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

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

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

Termites et savanes - une vue d'ensemble de l'histoire et des progrès de la recherche avec un accent particulier sur l'Afrique de l'Ouest et du genre *Macrotermes*

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

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

Termiten und Savannen – eine Übersicht zu Geschichte und Fortschritten der Forschung unter besonderer Berücksichtigung von Westafrika und der Gattung *Macrotermes*

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

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

1 Introduction

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

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

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

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

2 TERMITE BIOLOGY – A SHORT OVERVIEW

2.1 Research history

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

SMEATHMAN (1781) also commented on beneficial effects of termites, such as the removal of dead biomass, but these were thereafter mainly ignored or dismissed for a century until DRUMMOND (1886) compared the influence of termites in the tropics to the beneficial activities of temperate earthworms, inspired by Darwin's work on the latter (DARWIN 1881). Drummond's work, however, was largely ignored and disregarded, besides some rare contributions from the field of vegetation ecology. Nearly six decades later, a review by ADAMSON (1943) called for further research on the question whether termite activity is detrimental or beneficial to the ecosystem on a longer timescale, and addressed open questions. He particularly emphasised the need for research re-evaluating the effects of termites on soil fertility and soil erosion, and he remarked that large abandoned termite mounds may show increased fertility.

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

2.2 Termite ecology and classification

2.2.1 Termite diversity

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

2.2.2 Feeding groups

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

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

2.2.3 Caste differentiation

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

2.3 Termite mounds

2.3.1 Nests and mounds

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

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

2.3.2 Mound functions

It has been argued that termite mounds constitute a part of a colony superorganism in so far as they are a functional unit and no part can survive without the others (EGGLETON 2011). Besides protection against predators, termite mounds protect the colony from direct intrusion of rainwater and flooding, which would otherwise have catastrophic consequences. Damages by, e.g., rain or other organisms, are constantly repaired. The major challenge for a termite colony, however, is minimising variations in temperature and humidity. Especially in the fungus-cultivating genera, the most important function of the mound is creating and maintaining 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 & 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 & 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 & 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 paper, the genus *Macrotermes* in West Africa, constructs large mounds. The main function of *Macrotermes* mounds is to provide a protected and stable environment for the termite nest, including the fungus gardens. Termites transport and modify large amounts of soil over the lifetime of a colony to build and maintain their mounds, continuously engineering the soil environment of savanna landscapes in the process.

2.4 Focus species

2.4.1 Species distribution

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

2.4.2 Variability of mound types

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

However, mound architecture of the two species can overlap, as each species shows regional as well as local variability, with mounds being adapted to local environmental conditions (COLLINS 1979; KORB & 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, in the following, we do not differentiate between *M. subhyalinus* and *M. bellicosus*.

2.4.3 Soil composition of *Macrotermes* mounds

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

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

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

In addition to structural adaptation to local microclimate (KORB & 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) in Central Africa (MUJINYA et al. 2010, 2013, 2014; ERENS et al. 2015a), supporting the idea that the impact of termites on soil turnover and soil composition depends on the surrounding environment.

3 INTERRELATIONSHIP BETWEEN TERMITES AND THE SAVANNA ECOSYSTEM

3.1 Research history

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

the term "landscape ecology" (TROLL 1939). Further studies of landscape ecology in African savannas in the 1940s (THOMAS 1943; EGGELING 1947; MORISON et al. 1948) explored relationships between soils and vegetation, including the influence of termites. Later detailed studies of savanna vegetation were specifically interested in the synecology of plant communities on termite mounds (WILD 1952; MULLENDERS 1954; SCHMITZ 1963; JACKSON & GARTLAN 1965; 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 chemicophysical composition of termite mound soils (HESSE 1955; NYE 1955; WATSON 1962). Most recently, information from different scientific fields began to get integrated to address the role of termites in the savanna ecosystem (LEE & WOOD 1971; WOOD & SANDS 1978; WOOD 1988; ABE et al. 2000; SILESHI et al. 2010; BIGNELL et al. 2011), and the current scientific debate tries to identify the processes behind patterns in the savanna ecosystem which are caused by termites and their mounds (e.g., DANGERFIELD et al. 1998; LEVICK et al. 2010a; JOUQUET et al. 2011; OKULLO & MOE 2012a,b; BONACHELA et al. 2015). However, even today, termites can be seen as "neglected" soil and ecosystem engineers (JOUQUET et al. 2016).

3.2 Importance of termite mounds for the savanna ecosystem

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

3.2.1 Water availability

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

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

3.2.3 Nutrient enrichment

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

3.2.4 Clay enrichment

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

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

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

3.2.5 Soil turnover

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

3.2.6 Ecosystem engineering and effects on vegetation

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

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

A widely cited paper by Dangerfield et al. (1998), the 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.

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

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

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

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

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

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

3.2.7 Effects on animals and their feedbacks with vegetation

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

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

Termite mounds also affect other animals, both directly and indirectly through effects on the vegetation. Mounds themselves, and the often more dense vegetation on mounds compared to the surrounding savanna, provide food resources and sites for shelter, burrowing, foraging, thermoregulation, roosting, and breeding, as has been found for reptiles (Garden et al. 2010), birds (Dean et al. 1999; Joseph et al. 2011), and mammals (Fleming & Loveridge 2003). Several mammal species feed on termites, and a variety of animal species perch on mounds, take refuge in their cavities, directly exploit the mound material for minerals through geophagy, and prefer browsing or grazing on plants growing on termite mounds (e.g., Ruggiero & Fay 1994; Holdo & McDowell 2004; Loveridge & Moe 2004; Mobaek et al. 2005, Grant & Scholes 2006; Brody et al. 2010; Levick et al. 2010b; but also see Muvengwi et al. 2013; O'Connor 2013; van der Plas et al. 2013). The interactions of mounds, plants, and animals are suspected to cause feedback loops, similar to those observed for large trees (Dean et al. 1999). A summarising conceptual system analysis of this view, focussing on feedbacks creating and maintaining habitat heterogeneity of the savanna landscape, can be found in Sileshi et al. (2010). Thus, both for animals and plants, termite mounds can be described as keystone structures sensu Tews et al. (2004).

3.2.8 Benefits to humans – the example of West Africa

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

contents, however research so far is inconclusive (Ziegler 1997; Wilson 2003).

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

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

4 Termite mounds and vegetation patterns

4.1 Differences between mounds and the surrounding savanna

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

- The majority of characteristic mound species in West Africa is woody, which is in accordance with the notion that termite mounds are focal sites for woody plant regeneration as well as refugia for large trees to reach senescence (Joseph et al. 2011, 2013; Traoré et al. 2008b).

- Other characteristic mound species are geophytes, suggesting that water availability on mounds is not uniformly high, especially not in the compact topsoil layer. In addition to having higher water-storage capacity, geophytes in their dormant stage are likely more resistant to cracking/swelling cycles between dry and wet season, which might be another advantage in the face of higher expansible clay content in mound and pediment soil (Jouquet et al. 2002a,b, 2004; Mujinya et al. 2013).

- Studies analyzing the spatial distribution of species on mounds have shown spatial differentiation within mound microhabitats (Lawson & Jenik 1967; Kirchmair et al. 2012; Yamashina 2013), offering soil properties, microclimatic effects and protection from fire as possible explanations for the spatial distribution of species on mounds.

- Up to date, only very few studies (Erpenbach et al. 2013, Davies et al. 2014) have specifically addressed the fact that climatic gradients play a role in the degree of difference between the vegetation of termite mounds and the surrounding savanna. Also, landscape-scale gradients, e.g. based on underlying pedology, hydrology or microclimatic effects have rarely been addressed. Exceptions includes studies on mound composition and structure (Korb & Linsenmair 1998a,b; Abe et al. 2009a,b), vegetation composition in relation to soil changes mediated by termites or land use/grazing history (Davies et al. 2016; Erpenbach et al. 2016; Lagendijk et al 2016). It is of interest that some of these studies deliver evidence that the notion of termite mounds as being richer in nutrients than the matrix, thus being more densely vegetated by woody plants and more attractive to large herbivores does not hold true in all habitat contexts (Muvengwi et al. 2013; O'Connor 2013; Davies et al. 2016; Lagendijk et al 2016).

4.2 Creation of vegetation mosaics

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

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

4.3 Desertification

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

4.4 Landscape restoration

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

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

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

5 Vegetation of termite mounds across different scales and along a climatic gradient – the West African example

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

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

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

5.1.1 Gradient analysis of communities

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

5.1.2 Diversity analysis

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

5.1.3 Indicator species analysis

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

species: all were woody or at least subligneous, severals howed 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. According to the authors cited above, this might suggest further shared functional traits or preadaptations leading to selection against these species in the surrounding savanna or a competitive advantage of these characteristic species in the mound microhabitat.

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

5.2.1 Soil gradient analysis of communities

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

5.2.2 Analysis of community distances in response to soil

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

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

5.2.3 Indicator species analysis

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

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

5.3.1 Analysis of diversity patterns

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

5.3.2 Analysis of population dynamics

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

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

5.3.3 Analysis of soil composition

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

5.3.4 Analysis of plant dispersal modes

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

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

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

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

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

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