$_c$/kg]	n.s.	0.720	n.s.	n.s.
S value [mmol$_c$/kg]	n.s.	0.779	n.s.	0.789
V value [%]	0.881	0.829	0.706	n.s.
Medium sand$_{200—630\mu m}$[%]	n.s.	n.s.	-0.737	n.s.
Fine sand$_{63—200\mu m}$[%]	n.s.	n.s.	-0.816	n.s.
Fine silt$_{2—6.3\mu m}$[%]	n.s.	n.s.	0.742	n.s.
PSD $\sum$ clay$_{<2\mu m}$[%]	n.s.	0.719	0.718	n.s.

Characteristic mound species Indicator species analysis identified ten characteristic species for mound vegetation (Table II.3). Each of the four savanna type had different characteristic mound species, with very few overlaps (e.g. *Ampelocissus multistriata* in three savanna types). *Detarium* and *Crossopteryx* savannas had five and six characteristic species, respectively, while for the temporally waterlogged *Mitragyna* savannas and for *Terminalia* savannas, only one and two characteristic mound species, respecitvely, were detected. The characteristic species included several geophytes, which survive the annual burning and the following dry season in dormancy (*Ampelocissus multistriata*, *Asparagus flagellaris*, *Maerua oblongifolia*, *Stylochaeton hypogaeus*, *Chlorophytum blepharophyllum*).

Importance of soil parameters PLSR revealed that clay content had the strongest influence on vegetation differences between paired mound and savanna plots (Fig. II.3). This was indicated by difference in clay content having the largest squared loading weight (0.31) for the first latent variable (LV). The other variables contributing to the model for

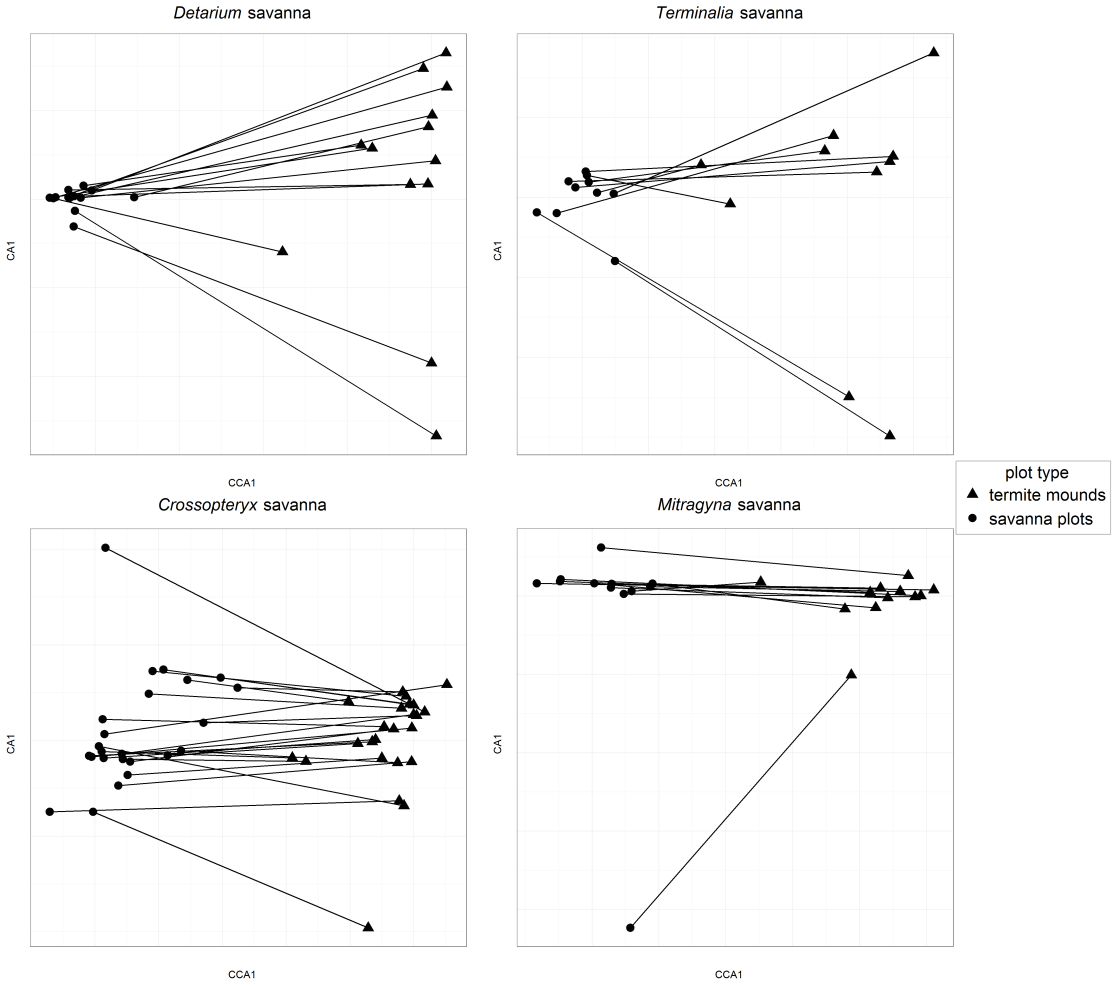

Figure II.2 CCAs for paired savanna and termite mound plots in four savanna types in Pendjari National Park. Paired plots are connected by lines. The 26 paired plots in *Detarium* savannas contained 162 spp., the 48 paired plots in *Crossopteryx* savannas contained 248 spp., the 20 paired plots in *Terminalia* savannas contained 163 spp., and the 24 paired plots in *Mitragyna* savannas contained 125 spp. For correlations, see Table II.2 and Supporting Information Table II.7.

Table II.3 Characteristic plant species of termite mound vegetation in four savanna types in Pendjari National Park. Only significant indicator values $\geq 60\%$ ($P < 0.05$, 1000 iterations) are given for each savanna type. Analyses were based on cover values of recorded species, estimated separately for two vegetation strata (h = herbaceous layer (including woody plants < 0.5 m); w: woody layer; the respective stratum is given after the species name). n.s.: not significant; *: indicator value < 60%; –: species absent.

	Detarium savanna type	*Crossopteryx* savanna type	*Terminalia* savanna type	*Mitragyna* savanna type
Chlorophytum blepharophyllum (h)	61.5%	n.s.	–	n.s.
Stylochaeton hypogaeus (h)	69.2%	*	–	n.s.
Combretum aculeatum (w)	69.0%	*	–	n.s.
Feretia apodanthera (w)	92.3%	66.3%	–	n.s.
Ampelocissus multistriata (h)	69.2%	70.8%	60.0%	n.s.
Feretia apodanthera (h)	*	79.2%	n.s.	n.s.
Capparis sepiaria (w)	n.s.	70.8%	–	*
Asparagus flagellaris (h)	*	69.3%	n.s.	n.s.
Maerua oblongifolia (h)	*	62.5%	n.s.	*
Maytenus senegalensis (h)	–	*	65.5%	n.s.
Flueggea virosa (w)	n.s.	n.s.	n.s.	72.8%

the first LV were, in descending importance, differences in pH, CEC_{pot}, Mg^{2+}, Ca^{2+} and silt content (Table II.4, Fig. II.4). A model including these six parameters explained 22% of the variation in vegetation differences between paired mound and savanna plots (Figs. II.3 a, II.4) using one LV. A more complete model including also differences in overall K^{+}, plant-available phosphorus, and sand content predicted 49% of the variation using two LV, 61% using three LV, and 63% using four LV.

Discussion

In this study, we analyzed vegetation data from different savanna types to investigate (i) variation in mound vegetation at a landscape scale, (ii) differences between termite mound and savanna vegetation composition, and (iii) the influence of soil parameters on differences between mound and savanna vegetation. Our findings show that the effect of *Macrotermes* mounds is not uniform across landscapes, and that termite-induced soil heterogeneity varies with underlying pedology and environmental context. In our study area, mound communities were especially distinct and homogeneous in temporarily inundated savannas on acidic soils.

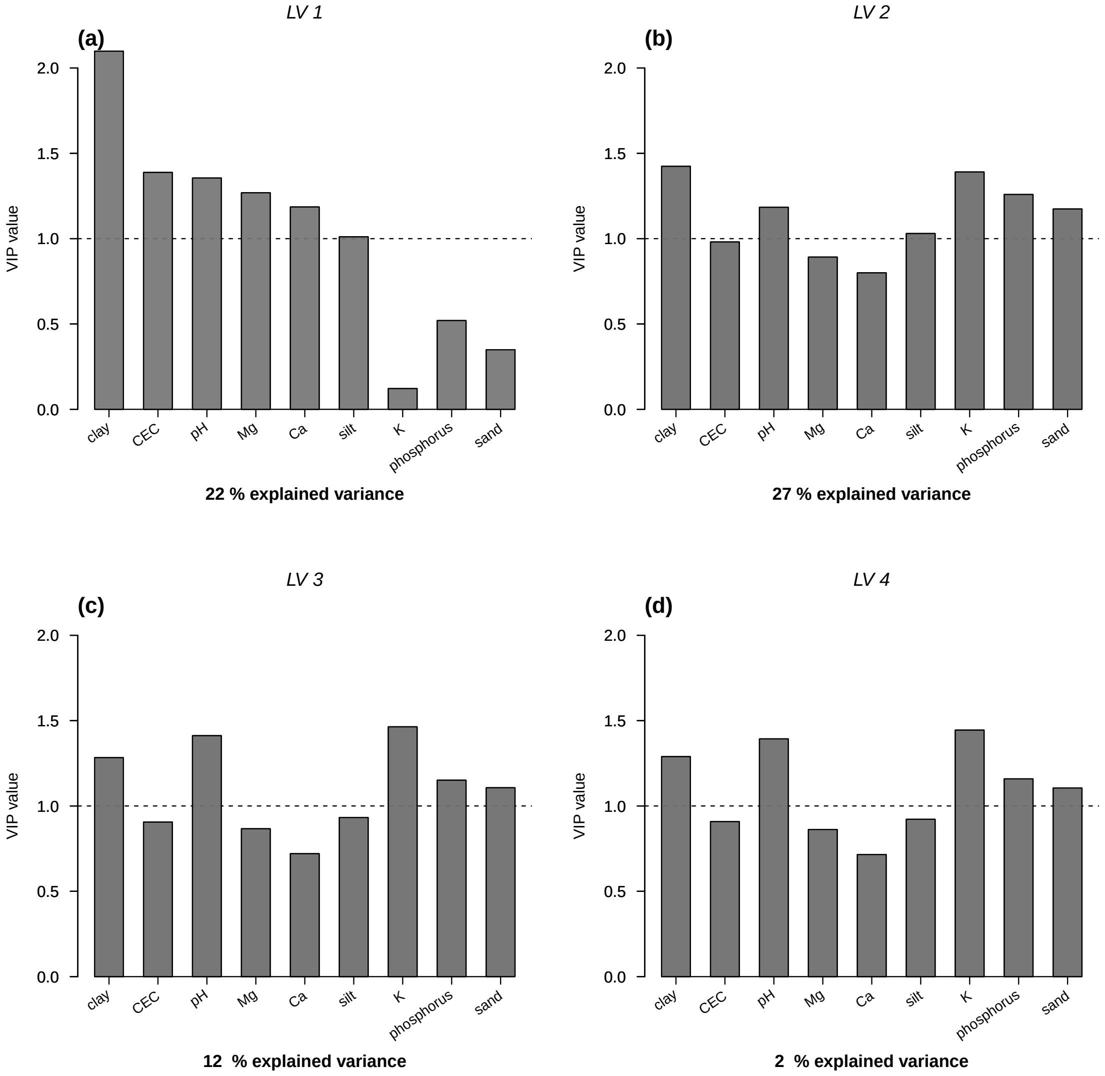

Figure II.3 PLSR variable importance in projection (VIP) for four components (latent variables, LV). PLSR explained about 63% of the original variation in distances in vegetation composition between mounds and the surrounding savanna. Only parameters with VIP values > 1 for at least one latent variable are shown. Squared loading weights contributing to VIP values are shown in Table II.5.

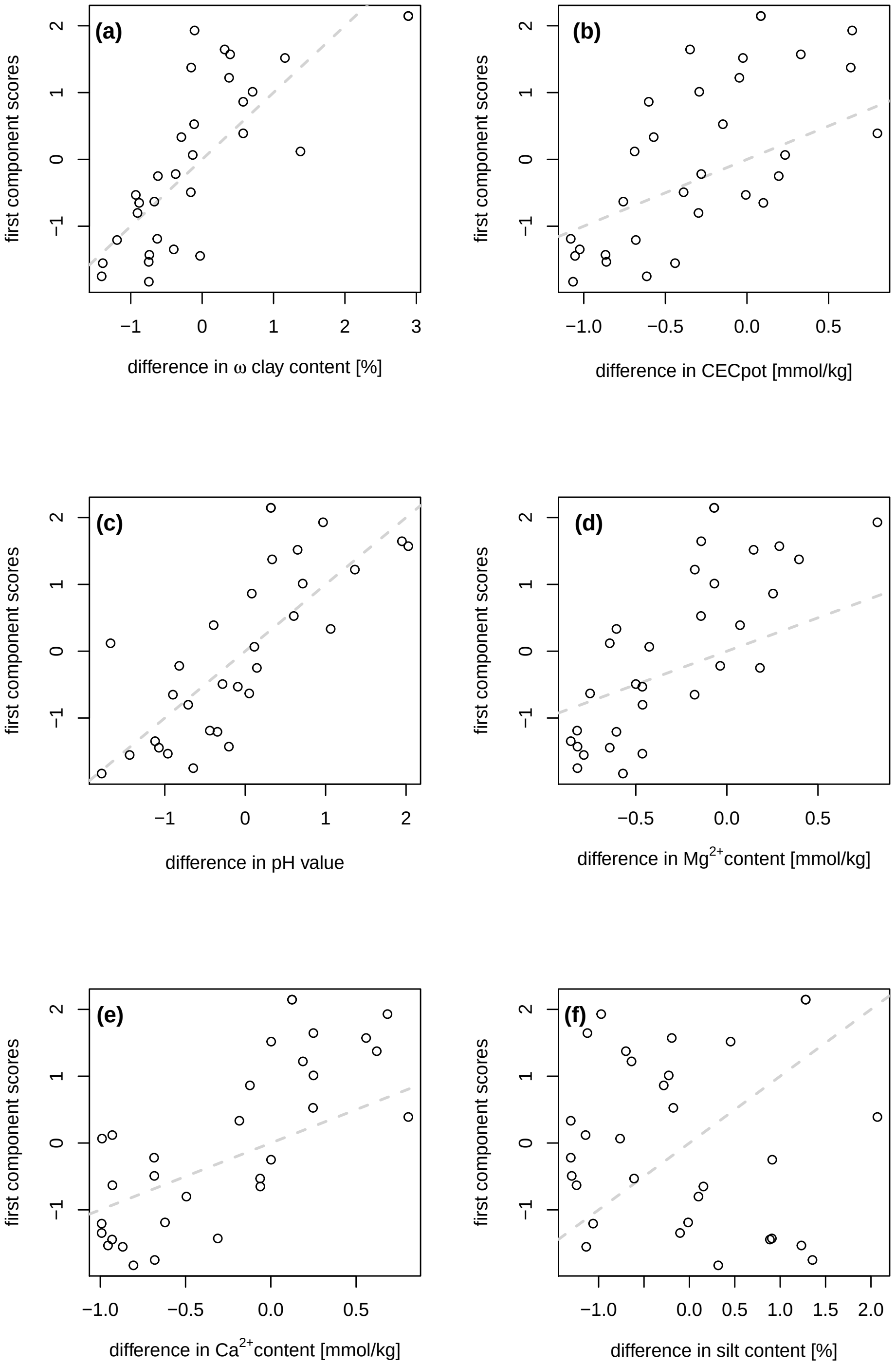

Figure II.4 PLSR results: relationships between the first latent variable and differences in soil parameters ((a) clay content, (b) cation exchange capacity (CEC_{pot}), (c) pH, (d) magnesium cation content, (e) calcium cation content, and (f) silt content) between savanna and mound plots. Dashed lines indicate perfect relation.

Table II.4 Basic statistics for the PLS regression model shown for four latent variable axes. Model coefficients are given for each latent variable axis (LV). RMSE: root mean square error, $RMSE_{cv}$: root mean square error after cross validation with 31 leave-one-out segments.

	LV 1	LV 2	LV 3	LV 4
pH_{H_2O}	0.016	0.016	-0.018	-0.023
P_{av} [%]	-0.006	-0.044	-0.068	-0.066
K_{av} [%]	0.009	-0.001	0.006	0.005
Carbon content [%]	0.008	0.032	0.041	0.048
C/N ratio	0.004	0.010	0.020	0.023
Organic subst. [%]	-0.004	-0.017	-0.050	-0.051
Na^+[$mmol_c$/kg]	0.003	-0.010	0.001	0.008
K^+[$mmol_c$/kg]	-0.001	-0.038	-0.025	-0.022
Ca^{2+}[$mmol_c$/kg]	0.014	0.028	0.033	0.035
Mg^{2+}[$mmol_c$/kg]	0.015	0.040	0.063	0.068
CEC_{pot}[$mmol_c$/kg]	0.016	0.044	0.064	0.070
PSD $\sum$ sand [%]	0.004	-0.020	-0.042	-0.049
PSD $\sum$ silt [%]	-0.012	-0.046	-0.056	-0.059
PSD $\sum$ clay [%]	0.024	0.049	0.062	0.059
RMSE	0.102	0.082	0.072	0.071
$RMSE_{cv}$	0.123	0.128	0.115	0.113
Cumulative variance in predictors [%]	27.88	38.32	45.18	65.21
Cumulative explained variance [%]	22.06	49.31	60.96	62.63

Vegetation differences between savanna types The systematic variation of mound vegetation with savanna type, as revealed by DCA, has not, to our knowledge, been demonstrated before. We found a clear influence of soil on landscape-scale variation of mound vegetation. In particular, we suggest that the pronounced differences in Na^+ and pH between *Mitragyna* savannas and the other savanna types are related to regular temporary inundation of *Mitragyna* savannas. Inundation should also directly influence the development of typical mound vegetation in this savanna type. Few woody plant species in West African savannas can cope with seasonal inundation, which explains the strong contrasts between *Mitragyna* savannas and the other savanna types and between mounds and savanna in this savanna type, in line with evidence from the Okavango delta showing that termite mounds support species that cannot survive in the seasonally flooded surroundings (Dangerfield et al. 1998; McCarthy et al. 1998). As most studies of mound soil report enrichment of fine particles from deeper soil layers (Sileshi et al. 2010), we expected clay enrichment to reduce vegetation differences between mounds. However, similar correlations of sand and silt contents with variation in both mound and savanna vegetation indicated that differences between mounds in different savanna types are influenced by local pedology. Even though differences in mound vegetation were not correlated with clay content itself, they were correlated with cation concentrations and $\mathrm{CEC}_{\mathrm{pot}}$, which could be interpreted as a result of differences in clay enrichment and possibly clay mineralogy.

Contrast between mound and savanna As expected, mound and savanna vegetation differed in all savanna types, in line with other studies from different parts of Africa (e.g., Blösch 2008; Erpenbach et al. 2013; Davies et al. 2014a,b), but correlations with soil parameters differed between savanna types. This indicates that local soil conditions influence both variation among mounds (as shown in DCA) and the contrast between mound and savanna.

Variation in mound vegetation was greater than expected, mostly exceeding variation in savanna plots, both overall and within savanna types (Fig. II.2). Several studies have reported higher plant richness on mounds than in the surrounding savanna, which might cause higher variation in mound vegetation composition (Moe et al. 2009; Okullo and Moe 2012; Joseph et al. 2013). However, in a recent study comparing mound and savanna vegetation along a climatic transect, we found that mound vegetation is not always richer in species than savanna vegetation (Erpenbach et al. 2013). Additionally, here we found high within-group variation in vegetation for both savanna plots and mounds *Crossopteryx* savannas.

Characteristic mound species The high number of characteristic geophytic species revealed on mounds is consistent with findings from an adjacent area showing higher abundance and frequency of geophytes on mounds (Kirchmair et al. 2012). Associations of particular plant species with mounds are mentioned in most floristic works from the range of *Macrotermes* (e.g., Hutchinson and Dalziel 1972; Arbonnier 2009) and in multiple recent case studies (Erpenbach et al. 2013; Joseph et al. 2013). Our results underline the importance of the mound microhabitat to both single species and plant communities. Further research is needed to determine if the association of certain plant species with termite mounds exemplifies coevolution, as has been speculated (Okullo and Moe 2012).

Importance of soil parameters Although the importance of the other eight parameters should not be underestimated, clay content stood out as the most important soil parameter influencing differences in vegetation between mounds and savanna (Figs. II.3 and

II.4, Tables II.4 and II.5). Clay particles not only provide a large surface for exchange processes, as captured by CEC, but also affect moisture storage (Hillel 1998). Depending on their mineralogy, clays show different sorption and desorption capacities for ions, and different capacities for swelling and water retention (Gaiser et al. 2000).

Table II.5 PLSR squared loading weights of retained predictors for four latent variables. Squared loading weights > 0.05 (in bold) are considered to contribute to the model if they score a VIP value > 1 (see Figure II.3). Soil parameters with squared loading weights < 0.05 in all latent variables are not shown.

	LV 1	LV 2	LV 3	LV 4
pH_{H_2O}	**0.13**	**0.08**	**0.32**	< 0.01
P_{av} [%]	0.02	**0.19**	0.02	**0.14**
K_{av} [%]	0.04	**0.09**	0.04	0.02
Carbon content [%]	0.04	0.04	< 0.01	**0.17**
Organic subst. [%]	0.01	0.01	**0.21**	**0.10**
Na^+[mmol$_c$/kg]	< 0.01	**0.06**	**0.08**	**0.18**
K^+[mmol$_c$/kg]	< 0.01	**0.25**	**0.22**	< 0.01
Ca^{2+}[mmol$_c$/kg]	**0.10**	< 0.01	< 0.01	0.02
Mg^{2+}[mmol$_c$/kg]	**0.12**	0.01	0.04	0.03
CEC_{pot}[mmol$_c$/kg]	**0.14**	0.01	0.02	**0.07**
PSD $\sum$ sand [%]	0.01	**0.17**	0.04	**0.08**
PSD $\sum$ silt [%]	**0.07**	**0.08**	< 0.01	0.01
PSD $\sum$ clay [%]	**0.31**	0.01	< 0.01	**0.16**

In addition to enriching mound soil with clay, termites might also modify clay mineralogy under certain conditions to a more expandable clay type (Boyer 1982; Jouquet et al. 2002a,b, but see also Jouquet et al. 2005; Mujinya et al. 2013), leading to a release of normally non-exchangeable inter-layer cations, especially K^+. Further K^+ might be released from plant matter transported to the mound by termites. In tropical and subtropical savannas, surface K^+ is quickly leached, and subsurface K^+ is mainly bound to illite and kaolinite clays and thus not directly available to plants. Termite mounds could also have retarding effects on K^+ leaching due to their effects on local ecohydrology (Turner 2006), although a recent study of a single mound showed no evidence of K^+ retardation (Erens et al. 2015). However, foliar concentrations of K^+ and other micronutrients have been shown to be higher on mounds (Seymour et al. 2014). Termite-modulated higher long-term K^+ availability on mounds could be important especially for water-use efficiency of plants, as K^+ is involved in various responses to drought and heat stress, including stomatal movements and root health maintenance (Marschner 2012). This relates to findings from a recent simulation study that plant water-use efficiency is a strong driver of divergence between mound and savanna vegetation patterns (Bonachela et al. 2015).

Clay enrichment and modification also increase pH, which in turn can increase phosphorus availability compared to surrounding, mostly acidic, soil environments, where phosphorus is immobilized by iron and aluminium oxides. However, previous studies have found contradictory results on the availability of phosphorus in *Macrotermes* mounds as compared to the surrounding savanna, and have noted that sorption by clay may actually reduce phosphorus availability in termite mound soil (López-Hernández et al. 2006; Seymour et al. 2014). In addition, Sileshi et al. (2010) pointed out conflicting evidence about the relative importance of enrichment of soil organic matter, nutrient enrichment and clay enrichment for termite mound vegetation. In our data, P_{av} was not consistently higher on mounds in all savanna types, but contributed to the model explaining differences between mound and savanna. We suggest that clay enrichment is the most important factor for differences between mound and savanna vegetation at the landscape scale, and that vegetation directly reacts to the relationships between clay content, potassium content, pH and phosphorus availability.

In addition to soil parameters, biotic interactions and the spatial distribution and density of mounds might help explain vegetation differences between mounds and savanna. It has been shown that distribution and density of mounds are affected by intraspecific competition (see, e.g., Korb and Linsenmair 2001; Grohmann et al. 2010), hydrology, geology, climatic constraints, and anthropogenic influences (see, e.g., Pringle et al. 2010; Davies et al. 2014b; Bonachela et al. 2015). High mound densities and regular mound distribution might facilitate directed plant dispersal towards mounds because of their role as sites for perching, nesting, and feeding (see, e.g., Jackson and Gartlan 1965; Joseph et al. 2011; Støen et al. 2013).

Conclusion

We demonstrated that even at a landscape scale, the influence of termite mounds depends on environmental context , as already shown at a regional scale across a climatic gradient in West Africa (Erpenbach et al. 2013). Future studies on termite mounds should thus take spatial and also temporal scale into account, as they are expected to influence study outcomes (van der Plas et al. 2013). We conclude that considering the local interplay environmental (e.g., pedological) factors, and their variation at the landscape scale, is essential for a comprehensive understanding of the influence of termite mounds on savanna vegetation heterogeneity.

Supporting Information

Table II.6 Pearson's correlation coefficient *r* between DCA axis scores and measured soil parameters of savanna and mound plots in Pendjari National Park. n: sample size for each plot type and soil parameter; n.s.: not significant ($P \geq 0.05$) after Bonferroni correction; –: not detected in samples.

	Savanna								Mound							
	DCA1				DCA2				DCA1				DCA2			
	r	n	t	p	*r*	n	t	p	*r*	n	t	p	*r*	n	t	p
pH_{H_2O}	-0.498	59	-4.332	0.006	-0.063	59	-0.477	n.s.	-0.174	59	-1.332	n.s.	-0.289	59	-2.281	n.s.
Conductivity [μS/cm]	-0.122	59	-0.932	n.s.	0.116	59	0.878	n.s.	0.139	58	1.047	n.s.	-0.395	58	-3.214	n.s.
P_{av}[%]	0.056	59	0.425	n.s.	-0.046	59	-0.347	n.s.	0.098	59	0.743	n.s.	-0.268	59	-2.098	n.s.
K_{av}[%]	-0.177	59	-1.358	n.s.	0.130	59	0.987	n.s.	0.096	59	0.724	n.s.	-0.261	59	-2.045	n.s.
Carbon [%]	-0.171	59	-1.307	n.s.	0.426	59	3.556	n.s.	0.260	59	2.032	n.s.	-0.312	59	-2.477	n.s.
Nitrogen [%]	-0.033	59	-0.248	n.s.	0.297	59	2.345	n.s.	0.216	59	1.671	n.s.	-0.321	59	-2.561	n.s.
C/N ratio	-0.268	59	-2.098	n.s.	0.248	59	1.934	n.s.	0.042	59	0.319	n.s.	-0.035	59	-0.262	n.s.
Carbonates [%]	–	59	–	–	–	59	–	–	-0.283	59	-2.227	n.s.	-0.227	59	-1.758	n.s.
Organic subst. [%]	-0.096	35	-0.554	n.s.	0.278	35	1.660	n.s.	0.548	35	3.762	n.s.	-0.013	35	-0.077	n.s.
Na^+[mmol$_c$/kg]	0.594	35	4.242	0.015	-0.104	35	-0.602	n.s.	0.407	35	2.558	n.s.	-0.324	35	-1.967	n.s.
K^+[mmol$_c$/kg]	-0.021	35	-0.120	n.s.	0.357	35	2.196	n.s.	0.251	35	1.491	n.s.	-0.044	35	-0.250	n.s.
Ca^{2+}[mmol$_c$/kg]	-0.210	35	-1.235	n.s.	0.359	35	2.211	n.s.	0.576	35	4.047	0.027	-0.027	35	-0.154	n.s.
Mg^{2+}[mmol$_c$/kg]	0.043	35	0.247	n.s.	0.282	35	1.687	n.s.	0.548	35	3.767	n.s.	0.005	35	0.028	n.s.
CEC_{pot}[mmol$_c$/kg]	-0.056	35	-0.321	n.s.	0.447	35	2.871	n.s.	0.588	35	4.179	0.019	-0.036	35	-0.205	n.s.
S value [mmol$_c$/kg]	-0.140	35	-0.811	n.s.	0.357	35	2.193	n.s.	0.588	35	4.172	0.019	-0.024	35	-0.137	n.s.
V value [%]	-0.175	35	-1.022	n.s.	-0.180	35	-1.050	n.s.	0.274	35	1.637	n.s.	-0.077	35	-0.441	n.s.
Coarse sand$_{630–2000\mu m}$[%]	-0.678	35	-5.293	0.001	-0.100	35	-0.575	n.s.	-0.740	35	-6.317	< 0.001	0.235	35	1.391	n.s.
Medium sand$_{200–630\mu m}$[%]	-0.597	35	-4.271	0.014	-0.461	35	-2.985	n.s.	-0.782	35	-7.219	< 0.001	-0.081	35	-0.465	n.s.
Fine sand$_{63–200\mu m}$[%]	-0.138	35	-0.803	n.s.	-0.218	35	-1.286	n.s.	0.168	35	0.979	n.s.	-0.202	35	-1.185	n.s.
Coarse silt$_{20–63\mu m}$[%]	0.613	35	4.462	0.008	0.405	35	2.546	n.s.	0.667	35	5.149	0.001	0.016	35	0.092	n.s.
Medium silt$_{6.3–20\mu m}$[%]	0.632	35	4.682	0.004	0.231	35	1.367	n.s.	0.144	35	0.836	n.s.	-0.146	35	-0.850	n.s.
Fine silt$_{2–6.3\mu m}$[%]	0.327	35	1.985	n.s.	0.063	35	0.365	n.s.	-0.348	35	-2.129	n.s.	-0.146	35	-0.847	n.s.
PSD $\sum$ sand [%]	-0.711	35	-5.800	< 0.001	-0.365	35	-2.255	n.s.	-0.708	35	-5.754	< 0.001	-0.021	35	-0.120	n.s.
PSD $\sum$ silt [%]	0.702	35	5.660	< 0.001	0.390	35	2.430	n.s.	0.676	35	5.273	0.001	-0.059	35	-0.340	n.s.
PSD $\sum$ clay$_{<2\mu m}$[%]	0.318	35	1.925	n.s.	0.081	35	0.465	n.s.	0.259	35	1.541	n.s.	0.090	35	0.517	n.s.

Table II.7 Pearson's correlation coefficient *r* between the first (constrained) CCA axis scores and measured soil parameters for plots in four savanna types (*Detarium*, *Crossopteryx*, *Terminalia*, *Mitragyna* savanna) in Pendjari National Park. Parameters shown have at least one significant correlation after Bonferroni correction. n: sample size for each plot type and soil parameter; n.s.: not significant at $P \leq 0.05$; –: not detected in samples.

	Detarium CCA1				*Crossopteryx* CCA1				*Terminalia* CCA1				*Mitragyna* CCA1			
	r	n	t	p	*r*	n	t	p	*r*	n	t	p	*r*	n	t	p
pH_{H_2O}	0.746	26	5.488	0.001	0.760	48	7.940	< 0.001	0.854	20	6.978	< 0.001	0.707	24	4.689	0.005
Conductivity [μS/cm]	0.767	26	5.849	< 0.001	0.729	47	7.151	< 0.001	0.743	20	4.713	0.008	0.900	24	9.683	< 0.001
P_{av}[%]	0.723	26	5.130	0.001	0.746	48	7.591	< 0.001	0.715	20	4.338	0.017	0.842	24	7.313	< 0.001
Carbonates [%]	–	26	–	n.s.	0.286	48	2.025	n.s.	0.753	20	4.854	0.006	–	24	–	n.s.
K^+[mmol$_c$/kg]	0.652	14	2.980	n.s.	0.733	22	4.815	0.004	0.679	20	3.927	0.040	0.828	14	5.117	0.011
Ca^{2+}[mmol$_c$/kg]	0.582	14	2.480	n.s.	0.750	22	5.065	0.002	0.579	20	3.016	n.s.	0.780	14	4.323	0.042
Mg^{2+}[mmol$_c$/kg]	0.495	14	1.973	n.s.	0.751	22	5.079	0.002	0.542	20	2.737	n.s.	0.719	14	3.583	n.s.
CEC_{pot}[mmol$_c$/kg]	0.041	14	0.142	n.s.	0.720	22	4.637	0.006	0.422	20	1.972	n.s.	0.662	14	3.062	n.s.
S value [mmol$_c$/kg]	0.613	14	2.687	n.s.	0.779	22	5.549	0.001	0.603	20	3.203	n.s.	0.789	14	4.449	0.034
V value [%]	0.881	14	6.452	0.001	0.829	22	6.634	< 0.001	0.706	20	4.231	0.021	0.724	14	3.636	n.s.
Medium sand$_{200–630\mu m}$[%]	-0.544	14	-2.246	n.s.	-0.250	22	-1.153	n.s.	-0.737	20	-4.628	0.009	-0.169	14	-0.593	n.s.
Fine sand$_{63–200\mu m}$[%]	0.079	14	0.273	n.s.	-0.282	22	-1.316	n.s.	-0.816	20	-5.980	0.001	-0.104	14	-0.362	n.s.
Fine silt$_{2–6.3\mu m}$[%]	-0.117	14	-0.409	n.s.	0.334	22	1.584	n.s.	0.742	20	4.702	0.008	-0.115	14	-0.402	n.s.
PSD $\sum$clay$_{<2\mu m}$[%]	0.595	14	2.566	n.s.	0.719	22	4.632	0.006	0.718	20	4.371	0.016	0.537	14	2.207	n.s.

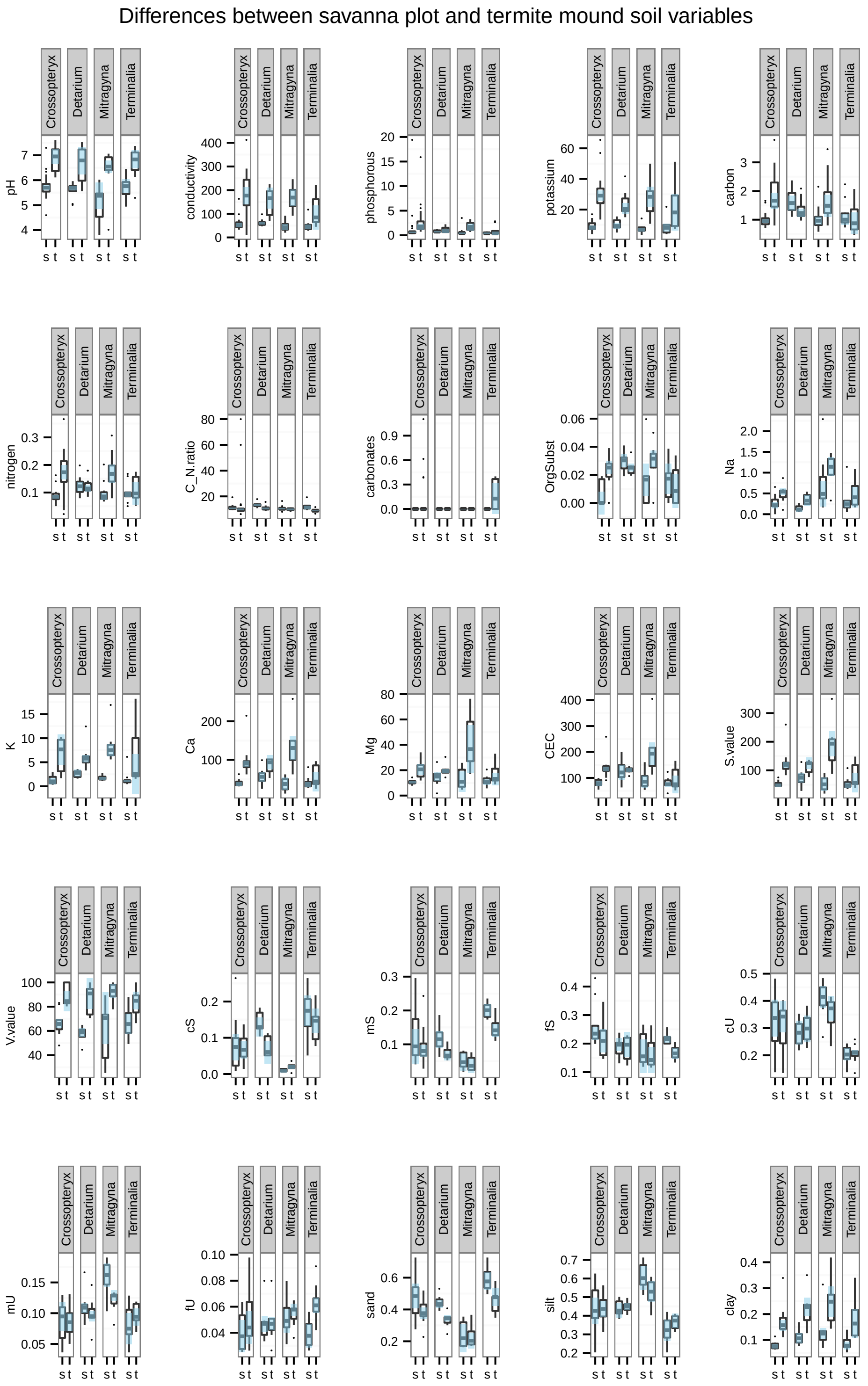

Figure II.5 Boxplots showing how differences in soil composition between termite mound (t) and savanna (s) plots vary with savanna type. Blue overlays show confidence intervals for measurements.

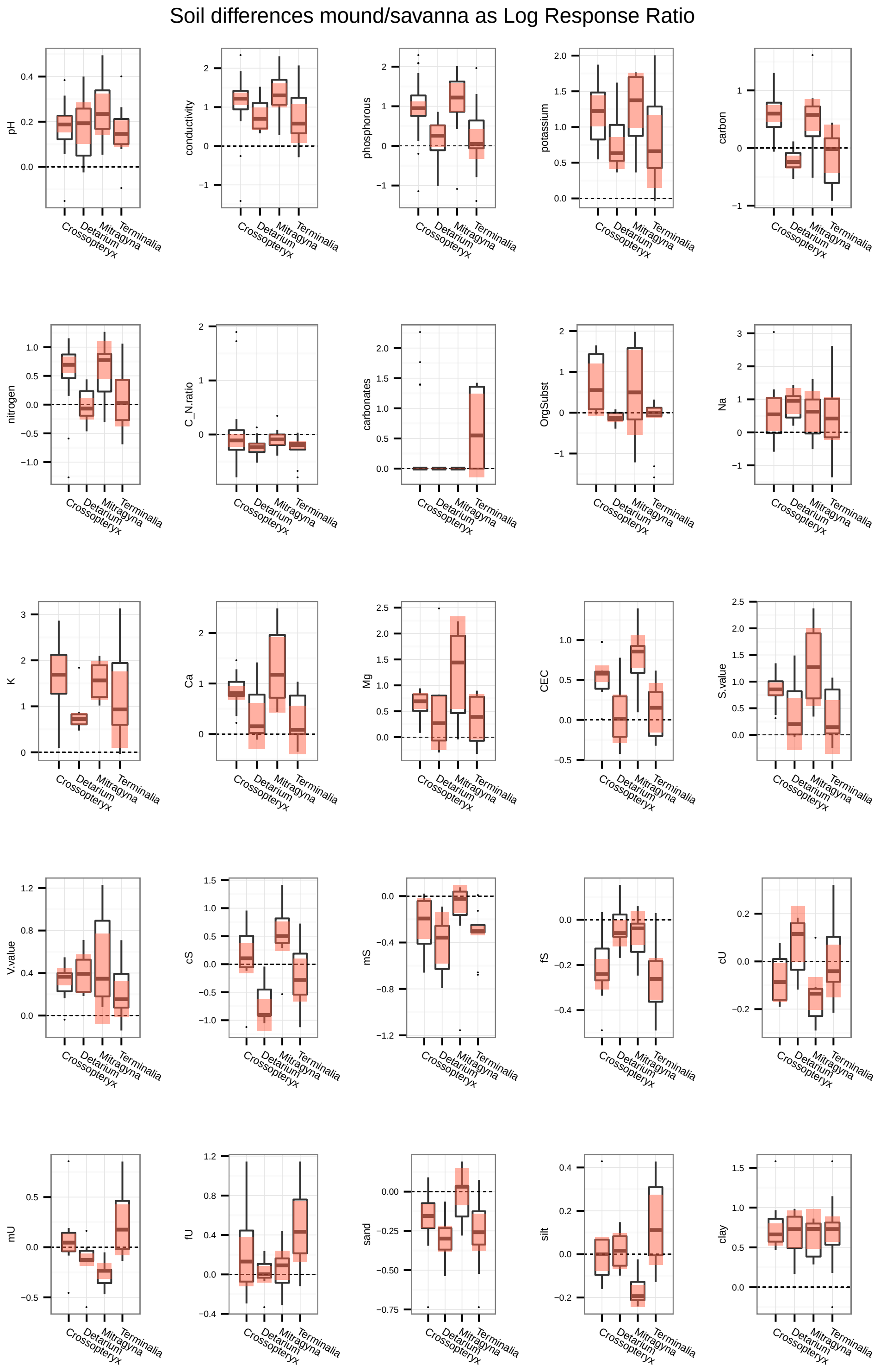

Figure II.6 Boxplots showing how differences in soil composition between mound and savanna plots vary with savanna type. Differences in soil composition are given as log response ratios. Red overlays indicate confidence intervals. Values above the dashed lines indicate higher values on mound plots; values below the dashed lines indicate higher values on savanna plots.

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Anlage 1

Erklärung über Anteile der Autoren/Autorinnen an den einzelnen Kapiteln der Promotionsarbeit

Titel der Publikation/ des Manuskripts:

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

Was hat der/die Promovierende bzw. was haben die Co-Autoren/Autorinnen beigetragen[#]	Name des/der jeweiligen Autors/Autoren/Autorin*
(1) Entwicklung und Planung AE (60%) and KH (40%) conceived and designed this study.	Arne Erpenbach, Karen Hahn
(2) Durchführung der einzelnen Untersuchungen/ Experimente AE conducted the fieldwork.	Arne Erpenbach
(3) Erstellung der Daten-sammlung und Abbildungen AE processed and analysed the data, and created all figures and tables.	Arne Erpenbach
(4) Analyse/Interpretation der Daten AE analysed and interpreted the data (80%). KH contributed to the interpretation of the data (20%).	Arne Erpenbach, Karen Hahn
(5) übergeordnete Einleitung/ Ergebnisse/Diskussion AE wrote the manuscript (80%), all authors commented equally on the manuscript.	Arne Erpenbach, Karen Hahn, Rüdiger Wittig

[#] Bei 2, 3 und 4 bitte kurze inhaltliche Angaben der jeweiligen Anteile, bei 1 und 5 reichen prozentuale Angaben

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III

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

Abstract

Termites are keystone species in savanna ecology, and their mounds are thought to be an important source of habitat heterogeneity and structural complexity of the savanna. *Macrotermes* termitaria have been shown to allow woody plant colonisation of landscapes otherwise dominated by C_4 grasses. In this study, we assess how resource-rich *Macrotermes* mounds affect juvenile woody plant and non-woody plant species diversity, community composition, biomass and population dynamics. We repeatedly sampled paired termite mound and savanna plots in Pendjari National Park (Sudanian vegetation zone, North Benin, West Africa) over the course of two years. Despite considerable overlap in their species pools, plant communities of mound and savanna plots were clearly separated in ordinations. Species richness and diversity of juvenile woody plants was consistently higher on termite mounds, while no differences could be detected for non-woody plants. Evenness of juvenile woody plants was generally lower on mounds, whereas density and basal area were higher on mounds. In contrast, we did not detect any influence of the mound microhabitat on colonisation, mortality and turnover of woody juveniles.

AE and KH conceived and designed this study. AE conducted the fieldwork, analysed and interpreted the data, and wrote the manuscript. KH contributed to the interpretation of the data, and all authors commented on the manuscript.

Therefore, we suggest that differences in the communities on and off mounds should be strongly influenced by directed diaspore dispersal through zoochory.

Introduction

Savanna systems occupy a large proportion of the global landmass (Sankaran et al. 2005). They are thought to be shaped by competition of woody plants and grasses for limiting resources, such as water and nutrients (Scholes and Archer 1997; Sankaran et al. 2005). Further factors affecting the dynamics of savanna vegetation include an interplay of climate, fire, and large herbivores (Bond 2008; Sankaran et al. 2008; Staver et al. 2011; Lehmann et al. 2014). It has long been suggested that termite mounds are key elements of woody plant establishment in savanna habitats (Troll 1936; Cole 1963), and thus contribute to defining the character of the savanna landscape. However, few studies so far have addressed recruitment and dynamics of juvenile woody plants on termite mounds as compared to the surrounding savanna. Recently, emphasis has been renewed that further studies are needed to understand the role of termite mounds in the process of woody plant establishment in savannas (Sileshi et al. 2010). New insights in this regard could also be beneficial to a better understanding of bush encroachment, which can be observed in many open savanna habitats worldwide (Sileshi et al. 2010).

Available evidence suggests that woody plants establish preferably on termite mounds (Cole 1963; Blösch 2008), and that their communities are shaped by fire and wildstock grazing. For instance, a recent study from East Africa showed higher densities of juvenile woody plants on termite mounds (Støen et al. 2013). Higher seedling densities on mounds have also been reported for West Africa (Traoré et al. 2008b), where at the same time strong temporal and seasonal variation of juvenile mortality was observed. Although a few studies on juvenile mound vegetation thus exist, the establishment, growth and mortality of juvenile woody plants on mounds compared to the surrounding savanna is overall poorly understood.

The aim of this study was to collect more data on vegetation dynamics on termite mounds, with a strong focus on juvenile woody plants. We contrasted data of juvenile woody plants against non-woody plants (including graminoids, geophytes, hemicryptophytes, and also semi-woody forbs and subshrubs) as their direct competitors. Our analysis was guided by several hypotheses related to differences in community composition and population dynamics between mounds and savannas. We expected (1) that plant communities on mounds are more diverse, and specifically show a higher within-group β-diversity than the surrounding savanna; and (2) that due to differences in mortality, colonisation, and diameter gain juvenile woody plants feature higher overall abundance, density, and biomass on termite mounds than in the surrounding savanna. All these factors should lead to a difference in woody plant species composition between mounds and savannas, as reported in many studies (Jackson and Gartlan 1965; Moe et al. 2009; Sileshi et al. 2010; Joseph et al. 2013a, 2014; van der Plas et al. 2013). We furthermore expected that soil characteristics would differ between mounds and savannas and could be used to explain the results regarding the hypotheses on diversity, abundance, biomass, and mortality. Moreover, we assumed that dispersal mode should affect woody plant establishment on mounds. Within the communities of juvenile plants, we expected animal-dispersed plants and plants with a mixed dispersal mode to be overrepresented on mounds compared to the surrounding savanna.

Material and Methods

Study area

We conducted our study in Pendjari National Park (PNP), North Benin (10° 30′–11° 30′N, 0° 50′–2° 00′E), in the vicinity of a permanent plot of the BIOTA West Africa project. PNP is situated at the limit of the North Sudanian Vegetation Zone (White 1983). In a paired plot design, we sampled twelve termite mounds and twelve corresponding savanna plots. The sampling sites were situated in an alluvial landscape on sceletic soil based on tillites. The area is dominated by *Terminalia avicennioides* and *Burkea africana* in the tree layer. The park area is under an annual early burning regime prescribed by its conservation authorities.

Sampling

For our sampling, we chose mound plots randomly and approximated their size by multiplying the longest diameter of each termite mound with its perpendicular axis diameter. Corresponding savanna plots of the same size as the paired mound plots were placed 15 m north of the mound plots, to minimize influence of termite activity (Levick et al. 2010; Okullo and Moe 2012a,b). Mound size varied between 5.5 m^2 and 37.7 m^2 (mean: 22.3 m^2 ± 8.0 SD). The average height of termite mounds was 1.5 m ± 0.5 SD. Vegetation data were recorded in four subsequent sampling periods in 2008 and 2009 at the beginning (end of May) and the end of the rainy season (end of October), respectively. Using these four samplings, we aimed at following individual plants over time to investigate juvenile dynamics. Nomenclature followed the African Plants Database (2014; http://www.ville-ge.ch/musinfo/bd/cjb/africa).

We considered woody plants with basal diameters < 5 cm as juveniles. We calculated diversity indices for each plot, including species richness for non-woody plants, and species richness, inverse Simpson index and evenness E_{var} after Smith and Wilson (1996) for juvenile woody plants. Furthermore, we estimated plant cover for all species present and recorded abundances and basal diameters of juvenile woody plants. We used the basal area for each individual as a proxy measure for juvenile biomass. Many individuals consisted of multiple stems, and while the identity of stems could not be ensured between two samplings, great care was taken to attribute stems to a particular individual. We measured colonisation as the number of plantlets emerging in a sampling that had not been present in the previous census. Mortality rate was calculated as the proportion of individuals that disappeared between two samplings, after excluding newly recruited individuals. Colonisation and mortality combined were treated as overall turnover between samplings. In addition to our field measurements, we compiled information on life form and dispersal type for each species present from the literature (Guinko 1984; Hovestadt 1997; Hovestadt et al. 1999; Aké Assi 2001). We sampled soil of both mounds and the surrounding savanna. Mound soil was sampled on the mound slope 1 m inwards of the mound's pediment limit (perceived as the outer limit of any visible alluvial fan). Savanna soil was sampled in 15 m distance to the mound's limit. To account for micro-scale heterogeneity, we pooled four topsoil subsamples of 10 cm^3 for each plot. Soil samples were air-dried and sieved to < 2 mm prior to analysis. Concentrations of plant-available phosphorus (P_2O_{5av}), plant-available potassium (K_2O_{av}), organic and inorganic carbon, nitrogen, as well as pH and conductivity were determined. Additionally, we determined potential cation exchange capacity (CEC_{pot}, with ion concentrations of sodium, potassium, calcium, and magnesium) and particle size distribution (PSD, as percentage of the sand, silt, and clay fractions).

Statistical analysis

We calculated species accumulation curves to ascertain if our sample was representative for the local species pool. Differences in species richness, diversity, and evenness between plot types (mound/savanna) and samplings (1-4) were analysed using Wilcoxon matched-pairs signed-rank tests. Further Wilcoxon matched-pairs signed-rank tests were used to assess differences in basal area, number of individuals and stems, mortality, colonisation and turnover rates, and dispersal modes of juvenile woody plant species between mounds and savannas. Differences in soil composition were analysed using paired Wilcoxon rank sum tests. When multiple tests were performed, we corrected probability values with Benjamini & Hochberg correction (Benjamini and Hochberg 1995) to account for the higher probability of Type I errors.

To examine β-diversity on plot community level, we used constrained distance-based analysis of principal coordinates (CAP, or constrained db-RDA). CAP allows linear and metrical analysis, while non-Euclidian distance metrics can be applied for the ordination (Anderson and Willis 2003). Using abundance data for juvenile woody plants, we calculated Bray-Curtis distances among all plots as a basis for further analysis. To account for pseudoreplication, we used repeated samplings as a conditioning factor. When analysing non-woody communities, we used Whittaker's β_W on presence/absence data as a distance measure among plots. Whittaker's β_W is eqivalent to Bray-Curtis distances for presence/absence data, and a dissimilarity analogon to Sørensen similarities. Blocked multiple response permutation procedure (MRPP) with permutations restricted by samplings was used to test for differences in mean β-diversity between plot types (Mielke and Berry 2001; McCune and Grace 2002). MRPP calculates the overall weighted mean of group mean distances δ for the original data set, and for permuted data. The expected delta Eδ is the mean of original dissimilarities (assuming no structure in groups). MRPP does not require normal distribution and is sensitive to both location and spread of the groups. All statistical analyses were performed with R 3.1.1 (R Development Core Team 2014), using the package *vegan* 2.0.10 (Oksanen et al. 2013).

Results

In our 24 plots, we recorded a total of 227 plant species from 55 families. On mounds, we found 173 species, and in the paired savanna plots we recorded 162 species. Mounds

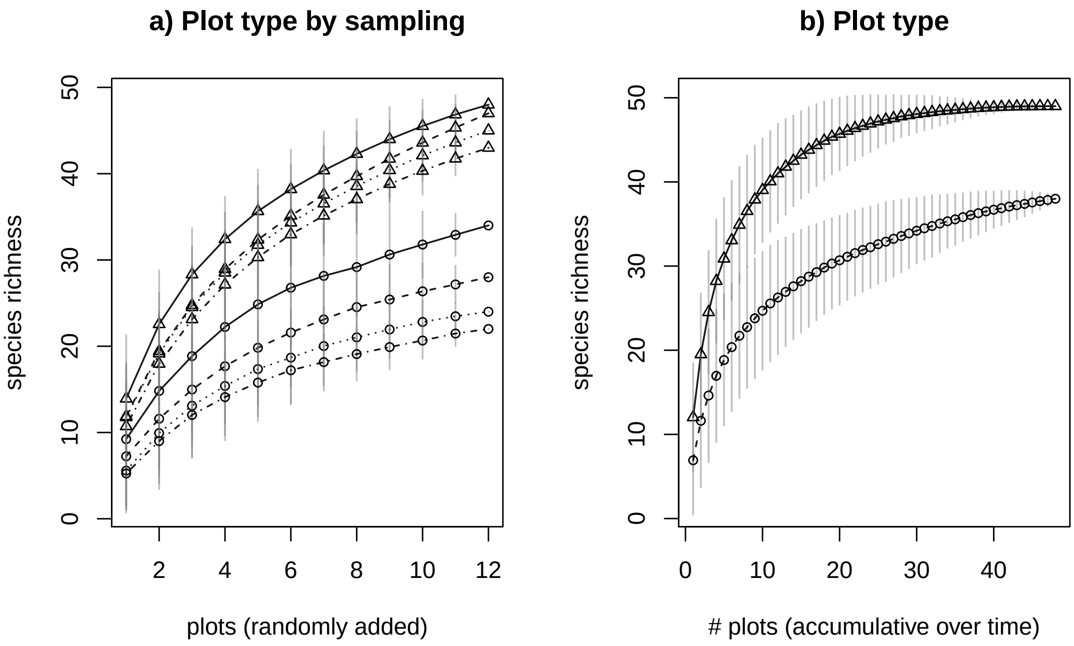

Figure III.1 Species accumulation curves (SAC) for mound and savanna plots. a) SAC per sampling for each plot type; b) SAC for each plot type, accumulative samples over time. △: mounds, ○: savannas, vertical lines represent 95% confidence interval for each SAC.

and savannas had 108 (48%) species in common, while 65 species were exclusively found on mounds (29%, from 31 families), and 54 species (24%, from 17 families) were only found in the adjacent savanna. Considering juvenile woody plants only, we found 57 species from 24 families in our plots (Supporting Information Table III.6), with 49 species on mounds, and 38 species in the paired savanna plots. Mounds and savannas had 30 species of juvenile woody plants in common (53%). We found 19 juvenile woody species from 14 families which were exclusive to mounds, while only eight of the juvenile woody species (from six families) were exclusive to the savanna plots. Species accumulation curves (Figure III.1) indicated sufficient sampling per plot type, and over time. In all four samplings, species richness and diversity were significantly higher on termite mounds than in the surrounding savannas (Wilcoxon rank sum test: $P < 0.05$, Figure III.2, Table III.1). Evenness was significantly higher in savannas than on mounds in the first two samplings.

Overall, very few species occurred frequently, i.e. on many plots. Among both woody plantlets and non-woody plants, the most frequently found species occurred in either plot type (Figure III.3). In contrast, species restricted to one particular plot type were par-

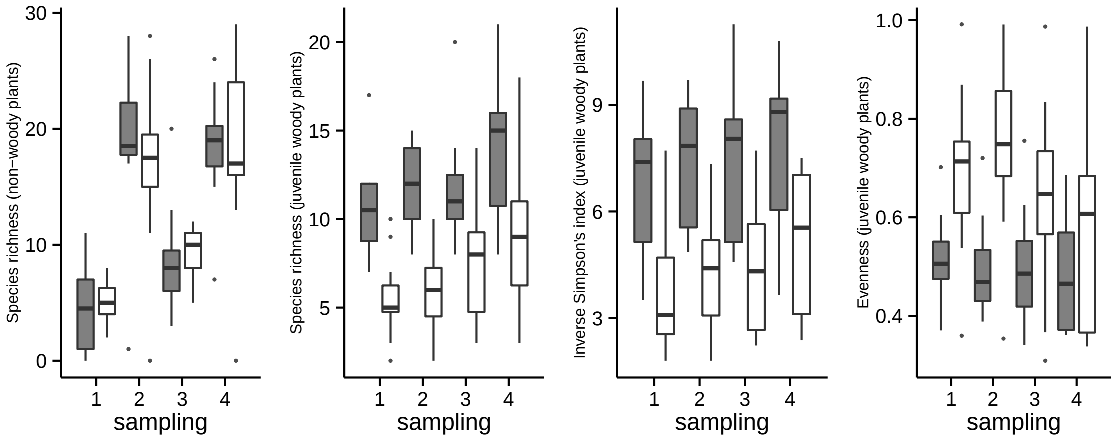

Figure III.2 Diversity of non-woody and juvenile woody plants on termite mounds (n = 12, dark grey boxes) and savanna plots (n = 12, white boxes) by sampling. For woody juveniles, differences between mounds and savannas are significant ($P < 0.05$), except for evenness in the third and fourth sampling period (Wilcoxon matched-pairs signed-rank test).

ticularly infrequent. Of the species exclusive to mounds, only four non-woody and four woody species were found to be present at more than four of the sampled termite mounds over the whole sampling period. No species exclusive to the savanna was recorded in more than three of the savanna plots. The most frequent juvenile woody species exclusive to mounds (*Clausena anisata*, *Feretia apodanthera*, *Grewia lasiodiscus*) occurred on six of the mounds each, the most frequent juvenile woody species exclusive to savannas (*Pteleopsis suberosa*) was found only in three savanna plots.

During our four sampling periods, we measured the basal area of 859 plant individuals on and off mounds. As most individuals showed more than one stem, we collected a total of 9382 stem measurements over time. Over the whole sampling period, the total number of individuals as well as the total number of stems and total basal area of juvenile woody plants was constantly and significantly higher on mounds than in the savanna plots between plot pairs (Table III.2). With one minor exception, all figures increased over time. Only the number of individuals in savanna plots at the second sampling was one individual less than at the previous sampling. Mortality was not significantly different between mound and savanna plot pairs, and neither between samplings nor over the whole sampling period. Colonisation, and therefore also overall turnover, were also not significantly different between plot pairs (Table III.3).

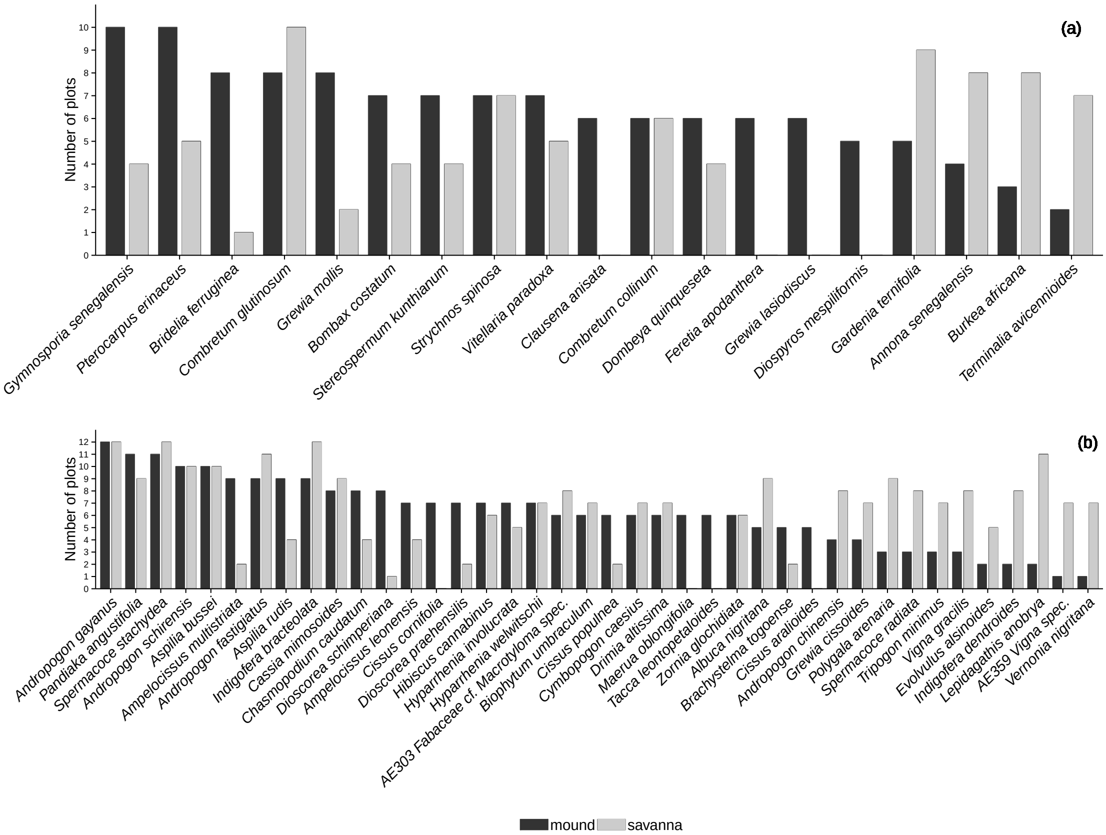

Figure III.3 Frequency of plant species, i.e. number of plots where a species was recorded on termite mounds (n=12) and savanna plots (n=12). (a) woody species, (b) non-woody species (herbaceous plants including graminoids, geophytes, hemicryptophytes, forbs and sub-shrubs). Only species present at more than four plots are included.

Table III.1 Species richness of non-woody plants (herbaceous plants including graminoids, geophytes, hemicryptophytes, forbs and subshrubs) and species richness, inverse Simpson index and evenness of juvenile woody plants on mound and savanna plots. Given are mean and standard deviation across plots for each of the four sampling times. Statistical values Z and P are derived from Wilcoxon matched-pairs signed-rank tests with Benjamini & Hochberg adjustment.

			Mound		Savanna			
		Sampling	Mean	SD	Mean	SD	Z	P value
non-woody plants	species richness	1	4.42	3.63	4.92	1.88	-0.56	0.577
		2	18.83	6.53	17.17	7.13	1.12	0.262
		3	8.83	4.37	9.17	2.17	-0.88	0.381
		4	18.50	4.80	18.25	7.51	0.30	0.760
woody plants	species richness	1	10.58	2.71	5.58	2.27	3.05	0.004
		2	11.83	2.25	5.75	2.34	3.19	0.004
		3	11.75	3.17	7.58	3.29	2.94	0.004
		4	13.92	3.75	8.92	4.19	2.68	0.007
	inverse Simpson index	1	6.73	1.92	3.89	1.89	2.88	0.005
		2	7.41	1.81	4.23	1.56	2.98	0.005
		3	7.23	2.16	4.46	1.92	3.05	0.005
		4	7.76	2.40	5.07	2.11	2.73	0.006
	evenness	1	0.51	0.09	0.69	0.16	-2.95	0.007
		2	0.49	0.10	0.75	0.18	-2.91	0.007
		3	0.49	0.12	0.64	0.19	-2.12	0.045
		4	0.47	0.11	0.59	0.22	-1.19	0.232

Community composition of juvenile woody plants differed between mounds and surrounding savanna plots, as indicated by CAP (Figure III.4a). Although the first axis for all plant species covered only 7.38% of the total variability of the juveniles dataset, groups were clearly separated. This was underlined by the MRPP analysis, which showed a significant, albeit small difference between the groups with a slightly lower mean β-diversity for termite mounds (effect size A = 0.06, δ = 0.75, Eδ = 0.8, p = 0.001, permutations = 999). CAP of presence-absence data for non-woody plants also showed mound and savanna groups (Figure III.4b). The first axis covered 4.41% of the total variability of the dataset. MRPP showed a significant difference in β-diversity for the groups with a slightly higher mean for termite mounds (effect size A = 0.03, δ = 0.79, Eδ = 0.81, p = 0.001, permutations = 999).

A comparison of dispersal modes between the communities showed significantly more animal-dispersed species on mounds (Figure III.5, Wilcoxon matched-pairs signed-rank test, adjusted $p < 0.05$ for each sampling, Table III.4), while both mixed dispersal mode and wind dispersal showed no significant differences between mound and savanna plots.

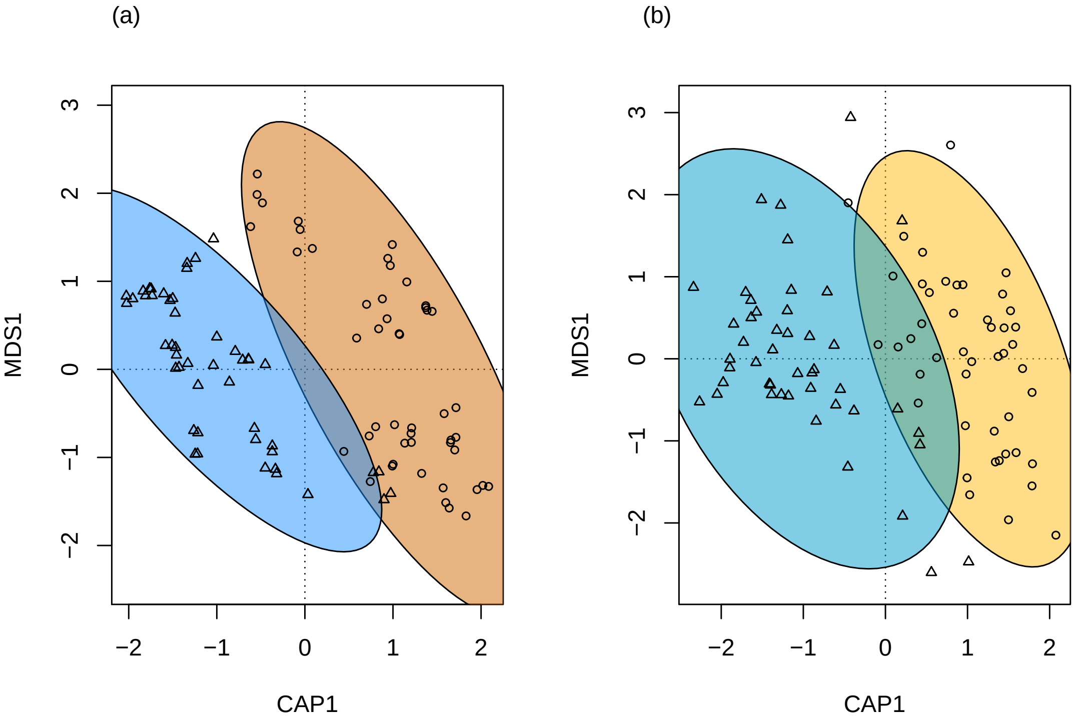

Figure III.4 Distance-based principal coordinate analysis for communities, constrained by plot type, (a) using Bray-Curtis distances on juvenile woody plants abundance data; (b) using Whittaker's β_w on non-woody species presence/absence data. △: mounds, ○: savannas, ellipses mark the 95% confidence interval for each group.

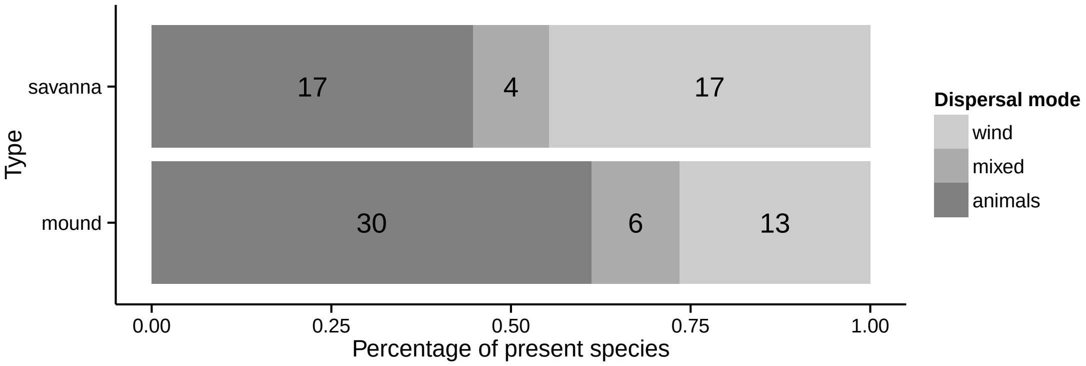

Figure III.5 Distribution of dispersal modes of juvenile woody plants on mound and savanna plots over all samplings. Numbers in the graph indicate the species count per dispersal mode according to the legend.

Table III.2 Basal area (cm^2), number of individuals and number of stems of juvenile woody plants on mound and savanna plots. Given are mean and standard deviation across plots for each of the four sampling times. Statistical values Z and P are derived from Wilcoxon matched-pairs signed-rank tests with Benjamini & Hochberg adjustment.

		Mound		Savanna			
	Sampling	Mean	SD	Mean	SD	Z	P value
basal area	1	41.31	22.68	24.12	26.65	2.98	0.012
	2	59.52	32.16	28.49	26.52	2.94	0.012
	3	44.55	27.02	26.83	32.35	2.49	0.025
	4	87.79	43.89	41.52	38.11	2.40	0.025
number of individuals	1	22.17	9.52	12.50	5.99	2.98	0.012
	2	27.50	11.83	12.42	6.22	2.94	0.012
	3	28.08	12.92	19.42	11.33	2.49	0.025
	4	35.50	15.75	24.67	16.71	2.40	0.025
number of stems	1	93.83	77.58	27.00	15.77	2.98	0.012
	2	133.50	132.49	37.92	17.72	2.94	0.012
	3	138.42	121.45	56.08	33.44	2.49	0.025
	4	222.33	283.97	72.75	45.77	2.40	0.025

With respect to soil composition, termite mounds showed significant differences from the surrounding savannas (Figure III.6, Table III.5). Physico-chemical analysis revealed that mound topsoil contained more plant-available potassium than savanna topsoil, and was enriched in clay. While the content of carbon and nitrogen did not differ significantly between mounds and savanna, the C:N ratio was significantly higher in savannas. Base saturation and base concentration were also significantly higher on mounds. Carbonates were absent in savanna soils, but present in mounds where they could in some cases already be detected visually as small carbonate-rich nodules.

Discussion

In this study, we used a repeated number of censuses and diameter measurements to gain more insight into patterns and processes within the community of juvenile woody plants and non-woody plants on and off termite mounds. While several of our hypotheses were confirmed, others had to be rejected or could not be adequately tested.

Biodiversity patterns

As expected, overall plant species richness and family richness were distinctly higher on mounds. Higher species richness on mounds was already reported in several studies

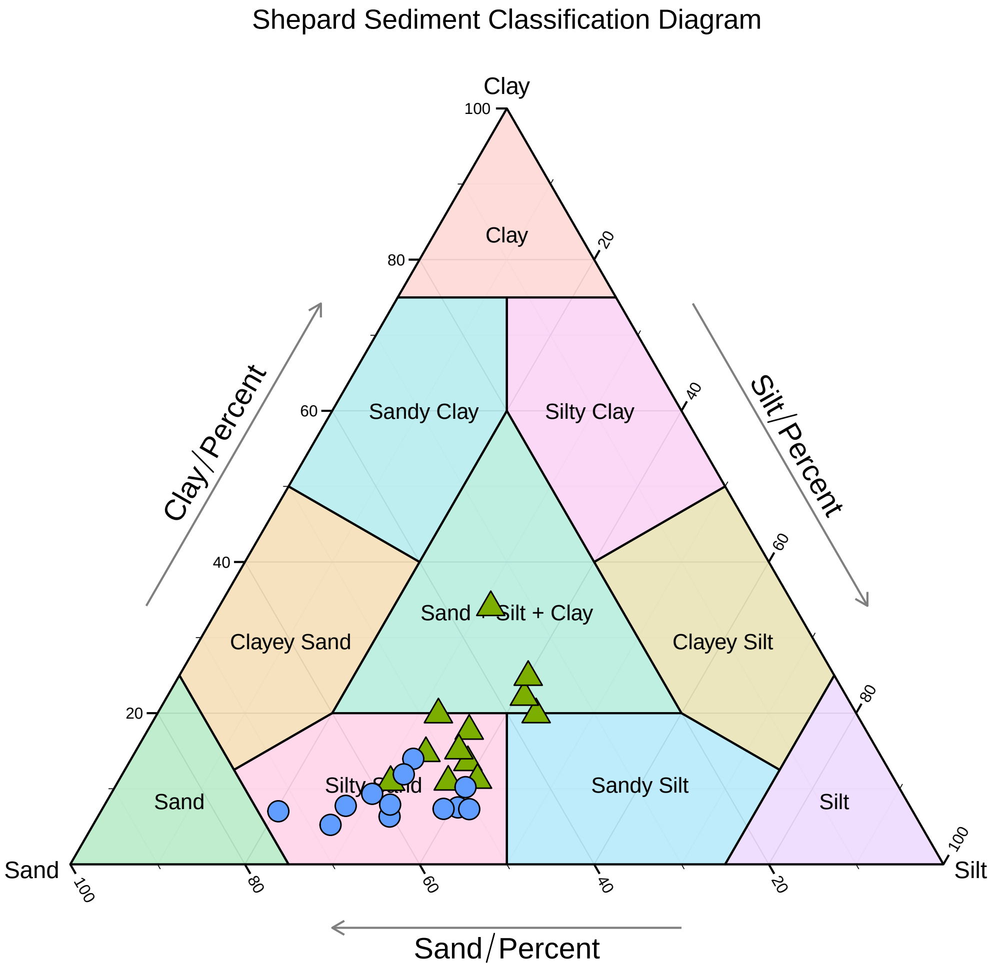

Figure III.6 Shepard diagram of termite mound and savanna plot soil samples. Mounds were characterized by higher clay content than the surrounding savanna plots. △: mounds, ○: savannas.

Table III.3 Mortality rate, colonisation rate and turnover rate of juvenile woody plants on mound and savanna plots. Given are mean and standard deviation across plots for each of the four sampling times. Statistical values Z and P are derived from Wilcoxon matched-pairs signed-rank tests with Benjamini & Hochberg adjustment.

		Mound		Savanna			
	Sampling	Mean	SD	Mean	SD	Z	P value
mortality	1-2	0.07	0.14	0.18	0.34	-0.29	0.772
	2-3	0.08	0.09	0.28	0.22	-2.07	0.096
	3-4	0.06	0.07	0.02	0.05	1.98	0.096
	1-4	0.05	0.09	0.16	0.27	-1.06	0.383
colonisation	1-2	0.20	0.16	0.30	0.34	0.07	0.941
	2-3	0.14	0.12	0.29	0.29	-0.88	0.918
	3-4	0.21	0.14	0.24	0.19	-0.40	0.918
	1-4	0.35	0.21	0.43	0.34	-0.68	0.918
turnover	1-2	0.16	0.11	0.26	0.33	0.14	0.891
	2-3	0.11	0.10	0.32	0.21	-2.17	0.120
	3-4	0.15	0.10	0.15	0.13	0.47	0.854
	1-4	0.25	0.15	0.36	0.28	-0.78	0.854

from our study region (Traoré et al. 2008a; Kirchmair et al. 2012; Erpenbach et al. 2013). Comparing paired plots, we detected higher species richness and diversity of juvenile woody plants on mounds than on the adjacent savanna plots (Figures III.1 & III.2, Table III.1). Higher plant species richness and diversity on mounds could be explained by several factors. First, termite mounds offer a more favourable environment for plants by providing higher nutrient and moisture availability in an otherwise deficient ecosystem (Adamson 1943; Konaté et al. 1999; Jouquet et al. 2006; Sileshi et al. 2010), which was also confirmed by our soil analysis. Second, mounds offer some degree of shelter and protection from disturbance such as fire and flooding (Lawson and Jenik 1967; McCarthy et al. 1998; Dean et al. 1999; Blösch 2008; Joseph et al. 2013b), which on one hand can be a direct effect of termite activity due to slight elevation above the surrounding surface and a sparsely vegetated pediment around the mound base. On the other hand, it can also be an indirect effect due to less available fuel, i.e. less dry herbaceous, and more lush woody biomass, on mounds. Third, higher small-scale heterogeneity in soil and microclimatic conditions on mounds should promote the coexistence of plant species with different habitat requirements (compare, e.g., Moe et al. 2009; Sileshi and Arshad 2012, and also more generally Moeslund et al. 2013 and Stein and Kreft 2014). All these conditions enable the occurrence of species on mounds that may otherwise be discriminated against in the savanna by environmental stressors and competition.

Table III.4 Dispersal mode differences in communities of mound and savanna plots, for each of the four samplings. Statistical values for Wilcoxon matched-pairs signed-rank tests, with Benjamini & Hochberg adjustment.

		Mound		Savanna			
Dispersal	Sampling	Mean	SD	Mean	SD	Z	P Value
animals	1	6.58	1.51	2.73	1.85	3.51	< 0.001
animals	2	7.42	1.73	2.42	1.68	4.11	< 0.001
animals	3	7.33	1.78	4.00	2.37	3.02	0.005
animals	4	8.67	2.67	4.00	2.24	3.29	0.002
mixed	1	1.14	0.38	1.50	0.71	-1.01	0.714
mixed	2	1.12	0.35	1.50	1.00	-0.65	0.938
mixed	3	1.12	0.83	1.00	0.00	0.00	0.001
mixed	4	1.56	0.73	1.40	0.55	0.30	0.938
wind	1	3.33	1.50	2.83	0.94	0.76	0.724
wind	2	3.67	0.98	2.83	0.72	2.18	0.070
wind	3	3.67	1.50	3.67	1.07	-0.27	0.938
wind	4	4.08	1.62	4.67	1.72	-0.99	0.680

Table III.5 Mean soil physical and chemical properties of 12 termite mounds and 12 paired adjacent savanna plots in Pendjari National Park. Values in mmol/kg unless otherwise indicated. Statistical values for Wilcoxon matched-pairs signed-rank tests with Benjamini & Hochberg adjustment.

	Mound		Savanna			
	Mean	SD	Mean	SD	V	P Value
pH	6.81	0.66	5.68	0.38	76.0	0.004
P_2O_{5av}	1.12	1.18	0.45	0.14	44.5	0.092
K_2O_{av}	22.78	13.75	8.55	4.73	77.0	0.003
C	1.01	0.48	1.13	0.45	29.0	0.456
N	0.11	0.04	0.10	0.03	54.0	0.255
C:N ratio	8.81	1.26	11.82	2.63	1.0	0.003
Carbonates [%]	0.12	0.33	0.00	0.00	3.0	0.371
Organic substance [%]	1.03	1.33	1.34	1.34	11.0	0.673
CEC_{pot}	97.60	37.82	78.64	20.37	61.0	0.092
Base concentration	86.37	39.31	53.03	19.63	69.0	0.021
Base saturation [%]	86.60	12.01	67.42	12.04	73.0	0.009
K^+	6.24	5.36	1.37	1.53	77.0	0.003
Na^+	0.50	0.35	0.29	0.28	49.0	0.168
Ca^{2+}	62.85	28.25	40.15	14.64	65.0	0.045
Mg^{2+}	16.77	7.24	11.22	3.91	66.0	0.038
Sand [%]	45.14	7.50	58.38	7.18	2.0	0.004
Silt [%]	37.00	4.15	33.14	6.48	61.5	0.084
Clay [%]	17.86	6.83	8.48	2.48	76.0	0.004

Contrary to our findings (Figure III.2, Table III.1), we had expected higher evenness on mound than savanna plots based on previous studies (Moe et al. 2009; Okullo and Moe 2012a). However, the latter study only included herbaceous plants, for which evenness could not be investigated in the current analysis. Van der Plas (2013) also reported higher evenness on mounds, which was however not statistically significant when accounting for false discovery rate. In contrast, several studies also reported significantly lower evenness of mound vegetation, including woody and non-woody plants (Loveridge and Moe 2004; Kirchmair et al. 2012; Støen et al. 2013). The lower evenness on mounds that we found in our study was likely caused by frequent and abundant species, like *Gymnosporia senegalensis*, and furthermore by species which were found infrequently, but in high abundance on mounds. For example, *Pseudocedrela kotschyi* and *Afzelia africana* occurred on only a single mound each, but with a maximum of 14 and 11 individuals, respectively, for a given sampling period.

With respect to community composition, the ordinations showed a clear separation of mound and savanna communities for both woody juvenile and non-woody plants (Figure III.4). However, the community differences were less strongly pronounced as expected, which we attribute to the high number of shared frequent species (Figure III.3). Surprisingly, our hypothesis of higher β-diversity on mounds compared with savanna plots was only confirmed for non-woody plants, but not for woody plants. Accordingly, the higher overall woody plant species richness we found on mounds should be influenced mainly by higher α-diversity and not, as expected, by joint contributions of α- and β-diversity. The lower β-diversity of woody plant species on mounds compared to savanna plots implies a more frequent reoccurrence of characteristic woody plant species on mounds. This makes sense considering that the three most-frequent woody plant species exclusive to mounds occurred on six mounds each, whereas the single most-frequent species exclusive to the savanna occurred only on three plots. Moreover, this trend towards a slightly more uniform typical "termite-mound vegetation" within juvenile woody plant communities is in accordance with findings from a related study that identified mainly woody plant species as characteristic mound species across multiple sites in West Africa (Erpenbach et al. 2013). Unsurprisingly, β-diversity between mound and savanna plots was consistently higher than among-group β-diversity for both woody and non-woody plants. This goes in line with our findings of 65 exclusive mound species and 54 exclusive savanna species, including both woody and non-woody species (also compare Figure III.3).

Population dynamics

In accordance with our hypothesis, basal area of juvenile woody plants was constantly and significantly higher on mound than on savanna plots in all samplings (Table III.2). This goes in line with the higher number of individuals and higher number of stems that we found on mounds. Basal area of woody plants is often used as a proxy for biomass and productivity (Catchpole and Wheeler 1992; Vanclay 1992). We expected higher productivity on mounds, as a large number of studies has reported higher soil nutrient levels on mounds (Jouquet et al. 2006; Sileshi and Arshad 2012). Also our own soil analysis revealed a better supply with potassium and other bases, and a more favourable (i.e., in this circumstance, smaller) C:N ratio on mounds than in the savanna. More fertile soil as well as higher water storage capacity due to higher clay content should thus promote productivity on mounds, similarly to the already mentioned promotion of plant diversity. These favourable conditions could also play a role in reducing mortality on mounds, as was suggested by Moe et al. (2009). Lower mortality, higher colonisation rates or a combination of both should be responsible for the higher abundance that we found on mounds. Mean mortality was generally lower on mounds than on savanna plots, even though the difference was not statistically significant (Table III.3). Surprisingly, we neither found any significant differences in colonisation and turnover rates between mound and savanna; however, more studies with increased statistical power are needed to confirm or reject these results and understand mortality and colonisation dynamics better. We would therefore suggest to focus on a selected set of frequent and abundant species in future analyses. This would make it possible to extend the scope of further analysis to species level, and to distinguish between effects of biotic interaction among plants (e.g., density-dependent mortality, inter- and intraspecific competition) and of other influential environmental factors (e.g., fire, water availability, herbivory) on juvenile woody plants on mounds. It is likely that intraspecific density affects several species on mounds, as density-dependent mortality has already been shown for *Acacia erythrocalyx* (Traoré et al. 2008b). Moreover, not only mortality, but also species-specific biomass gain should be influenced by density as well as other mound-mediated factors. Unfortunately, in our dataset, the analysis of basal area gain as a biomass proxy was impeded. Continuous diameter measurements could only be conducted for one third of the 859 sampled individuals, due to high turnover rates and die-back of juveniles. Only four woody species were present both at more than four plots and at all four samplings, but not necessarily with the same individuals. In combination with low overall frequency and abundance of each species, this hampered an adequate testing of our hypothesis. Currently available experimental research indicates that differences in soil nutrients between mound and savanna influence neither the number of seedlings nor the growth rates of selected species (Müller 2013). However, the experiment was performed under greenhouse conditions, and soil handling might have influenced the outcome. An experimental study of two herbaceous model species found that *in situ* biomass gain was higher on mounds than in the surrounding savanna, while biomass gain was higher on potted savanna soil than handled mound soil, presumably due to soil handling (Grohmann et al. 2010). However, experimental research *in situ* is highly challenging: in an experimental approach run simultaneously to our survey presented in this study, less than 1 % of all germinated seedlings (N = 1000) in a random block design with *in situ* and *ex situ* replicates survived long enough to obtain biomass measurements. As population dynamics on mounds and their impact on plant growth and survival of seedlings and saplings remain poorly understood, further research focussing on juvenile plants is desperately needed.

Regarding dispersal modes, we found that animal-dispersed species were overrepresented in the communities of juvenile woody plants on mounds, as predicted (Figure III.5, Table III.4). In contrast, we did not detect differences in the proportion of wind-dispersed species and species with a mixed dispersal mode. It has been shown that protection from fire can lead to a prevalence of animal-dispersed colonisers in a savanna landscape (Swaine et al. 1992), and the importance of termite mounds as refugia from severe fire has recently been emphasised (Traoré et al. 2008a; Joseph et al. 2013b). Based on these findings, we would, however, expect a stronger effect of mounds as more fire-protected habitats on seedling mortality than was found in our study. We therefore suggest that directed dispersal by animals is a driving force behind the higher number of individuals and species, and also lower evenness on mounds. Due to the high structural complexity of mounds, they are attractive to animals already in an unvegetated stage. After establishment of woody plants, attractiveness should be increased through the high structural complexity of mound vegetation, which has been shown to harbour a large proportion of species with a climbing and scrambling habitus, and higher vegetation density (Moe et al. 2009; Erpenbach et al. 2013). Such structural complexity can provide shelter, thermoregulation, roosting and nesting sites, and more heterogeneous food resources (Lawton 1983). The resulting high attractiveness of mounds has been shown for various taxa (Fleming and Loveridge 2003; Moe et al. 2009; Brody et al. 2010; Garden et al. 2010;

Joseph et al. 2011; but see also van der Plas et al. 2013). Thus, structural complexity of mounds and mound vegetation can potentially lead to higher input of animal-dispersed diaspores, leading to higher dominance of some well-dispersed species and higher individual density, but also to higher species richness than in the surrounding savanna. Animal-dispersed species are often thought to have better long-distance dispersal ability than wind-dispersed species (Hovestadt et al. 1999; Hovestadt and Poethke 2005). Considering that some species often found on mounds, e.g. *Diospyros mespiliformis*, also typically occur in gallery forests and forest islands within the savanna habitat (Hovestadt et al. 1999), the mound microhabitat could be considered an important stepping stone for populations of these otherwise spatially disconnected habitats.

Further long-term studies are needed to understand population dynamics on mounds and surrounding savanna habitats in more detail. Still, the outcomes of our study and of previous research emphasize that termite mounds represent crucial habitats for both plant and animal species and provide essential contributions to spatial structure and complexity in savanna systems.

Supporting Information

Table III.6 List of juvenile woody species found on mounds and savannas over the whole sampling period.

Family	Species	Mound	Savanna
Anacardiaceae	*Lannea acida*	+	+
Anacardiaceae	*Ozoroa insignis*	+	
Annonaceae	*Annona senegalensis*	+	+
Bignoniaceae	*Stereospermum kunthianum*	+	+
Bombacaceae	*Bombax costatum*	+	+
Caesalpiniaceae	*Afzelia africana*	+	
Caesalpiniaceae	*Burkea africana*	+	+
Caesalpiniaceae	*Cassia sieberiana*	+	
Caesalpiniaceae	*Detarium microcarpum*	+	+
Caesalpiniaceae	*Piliostigma thonningii*	+	+
Caesalpiniaceae	*Tamarindus indica*	+	
Celastraceae	*Gymnosporia senegalensis*	+	+
Combretaceae	*Anogeissus leiocarpa*	+	
Combretaceae	*Combretum adenogonium*	+	+
Combretaceae	*Combretum collinum*	+	+
Combretaceae	*Combretum glutinosum*	+	+
Combretaceae	*Combretum molle*	+	+
Combretaceae	*Combretum nigricans*	+	+
Combretaceae	*Guiera senegalensis*		+

Table III.6 continued

Family	Species	Mound	Savanna
Combretaceae	*Pteleopsis suberosa*		+
Combretaceae	*Terminalia avicennioides*	+	+
Combretaceae	*Terminalia laxiflora*		+
Ebenaceae	*Diospyros mespiliformis*	+	
Euphorbiaceae	*Bridelia ferruginea*	+	+
Euphorbiaceae	*Flueggea virosa*	+	
Fabaceae	*Pericopsis laxiflora*	+	
Fabaceae	*Philenoptera laxiflora*	+	+
Fabaceae	*Pterocarpus erinaceus*	+	+
Fabaceae	*Xeroderris stuhlmannii*		+
Loganiaceae	*Strychnos innocua*		+
Loganiaceae	*Strychnos spinosa*	+	+
Malvaceae	*Cienfuegosia heteroclada*	+	
Meliaceae	*Pseudocedrela kotschyi*	+	+
Meliaceae	*Trichilia emetica*	+	+
Mimosaceae	*Acacia dudgeonii*	+	
Mimosaceae	*Acacia gourmaensis*	+	+
Mimosaceae	*Acacia hockii*	+	+
Mimosaceae	*Dichrostachys cinerea*	+	
Mimosaceae	*Prosopis africana*		+
Moraceae	*Ficus sur*	+	
Olacaceae	*Ximenia americana*	+	+
Polygalaceae	*Securidaca longepedunculata*		+
Rubiaceae	*Crossopteryx febrifuga*	+	+
Rubiaceae	*Fadogia cienkowskii*		+
Rubiaceae	*Feretia apodanthera*	+	
Rubiaceae	*Gardenia aqualla*	+	
Rubiaceae	*Gardenia erubescens*	+	+
Rubiaceae	*Gardenia ternifolia*	+	+
Rutaceae	*Clausena anisata*	+	
Rutaceae	*Zanthoxylum zanthoxyloides*	+	
Sapotaceae	*Vitellaria paradoxa*	+	+
Simaroubaceae	*Quassia undulata*	+	
Sterculiaceae	*Dombeya quinqueseta*	+	+
Sterculiaceae	*Sterculia setigera*	+	
Tiliaceae	*Grewia lasiodiscus*	+	
Tiliaceae	*Grewia mollis*	+	+
Verbenaceae	*Vitex madiensis*	+	
Zygophyllaceae	*Balanites aegyptiaca*	+	+

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