Termite mediated heterogeneity of soil and vegetation patterns in a semi-arid savanna ecosystem in Namibia

Dissertation zur Erlangung des

naturwissenschaftlichen Doktorgrades

der Julius-Maximilians-Universität Würzburg

vorgelegt von

Constanze Grohmann

geboren in der Hansestadt Lübeck

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Um es vorweg zu nehmen: Die Namib schluckte mich mit Haut und Haaren. Dort war ich glücklich und ruhig in mir. Wer die Wüste nicht selbst erlebt hat, ihre Weite und ihren Frieden, ihre Härte und Unerbittlichkeit, wird es nicht verstehen, und ich werde es ihm nicht erklären können. Ich kann ihm nur sagen, dass ich seither ein kleines Stück Wüste in mir trage. Und es ist ein größerer Schatz für mich als manches Schulwissen.

Barbara Imgrund

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Grohmann C. and Linsenmair K.E. (in prep.). Biodiversity of termite species along a rainfall gradient in Namibia.

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Zusammenfassung

Termiten sind die bedeutendsten Ökosystem-Ingenieure in den Böden arider und semi-arider Gebiete. Sie beschleunigen Zersetzungsprozesse und damit auch die nachfolgende Mineralisation von Nährstoffen durch Bakterien und Pilze. Durch den Bau ihrer Galerien, Nester und Hügel fördern sie die Umwälzung des Bodens und beeinflussen die Nährstoffverteilung, die Textur sowie die hydrologischen Eigenschaften der Böden. Durch diese Prozesse erhöhen sie die Heterogenität in den von ihnen bewohnten Ökosystemen.

Die vorliegende Arbeit beschäftigt sich vorrangig mit dem Einfluss von Termiten auf Ökosystemfunktionen eines semi-ariden Ökosystems. Als Grundlage dazu habe ich die Diversität von Termitentaxa und ihre Abhängigkeit von Niederschlagsmenge, Vegetationsmustern und Landnutzungssystemen auf verschiedenen Untersuchungsflächen in Namibia bestimmt. In dem darauffolgenden Teil der Arbeit habe ich mich auf die pilzzüchtende und hügel bauende Art *Macrotermes michaelseni* (Sjöstedt, 1914) konzentriert, eine Art, die in vielen afrikanischen Savannen in hoher Abundanz vorkommt. Ich habe mich damit beschäftigt, wie diese Art die räumliche Heterogenität von Böden und Vegetationsmustern beeinflusst. Durch wiederholtes Sammeln an 13 verschiedenen Untersuchungsgebieten in Namibia konnte ich 17 Termitentaxa aus 15 Gattungen erfassen. Während die Landnutzung einen unwesentlichen Einfluss auf die Termitenfauna hatte, konnte die Variation in der Taxadiversität zu 96% durch den mittleren jährlichen Niederschlag erklärt werden und zu 81% durch den Simpson-Diversitäts-Index der Gefäßpflanzen. Die Anzahl der Termitentaxa nahm mit diesen beiden Variablen zu.

Im Gegensatz zu vorherigen Studien an *Macrotermes* Hügeln in verschiedenen Regionen Afrikas, enthielten Bodenproben der untersuchten Hügel in der zentralen namibischen Savanne viel höhere Stickstoffgehalte im Vergleich zum Ausgangsmaterial. Weitere Analysen ergaben, dass der hohe Stickstoffgehalt in dem Hügelmaterial vor allem auf Nitrat zurückzuführen ist. Da Nitrat leicht wasserlöslich ist, gelangt es wahrscheinlich durch von Evaporation angetriebene Wasserbewegungen an die Hügeloberfläche und reichert sich dort an. Die untersuchten Termitenhügel in Namibia enthielten zudem höhere Sandgehalte im Vergleich zu den Hügeln der von mir ausgewerteten vorherigen Studien. Durch den höheren Anteil von Grob- und Mittelporen kann sich Wasser in sandigen Böden schneller bewegen als in tonigen Böden. Dadurch bedingt können in den untersuchten Hügeln Evaporation und Nitratakkumulation in hohen Raten erfolgen.

Um die Menge des von den Termitenhügeln erodierenden Materials zu ermitteln, habe ich jeweils vier stabile, 65 cm breite Plastikbeutel an 14 Hügeln befestigt und mit diesen das Bodenmaterial aufgesammelt, das während fünf Regenereignissen von den Hügeln abgeschwemmt wurde. Hochgerechnet auf den Gesamtumfang der Hügel bedeckte das pro Jahr von einem bewohnten Hügel erodierte Material theoretisch einen 1 m breiten Kreisring um den Schwemmkegel des Hügels 2,4 mm hoch. Der entsprechende Wert für unbewohnte Hügel betrug 1,0 mm. Projiziert auf eine Fläche von einen Hektar erodierten insgesamt etwa 245 kg Hügelmaterial pro Jahr. Dabei muss berücksichtigt werden, dass dies nur eine ganz grobe Schätzung ist, da die Erosionsrate von verschiedenen Faktoren wie der Regenintensität, der Körnung des Bodens und des Zeitpunkts innerhalb der Regensaison abhängt. Um zu erfassen, bis zu welcher Distanz der erodierte Boden die chemische Zusammensetzung des Umgebungsbodens beeinflusst, habe ich aus jeweils 0–10 cm Tiefe

Proben in 1, 5 und 25 m Entfernung sowie als Kontrolle von den Hügeln selbst genommen. Mit Hilfe nichtmetrischer multidimensionaler Skalierung konnte ich zeigen, dass sich die Bodeneigenschaften des Hügelmaterials stark von denen des Umgebungsbodens unterschieden. Innerhalb der Hügelproben variierten die Bodeneigenschaften nur gering. Ebenso konnte ich zwischen den Proben, die aus den drei Entfernungen stammten, keine starken Unterschiede feststellen. Aus diesen Ergebnissen schlussfolgere ich, dass der von den Termitenhügeln erodierende Boden sich durch den Bau von unterirdischen Gängen und „sheetings“ (Konstruktionen aus Bodenmaterial, mit denen einige Termitenarten ihre Nahrungsstücke umziehen) schnell mit tieferen Bodenschichten mischt. Infolgedessen sammelt sich das Hügelmaterial nicht in der näheren Umgebung des Hügels an.

Um herauszufinden, wie das Pflanzenwachstum durch Termitenhügelmaterial beeinflusst wird, haben wir die Anzahl und Biomasse von Gräsern und Kräutern erhoben, die *in situ* an der Basis von Hügel wuchsen. Während die Individuenzahl der Gräser und die der Kräuter signifikant geringer waren, war die Gesamtbiomasse der Pflanzen, die an der Hügelbasis wuchsen, signifikant höher im Vergleich zu benachbarten Flächen. Umgekehrte Ergebnisse wurden durch Versuche erzielt, bei denen Radieschen (*Raphanus sativus* subsp. s*ativus*) und Sorghum (*Sorghum* sp.) Pflanzen in Folientöpfen herangezogen wurden. Beide Arten wuchsen signifikant schlechter auf Hügelerde im Vergleich zu Umgebungsboden. Die widersprüchlichen Ergebnisse im Bezug auf die Biomasse der *in situ*- und Wachstums-Experimente werden wahrscheinlich durch die Zerstörung der ursprünglichen Bodenstruktur während des Umfüllens der Erde in die Folientöpfe verursacht. Zudem verstärkte das Gießen der Pflanzen die Verdichtung des Materials. Im Gegensatz dazu sind *Macrotermes* Hügel von vielen Makroporen durchzogen, die für die Durchwurzelung der komprimierten Böden essentiell zu sein scheinen.

Im letzten Teil der vorliegenden Arbeit befasse ich mich mit der Frage, wie *M. michaelseni* Bauten verteilt sind und welche Faktoren dafür verantwortlich sind. Frühere Studien haben gezeigt, dass die Hügelgröße mit der Größe der Kolonie korreliert ist, die den jeweiligen Hügel bewohnt. Mit verschiedenen Mehrskalenverfahren konnte ich darlegen, dass größere bewohnte Hügel regulär verteilt waren. Außerdem waren Hügel, die enger zusammen standen, kleiner als der Durchschnitt der Hügel. Dieses deutet darauf hin, dass intraspezifische Konkurrenz die Verteilung und Größe der Hügel und deren Kolonien reguliert. Frühere Studien an *Odontotermes* Hügeln haben gezeigt, dass diese lokale Zentren der Primärproduktion und der Abundanz von Tieren sind. Mit darauf basierenden Simulationen konnte nachgewiesen werden, dass eine reguläre Verteilung von Hügeln im Vergleich zu einer zufälligen Anordnung zu einer größeren Gesamtproduktivität des Ökosystems führt. Da in der vorliegenden Arbeit die Pflanzenbiomasse an den Hügeln höher war als an benachbarten Stellen, könnte dieses auch für *M. michaelseni* Hügel zutreffen.

Aus den Ergebnissen dieser Arbeit ziehe ich die Schlussfolgerung, dass *M. michaelseni* durch ihre Hügelbauaktivitäten die Verteilungsmuster von Bodennährstoffen in der zentralen namibischen Savanne stark beeinflusst. Die Termiten erzeugen deutliche Kontraste in Bezug auf Nährstoffgehalt und Vegetationsmuster zwischen Hügelboden und benachbarten Stellen und erhöhen so die Heterogenität ihrer Habitate. Von früheren Studien ist bekannt, dass Habitatheterogenität eine hohe Artendiversität erzeugt. Eine hohe Diversität wiederum ist mit der Biomasseproduktion positiv korreliert und hat einen positiven Einfluss auf Ökosystemdienstleistungen. Schlussendlich unterstreicht die vorliegende Arbeit die Bedeutung von *M. michaelseni* für Ökosystemfunktionen in der Savanne Zentralnamibias.

Abstract

Termites are the most important soil ecosystem engineers of semi-arid and arid habitats. They enhance decomposition processes as well as the subsequent mineralisation of nutrients by bacteria and fungi. Through their construction of galleries, nests and mounds, they promote soil turnover and influence the distribution of nutrients and also alter texture and hydrological properties of soils, thereby affecting the heterogeneity of their ecosystem.

The main aim of the present thesis was to define the impact of termites on ecosystem functioning in a semi-arid ecosystem. In a baseline study, I assessed the diversity of termite taxa in relation to the amount of precipitation, the vegetation patterns and the land use systems at several sites in Namibia. Subsequently, I focussed on a species that is highly abundant in many African savannas, the fungus growing and mound building species *Macrotermes michaelseni* (Sjöstedt, 1914). I asked how this species influences the spatial heterogeneity of soil and vegetation patterns. From repeated samplings at 13 sites in Namibia, I obtained 17 termite taxa of 15 genera. While the type of land use seems to have a minor effect on the termite fauna, the mean annual precipitation explained 96% and the Simpson index of vascular plant diversity 81% of the variation in taxa diversity. The number of termite taxa increased with both of these explanation variables.

In contrast to former studies on *Macrotermes* mounds in several regions of Africa that I reviewed, soil analyses from *M. michaelseni* mounds in the central Namibian savanna revealed that they contain much higher nitrogen contents when compared to their parent material. Further analyses revealed that nitrate forms a major component of the nitrogen content in termite mounds. As nitrate solves easily in water, evaporation processes are most probably responsible for the transport of solved nitrates to the mound surface and their accumulation there. The analysed mounds in central Namibia contained higher sand proportions compared to the mounds of the former studies. Through the higher percentage of coarse and middle sized pores, water moves more easily in sandy soils compared to more clayey soils. In consequence, evaporation-driven nitrate accumulation can occur in the studied mounds at high rates.

Hochgerechnet auf den Gesamtumfang der Hügel bedeckte das pro Jahr von einem bewohnten Hügel erodierte Material theoretisch einen 1 m breiten Kreisring um den Schwemmkegel des Hügels 2,4 mm hoch. Der entsprechende Wert für unbewohnte Hügel betrug 1,0 mm.

To assess the amount of soil that erodes from termite mounds, I fastened four strong, 65 cm wide plastic bags at 14 mounds each and collected the soil that eroded during five rainfall events. Projected to the total mound circumference, the amount of soil eroded covers theoretically a 1 m wide circular ring around the pediment of an inhabited mound up to a height of 2.4 mm per year. For uninhabited mounds, the height of this soil layer would be 1.0 mm. Per hectare, roughly 245 kg eroded per year from the mounds. However, as the erosion rate depends on several factors such as rainfall intensity, soil texture and point of time within the rainy season, this is only a vague estimate. In order to determine up to which distance the soil erosion from the mounds still influences the chemical characteristics of the adjacent topsoil, I took samples from depth of 0–10 cm at 1, 5 and 25 m distances, respectively, from four different mounds and from the mounds themselves. The non-metric

multidimensional scaling of the soil properties showed strong differences between mound and off-mound samples. Soil characteristics within the samples from the mounds did not differ largely. Similarly, I found no strong differences between the samples taken from the different distances from the mound. From these results I conclude that through the construction of foraging galleries and sheetings (soil constructions with which some termite species cover their food items), the soil eroding from termite mounds is quickly mixed with deeper soil layers. In consequence, mound material does not accumulate in the mound's vicinity.

In order to reveal how plant growth is influenced by termite mound material, we assessed the number of grass and herb individuals as well as the biomass of plants growing *in situ* on the base of mounds compared to adjacent sites. While the numbers of both grass and herb individuals were significantly lower compared to adjacent sites, the total biomass of plants growing on the base of mounds was significantly higher. Reverse results were obtained by pot experiments with radish (*Raphanus sativus* subsp. s*ativus*) and sorghum (*Sorghum* sp.) growth. Both species grew significantly weaker on mound soil compared to adjacent soil. The contradictory results concerning the biomass of *in situ* and pot experiments are most probably caused by the disturbance of the original soil structure during the potting process. The material was subsequently compacted through watering the plants. In contrast, *Macrotermes* mounds are pervaded by many macropores which seem to be essential for the plant roots to penetrate the soil.

In the last part of this thesis, I posed the question how mounds of *M. michaelseni* are distributed and what factors might be responsible for this pattern. Former studies showed that mound size is correlated with the size of its inhabiting colony. With several multi-scale analyses, I revealed that larger inhabited mounds were regularly distributed. Additionally, mounds which were closer together tended to be smaller than on average. This indicates that intraspecific competition controls the distribution and size of colonies and their mounds. Former studies concerning *Odontotermes* mounds substantiated that they are local hotspots of primary productivity and animal abundance. Based on these findings, simulations revealed that a regular distribution of these mounds leads to a greater ecosystem-wide productivity compared to a random arrangement. As in the present study, plant biomass was higher at the mounds compared to off-mound sites, this might hold true for *M. michaelseni* mounds.

From the results of this thesis, I draw the conclusion that through their mound building activities, *M. michaelseni* strongly influences the distribution patterns of soil nutrients within the central Namibian savanna. These termites create sharp contrasts in nutrient levels and vegetation patterns between mound soils and off-mound soils and enhance the heterogeneity of their habitats. Former studies revealed that habitat heterogeneity is important in generating species diversity and species richness in turn is correlated positively with biomass production and positively affects ecosystem services. In conclusion, the present thesis underlines the importance of *M. michaelseni* for ecosystem functioning of the central Namibian savanna.

Chapter I

General introduction

The aim of the present thesis was to consider the influence termites have on their ecosystem. Therefore, I first assessed the biodiversity of termites. Subsequently, I focussed on the mound building species *Macrotermes michaelseni* (Sjöstedt, 1914), which is abundant in many semi-arid savannas of Africa, and analysed how this species increases the heterogeneity in soil and vegetation patters. In this first chapter, I present an overview on the broader context and the current knowledge of the topics this thesis deals with. I then give a short outline of the thesis and summarise the main aims and methods of the following chapters. After an introduction to the BIOTA-project in which this thesis was embedded, a short description of the main study sites follows at the end of this chapter.

Introduction

Darwin (1881) described the importance of earthworms for soil formation. From his observations, he concluded that earthworms played an "important … part in the history of the world". As many as 115 years later, a precise definition of such species influencing the processes in an ecosystem was given by Jones et al. (1994). According to these authors, "**ecosystem engineers** are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In doing so, they modify, maintain and create habitats". Apart from earthworms, another familiar example of an ecosystem engineering species that visibly changes habitats is the beaver (*Castor* sp.). By constructing dams, it alters the hydrology of large areas. In consequence of this, the flow rate, material transport and nutrient cycle are modified, as are the composition of plant and animal communities.

In the present thesis, I focus on the most important soil ecosystem engineers of drylands. According to the Millennium Ecosystem Assessment (2005), **drylands** comprise all lands where the climate is classified as dry subhumid, semiarid, arid or hyper-arid. They comprise 41% of the global terrestrial area and are inhabited by 35% of the global population (data from 2000, Millennium Ecosystem Assessment 2005). Desertification, intensive use of land and climate change are much greater threats to dryland ecosystems and the ecosystem services provided by them, compared to other ecosystems (Millennium Ecosystem Assessment 2005). **Soil organisms** are essential for the functioning of natural and managed ecosystems and the productivity of land (Barrios 2007). Their relevance for soil fertility originates from their influence on water movement, aeration and nutrient levels as well as on their influence on decomposition processes.

The most important soil ecosystem engineers of drylands are **termites** (Wood and Sands 1978, Holt and Coventry 1990, Whitford 1991, Whitford et al. 1992, Dangerfield 1997). The processes termites promote via their feeding and nesting behaviour were reviewed by Lee and Wood (1971), Wood and Sands (1978), Lobry de Bruyn and Conacher (1990) and Holt and Lepage (2000). They enhance decomposition processes and subse-

quently control the mineralization of nutrients by associated microorganisms. Via the constructions of foraging galleries within the soil, soil porosity increases, as does the infiltration of rainwater into deeper soil layers and the aeration of the soil.

The ecosystem engineering concept remains in the focus of current research, as since the "**Biodiversity-Ecosystem Function Paradigm**" (Naeem 2002), the importance of maintaining biodiversity is often underpinned by the active role biota are playing in governing environmental conditions. More specifically, within this paradigm, a specific ecosystem function is seen as a function of the density of each species, the biotic interactions among species, biogeochemical processes and the abiotic environment. Hence, species diversity and the role each species plays in its ecosystem have to be considered at the same time to understand the functioning of an ecosystem and the services it provides for human well-being.

Over 2.600 termite species in 281 genera are described globally (Kambhampati and Eggleton 2000). Their **diversity**, abundance and biomass have been found to decrease with increasing latitude (Eggleton and Bignell 1995, Eggleton 2000). In southern Africa, 54 genera comprising 165 species are described (Uys 2002). During the "National Survey", an extensive survey of termites in southern Africa, 33 of these genera were found in Namibia (Coaton and Sheasby 1972), with an unknown number of species, as many termite genera need taxonomic revisions (Uys 2002). As the climate becomes more arid, shifts in functional groups occur. In Africa and Asia, humivorous taxa, which can often be found in the subfamilies Apicotermitinae, Termitinae and Nasutitermitinae, are often replaced by those of the fungus growing Macrotermitinae (Bignell and Eggleton 2000). Of the subfamily Macrotermitinae, especially *Macrotermes* species build large, conspicuous mounds, which are characteristic for many African savannas. In Namibia, four *Macrotermes* species occur (Ruelle et al. 1975). *M. michaelseni* is widely distributed in the central and northern parts of Namibia. It is replaced by *Macrotermes natalenis* at the eastern and southern border of its distribution area, while *M. subhyalinus* replaces *M. michaelseni* at its western distribution area. *Macrotermes vitrialatus* is sparsely distributed in the north-eastern and north-western parts of Namibia. Of these four species, *M. michaelseni* builds the most prominent mounds with 79% of them being 1.5—6 m in height and only 21% being less than 1.5 m in height (Coaton and Sheasby 1972). Mounds built by *M. subhyalinus* are lower than those of *M. michaelseni* but slightly higher than those of *M. natalensis*. In Namibia, *M. vitrialatus* builds mounds of varying sizes (Ruelle et al. 1975).

The effect of termites on their ecosystem is largely based upon the construction of soil sheetings, galleries, nests and mounds (Lobry de Bruyn and Conacher 1990, see blue labels in Fig. 1). **Sheetings** (Fig. 2) are built by many termite species around food items to protect themselves to a certain extent from predators and, moreover, to prevent desiccation and to maintain a constant micro-climate while foraging (Wood and Sands 1978, Rouland et al. 2003). The soil particles used for these constructions are selected from the topsoil (Jouquet et al. 2002). As for all constructions other than the fungus combs, Macrotermitinae use saliva to cement the soil particles (Wood 1988, Fig. 3). Soil sheetings are fragile constructions which are easily redistributed to the surrounding soil surface by rain, wind and trampling by larger animals (Wood and Sands 1978, Bagine 1984, Wood 1988, Holt and Lepage 2000). Sheetings of termite species in general are not only redistributed easily, but large portions can also be built within a short time (Ferrar 1982, Bagine 1984). Consequently, via the construction of sheetings, *Macrotermes* species promote the turbation of soil

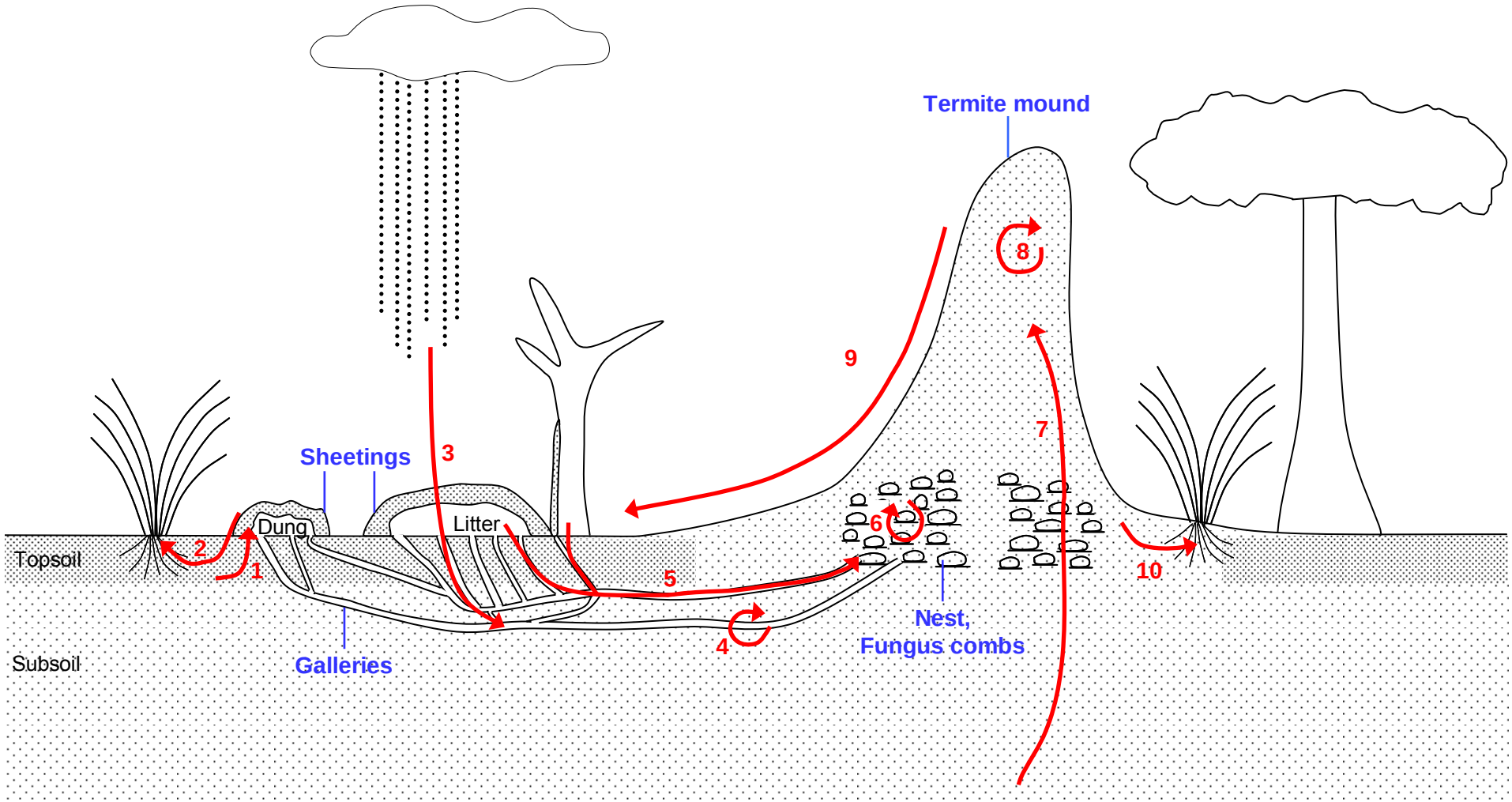

Fig. 1: Scheme of constructions (blue labels) built by *Macrotermes* species and processes (red arrows) mediated by them as discussed in the literature. 1: soil turbation via the construction of sheetings; 2: uptake of nutrients from the sheetings by plants; 3: increase of infiltration rates; 4: aeration of the soil; 5: relocation of organic matter; 6: decomposition; 7: soil turbation via the construction of mounds with subsoil; 8: mineralisation and enrichment of nutrients; 9: erosion and redistribution of mound material; 10: uptake of nutrients from the mound material by plants.

material (Rouland et al. 2003; no. 1 in Fig. 1). Jouquet et al. (2002) showed that the sheetings of *Odontotermes* contain more nutrients, particularly carbon and exchangeable cations, than the underlying soil. Additionally, soil sheetings of *Macrotermes* and *Odontotermes* species contain large amounts of inorganic nitrogen (Ndiaye et al. 2004). Thus, sheetings might enhance the growth of plants which root at sites with high termite activities (no. 2 in Fig. 1).

To reach their food items, termites build many interconnected tunnels in the soil. In this thesis, I name these tunnels that are built below the soil surface **galleries**, which is the most commonly used term. However, the usage of this term is not consistent within the literature, as some authors also or exclusively name the gangways beneath soil sheetings galleries. The galleries and their openings at the soil surface (Fig. 4) enhance the infiltration of rainwater into the soil manifold (Graiff 2010, D. Kaiser, unpublished data; no. 3 in Fig. 1) and most probably improve the water storage capacity of the soils. The galleries additionally increase the aeration of the soil (no. 4 in Fig. 1) and thus allow plant roots to easily penetrate the soil.

Via foraging activities, large amounts of organic matter are relocated and taken to the termites' **nest** (no. 5 in Figs. 1, 5, 6). The primary food source of *Macrotermes* species consists of dead wood, grass litter and dung (Dangerfield and Schuurman 2000). This food rapidly passes through the gut of the termites and the material is then expelled as so called primary faeces onto the fungus combs. The fungus combs consist of more or less degraded plant material that is pervaded by a basidiomycete fungus of the genus *Termitomyces* (Westhuizen and Eicker 1991, Osiemo et al. 2010; Fig. 7). The fungus degrades plant structural compounds such as lignin (Rouland-Lefèvre 2000). Hence, in the fungus gardens, the food items are decomposed (no. 6 in Fig. 1). Further decomposition occurs as the termites ingest the old parts from the bottom of the fungus combs (Rouland-Lefèvre 2000). In *M. bellicosus* nests, Hinze et al. (2002) found the final faeces in form of a homogenous, dark brown, sticky mass deposited in special chambers.

Badertscher et al. (1983) showed for *M. subhyalinus* that young workers stay in the nest and feed on plant material that was collected by older workers and on fungus nodules (Fig. 8). They deposit their primary faeces on the fungus combs. Old workers in contrast eat fungus comb material, earth and some plant material, while soldiers are fed by the workers with fungus comb material. The authors also assume that young workers feed the larvae (Fig. 9) with a secretion from their salivary glands. This pattern might differ between *Macrotermes* species. Hinze et al. (2002) found for *M. bellicosus*, that many more major workers than minor workers have primary food in their gut and major workers are mainly involved in building the fungus comb. Plant material in the gut of workers was often found along with fungal conidia. Those workers which fed on secondary food revealed the highest protein content in their labial glands. From this, Hinze et al. (2002) conclude that there might be two different kinds of nurses in the queen cell (Fig. 10), workers which provide stomodeal nodule material and workers which feed on the fungus comb and feed saliva to the reproductives.

To build their **mounds**, *Macrotermes* species use subsoil (Harris 1956, Holt and Lepage 2000; no. 7 in Fig. 1). In contrast to topsoil, subsoil often contains more inorganic nutrients and offers higher clay contents. If the clay content of the subsoil is low, termites select clay minerals for their constructions (Jouquet et al. 2002). Through the use of subsoil and salivary content, termite mounds contain more nutrients than the adjacent topsoil (Wood 1988). The organic compounds of the mound material are mineralized by bacteria and fungi present in the mound walls (Holt and Lepage 2000; no. 8 in Fig. 1).

Fig. 2: Sheetings built by *M. michaelseni* around the stem of a dead tree.

Fig. 3: *Odontotermes okahandjae* worker raising their nest system.

Fig. 4: Foraging hole of *Baucaliotermes hainesi.*

Fig. 5: Opened termite mound of *M. michaelseni*. In the lower part of the mounds, the central nest system is located. The whitish fungus combs are lying on flat, earthen shelves. Above the fungus garden, truncated air channels can be seen.

Fig. 6: Central nest system of a *M. michaelseni* mound. On the left hand side, whitish fungus combs are lying on flat, earthen shelves. On the right hand side, the truncated queen cell is located in the middle of a massive block of soil. The queen cell was located roughly in the centre of the fungus gardens.

The mound soil is gradually eroded by rain and wind and thereby redistributed to the surrounding terrain (no. 9 in Fig. 1, Fig. 11). At a site with 1,100 mm precipitation per year, Lepage (1984) calculated the **erosion** from *Macrotermes bellicosus* mounds in West Africa to be 0.37 m^3 $mound^{-1}$ $year^{-1}$, respectively 9.4 m^3 ha^{-1} $year^{-1}$, representing an average soil thickness of 1.5–2 mm over two years. Further data on soil erosion from *Macrotermes* mounds are lacking. Aloni and Soyer (1987) report erosion rates from *Cubitermes* mounds to be 3 t ha^{-1} $year^{-1}$ at a site with roughly 1,000 mm rainfall per year in the Democratic Republic of the Congo. Bonell et al. (1986) measured the substrate loss from *Amitermes vitiosus* mounds by rain to be 475 kg ha^{-1} $year^{-1}$ in Australia at a site with 600 mm precipitation per year. However, it is difficult to transfer these data to *Macrotermes* mounds of other regions, as the severity of erosion depends on the termite taxon, shape of the mound, rainfall intensity (Bonell et al. 1986), size of raindrops (Parsons and Gardian 2000), soil texture (C. Grohmann, unpublished data) and point of time within the rainy season.

In correlation with the higher nutrient status of *Macrotermes* mounds, **plant growth** at the mounds (no. 10 in Fig. 1) is often enhanced (Arshad 1982, Pomeroy 1983). Similarly, Watson (1977) showed that increased plant growth in potted mound soil is correlated with higher nutrient levels and better soil water storage capacity of the mound material compared to adjacent soil. In contrast to these results, Kang (1978) and Graiff (2010) observed poorer plant growth in potted mound soil compared to adjacent soil. Both authors regarded this as a direct effect of the poor aeration of the mound soil once its natural structure is disturbed, as happens during the potting process. The hardness of such soils is hampering the growth of plant roots.

Through their mound building activities and its impact on plant growth, termites enhance the **heterogeneity** of their ecosystems. Recent studies demonstrate that termite mounds in African savannas generate the spatially heterogeneous distribution of e.g. plant species composition and diversity, atmospheric N-fixation rates and animal abundances (Traoré et al. 2008, Moe et al. 2009, Brody et al. 2010, Fox-Dobbs et al. 2010, Pringle et al. 2010).

The impact of termite mounds on ecosystem functioning is additionally determined by their **distribution** patterns. Evenly spaced *Odontotermes* mounds produce greater abundance, biomass and reproductive output of consumers across all trophic levels than one would expect in landscapes with randomly distributed mounds (Pringle et al. 2010). So far, studies on the spatial distribution of *Macrotermes* mounds yielded contradictory results. A clumped distribution was found by Meyer et al. (1999), whereas no significant deviations from a random pattern were revealed by Collins (1981), Schuurman and Dangerfield (1997) and Turner (2000). A regular distribution was verified by Darlington (1982), Lepage (1984), Kaib et al. (1997) and Pomeroy (2005) and is often addressed to be caused by intraspecific competition.

The main aim of the **present doctoral thesis** was to analyse the impact of termites on ecosystem functioning in a semi-arid ecosystem. In a baseline study, I examined the biodiversity of termite taxa at several sites in Namibia and tested their dependence on the mean annual precipitation. I then exemplarily focussed on two sites where *M. michaelseni* seemed to play an extraordinarily large role as an ecosystem engineer through its mound building behaviour. At these sites, I investigated the impact of *M. michaelseni* on the spatial heterogeneity of soil and vegetation patterns. Finally, I assessed the spatial distribution patterns of *Macrotermes* mounds and deduced its causes and consequences.

Fig. 7: Fruiting bodies (basidiocarps) of the termite fungus *Termitomyces* sp. growing on a *M. michaelseni* mound. Vernacular, they are called "Omajuvas" in Namibia. The fruiting body is part of the sexual phase of the fungus.

Fig. 8: Fungus comb of *M. michaelseni* with white nodules (conidia). The comb consists of more or less degraded plant material that is pervaded with hyphae of the basidiomycete fungus *Termitomyces* sp. The conidia are asexual reproductive structures of the fungus.

Fig. 9: Larvae and nymphs of *M. michaelseni* in a chamber of the mound.

Fig. 10: Queen of M. michaelseni in the opened queen cell with major soldiers (e.g. in front), minor soldiers (e.g. at top right) and workers (e.g. at the queen's right side).

Fig. 11: Partly eroded *M. michaelseni* mound. The chimney broke down and fell towards the front part of the picture. Thereby, air channels were exposed at the top of the mound. Length of the yellow spirit level: 45 cm.

Thesis outline

Chapter II of this thesis ("**Biodiversity of termites along rainfall gradients in Namibia**") deals with the termite taxa occurring on 13 sites in Namibia. Most of these sites differ in the mean annual precipitation they receive and the type of land use system that is prevailing. The main aim of this chapter is i) to compile a termite taxa list for these sites, ii) to reveal the main abiotic factors responsible for termite taxa diversity and iii) to test the hypotheses that termite diversity decreases with decreasing rainfall, decreasing vegetation cover and increasing anthropogenic land-use. To this end, during three and five field campaigns respectively (depending on the study site), I collected specimens according to a standardised sampling protocol that combined several methods.

In Chapter III, IV and V, I demonstrate the influence of termites on their ecosystem exemplarily by means of the fungus-growing and mound-building species *M. michaelseni* in the central Namibian savanna.

Chapter III ("***Macrotermes michaelseni* mounds enhance the spatial heterogeneity of nitrogen distribution**") concerns numbers 7, 8 and 9 of Fig. 1. The goal is to characterise the influence *M. michaelseni* has on the soil characteristics by its mound-building behaviour. First, I compare several soil properties of mound soils and off-mound soils. I then assess the rate of soil that erodes from the mounds by rain and the distance up to which a substantial impact of the eroding soil on the surrounding topsoil can be verified. From this, I infer the spatial influence mounds have on their surroundings. With the aid of additional analyses as the temporal variation in mound characteristics, I draw conclusions on the processes that are responsible for the observed differences in mound soils and off-mound soils.

In **Chapter IV** ("**Impact of *Macrotermes michaelseni* on soil fertility and plant growth**"), numbers 1, 2, 10 and to a certain degree number 4 of Fig. 1 are affected. The focus of this chapter is the question how *M. michaelseni* changes vegetation patterns through the construction of mounds and sheetings. In pot experiments, the growth rates of radish and sorghum plants on mound soil, sheeting soil and off-mound soil were measured and compared with *in situ* vegetation patterns at mounds. Analyses of the soils and plants were conducted to reveal the factors that were responsible for observed differences between the soil types.

Chapter V ("**Multi-scale pattern analysis of *Macrotermes* mounds**") stresses how intraspecific competition regulates the spatial distribution of *Macrotermes* mounds. This is done with regard to their size, as a surrogate for the size of the colony that inhabits the mound. In the context of this thesis, the question on distribution patterns of *Macrotermes* mounds is crucial. According to chapter III and IV, termite mounds heavily influence soil and vegetation patterns. In consequence, the density and spatial arrangement of mounds determine their quantity and the spatial arrangement on these patterns.

Chapter VI contains the **general discussion** of this thesis. I first discuss chapter II and bring the results in context with the following chapters. The contributions of chapters III to V to the current knowledge of termite mediated processes are then discussed on the basis of the schema that was presented in Fig. 1.

The BIOTA-project

This study was part of the large and interdisciplinary research program "Biodiversity Monitoring Transect Analysis in Africa" (**BIOTA**, www.biota-africa.org). BIOTA was funded by the German Federal Ministry of Education and Research from 2000 to 2010 and contributed to the "Convention on Biological Diversity" (CBD) of the United Nations. The main objectives of BIOTA were to assess and monitor biodiversity and its responds to land use and climate changes. The processes and mechanisms that are responsible for biotic changes were analysed, schemes for interventions were developed and tools for a sustainable land management that conserves biodiversity and its functions were established. Based on the achieved findings, decision making tools for land users and policy makers were developed.

BIOTA comprised four subprojects, each of them focussing on a different region of Africa. Within "**BIOTA Southern Africa**", roughly 200 participants from Germany, Namibia and South Africa were involved. Two different transects were established, along which several study sites (so called "Observatories") were located. The main transect runs from northern Namibia to the Cape Peninsula in southwest South Africa and is characterised by an extensive rainfall gradient. The northern end of this transect is located in a summer rainfall regime. The Woodland Savanna at this site receives 536 mm rainfall per year (global interpolations from WorldClim (Hijmans et al. 2005) for the period 1950–2000). Within Namibia, the rainfall decreases southwards. The Observatories close to the Namibian - South African border are lying in the transition zone between summer rainfall (Nama Karoo) and winter rainfall (Succulent Karoo) and receive less than 100 mm rainfall per year. Further south, within the winter rainfall regime of South Africa, the rainfall increases up to 689 mm per year (global interpolations from WorldClim (Hijmans et al. 2005) for the period 1950–2000) in the Fynbos biome of the Cape Peninsula. The second transect leads from west to east in the middle of Namibia. The Observatories at the Atlantic coast receive less than 20 mm rainfall per year. This transect then leads through the Namib Desert and the escarpment to the Thornbush Savanna in east Namibia with almost 400 mm rainfall per year. This information and the outcomes of BIOTA Southern Africa are published in the three-volume book "Biodiversity in southern Africa" (Jürgens et al. 2010, Schmiedel and Jürgens 2010, Hoffman et al. 2010).

Study sites

The biodiversity study presented in chapter II of this thesis was conducted on **13 different BIOTA-Observatories**. We selected solely sites that are located in the summer rainfall regime of Namibia. Amongst these, we excluded sites with similar abiotic conditions to achieve that the selected ones adequately represent different rainfall and land use intensities along the two transects. The location of each site is sketched in the map of Namibia in Fig. 12. Further information on the abiotic and biotic characteristics of these sites is given in Table 1 of chapter II and by Jürgens et al. 2010).

Chapters III to V focus on the **Thornbush Savanna biome** of central Namibia. The field works for these chapters were done at the Observatories Toggekry (chapters III and V) and Otjiamongombe (chapter IV). Savannas are characterised by an extensive cover of grasses with scattered trees. The Thornbush Savanna of central Namibia is used for cattle and game farming and trophy hunting; the proportion of the latter business increased largely during

the last decade. Intensively used farms show a reduced cover of perennial grasses and their productivity is additionally threatened by soil erosion and shrub encroachment. Common plant species of this region are *Stipagrostis uniplumis*, *Acacia tortilis*, *Acacia mellifera*, *Boscia albitrunca*, *Eragrostis* sp. and *Monechma genistifolia*.

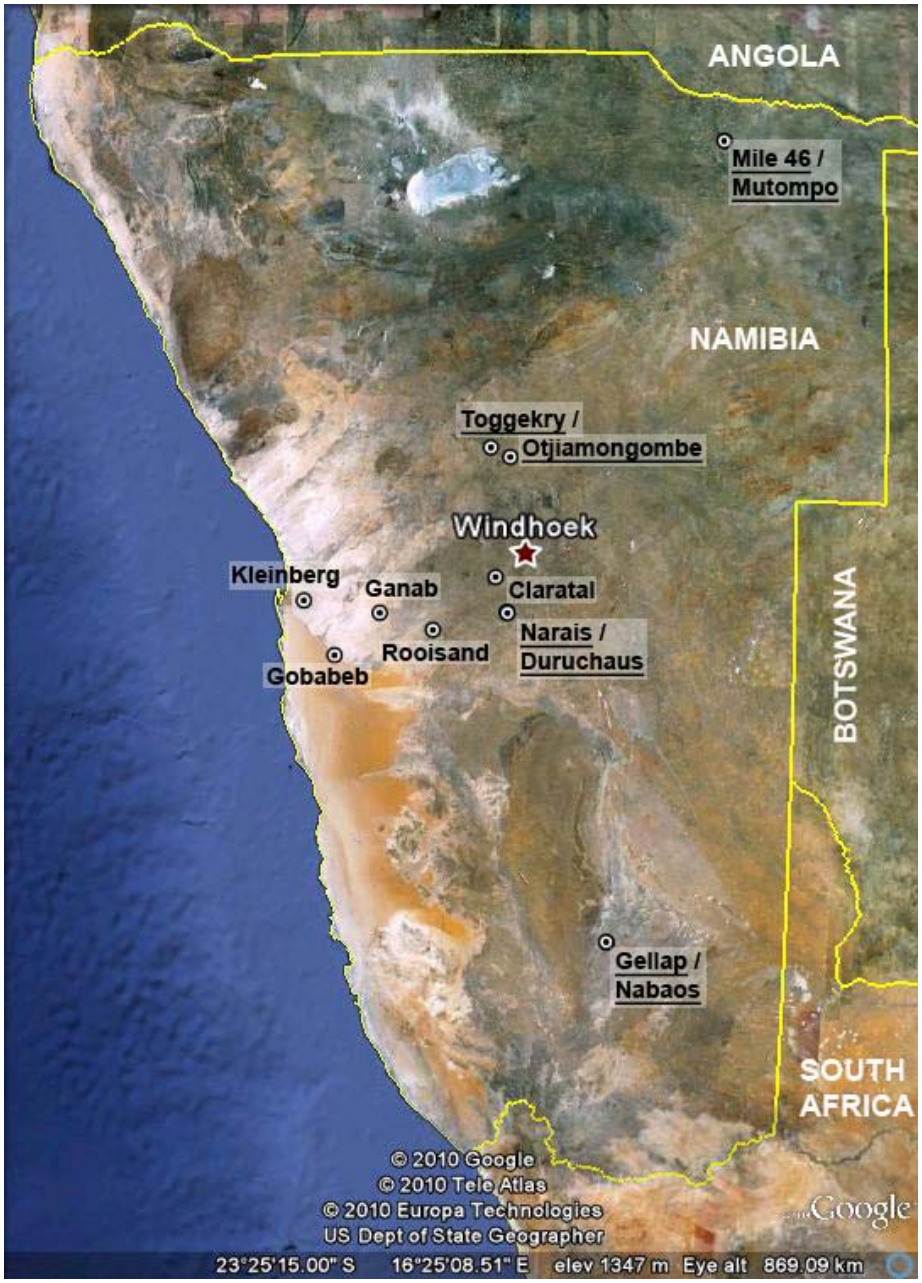

Fig. 12: Map of Namibia showing the locations at which the termite diversity was assessed. At the underlined sites, two farms with different land use systems are located close to each other.

The following descriptions of the Observatories Toggekry and Otjiamongombe cite passages of Jürgens et al. (2010), which were written to 90% by me, with A. Gröngröft and D.H. Haarmeyer as co-authors. At Toggekry, a BIOTA weather station was located. As the station was broken down during long periods during this study, the climate data I give here are based on global interpolations from WorldClim (Hijmans et al. 2005, see

http://www.worldclim.org) for the period 1950–2000, see also Jürgens et al. (2010) and Table 1 in chapter 2 of the present thesis. As the two main study sites (Toggekry and Otjiamongombe) are located 24 km from each other and hence exhibit similar climate patterns, I give the mean values of both sites.

Toggekry and Otjiamongombe receive on average 395 mm precipitation per year, but the amount varies largely between years. For example, at the farm house of Otjiamongombe, as less as 136 mm were recorded in 1995 in contrast to 808 mm in 2006. Roughly 90% of the annual precipitation is falling during the summer month. The mean annual temperature is 19°C. During the coldest month, the mean of the daily minimum temperature is 4°C, while the mean of the daily maximum temperature during the warmest month is 32°C.

The BIOTA Observatory **Toggekry** (commonly named Omatako) is situated approximately 60 km northwest of Okahandja in the Otjozondjupa region. The mean altitude is 1,519 m a.s.l. and the topography is flat to gently undulating. The soils are sandy to loamy and differ in colour from grey to reddish. The open Thornbush Savanna is dominated by *Acacia* species and grasses and bush encroachment by *Acacia mellifera* occurs in some areas. Over the last two decades, the farming system has changed from a commercial cattle farm to a hunting farm and the area of the farm has increased to approximately 15,000 ha. The "Omatako Hunting Ranch" is a family business and, amongst game species that are typical for that region, is host to species such as Sable Antelope (*Hippotragus niger*), Eland (*Taurotragus oryx*), Black- and Blue Wildebeest (*Connochaetes gnou*, *C. taurinus*, Mountain- and Burchell's Zebra (*Equus zebra hartmannae*, *E. burchelli*), Giraffe (*Giraffa camelopardalis*) and Black Rhinoceros (*Diceros bicornis*). Mounds built by the termite *Macrotermes michaelseni* are a widespread feature of the landscape on the farm and in the region.

The BIOTA Observatory **Otjiamongombe** (commonly called Erichsfelde) is located approximately 40 km north of Okahandja in the Otjozondjupa region. It lies 24 km southeast of the BIOTA Observatory Toggekry at a mean altitude of 1,495 m a.s.l. and, similar to Toggekry, the topography is almost flat. The Observatory is slightly inclined towards the north and is dissected by a small rivier. The unconsolidated substrates are mainly loamy in their texture. Adjacent to the rivier, a calcrete layer is exposed at the soil surface. The vegetation of this predominantly open Thornbush Savanna is dominated by *Acacia* species and grasses. Depending on the habitat and the intensity of disturbance by grazing and trampling animals, annuals can dominate over perennial climax grasses in the herbaceous layer. The 13,000 ha farm is privately owned and used for cattle farming, with a small proportion of income gained from hunting. Large herds of games species that are typical in this region occur on this farm, e.g. Oryx (*Oryx gazella*), Kudu (*Tragelaphus strepsiceros*), Eland (*Taurotragus oryx*) and Warthog (*Phacochoerus aethiopicus*). Mounds built by the termite *M. michaelseni* are widespread at this Observatory, as they are in the whole region.

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Chapter II

Biodiversity of termites along rainfall gradients in Namibia

Abstract

Termites have a strong impact on ecosystem functioning. They decompose large amounts of plant material, promote soil turnover and enhance the infiltration rate of rainwater through their building activities. We sampled termites at 13 sites along rainfall gradients in Namibia and identified 17 termite taxa belonging to 15 genera. No strong responses by termite fauna to the type of land-use were detected, probably due to the small sample size. Latitude, altitude and mean annual precipitation independently explained a significantly larger proportion of the variation of termite taxa diversity than expected by chance. Termite diversity increased with increasing precipitation and increasing Simpson index of vascular plant diversity at the sites. Mean annual precipitation explained more than 90% of the variation in taxa diversity and the Simpson diversity index of vascular plants explained 81%. Most probably, not only one factor, but a combination of climatic, pedological and botanical influences explains the variation in termite diversity across the study sites.

Keywords
Diversity, Ecosystem engineer, Isoptera, Land-use, Precipitation

Introduction

Termites strongly modify the ecosystems in which they live. They decompose large amounts of plant material (Collins 1981, Schuurman 2005) and therefore strongly influence the subsequent mineralization of nutrients by bacteria and fungi (Holt and Lepage 2000). Via their building of galleries, nests and, depending on the species, mounds, they promote soil turnover and hence influence the distribution of nutrients, the texture and the hydrological properties of soils (see reviews by Brian 1978, Wood and Sands 1978, Bignell and Eggleton 2000). Since termites have such a strong impact on ecosystem functioning they are counted amongst the so called "ecosystem engineers", which modulate the availability of resources to other species (Jones et al. 1994, Dangerfield et al. 1998, Lavelle 2002).

There is strong evidence from the literature that ecosystem properties greatly depend on the diversity, distribution and abundance of organisms (Hooper et al. 2005). This should especially hold true for ecosystem engineering species. Pringle et al. (2010) analysed termite mounds, which are hotspots of plant growth and animal abundance, and proved that their regularly distributed pattern enables a high abundance of mounds. In turn, this leads to high abundance, biomass and reproductive output of consumers across trophic levels.

On a global scale, termite diversity has been found to decrease with increasing latitude (Eggleton 2000) with the highest species richness of 50–80 species per hectare occurring in lowland tropical forests (Eggleton and Bignell 1995). Parallel to this decline in termite diversity, the abundance and biomass of termite colonies also declines towards the higher latitudes (Bignell and Eggleton 2000).

The abiotic factors responsible for the decreasing species richness with increasing latitude are not fully understood, although Bignell and Eggleton (2000) speculate that a drop in insolation and rainfall causes this pattern. Direct comparisons of termite species diversity at sites with different rainfall patterns are rare in the literature. Buxton (1981) revealed that the number of termite species declined along a gradient with decreasing rainfall in semi-arid southern Kenya. Zeidler (1997) analysed the genera distribution data obtained by Coaton and Sheasby (1972) and found a strong dependence of genera richness on the amount of annual precipitation in Namibia. In addition to rainfall, annual temperature and temperature range might also play large roles as activity patterns of termites such as e.g. *Hodotermes mossambicus* (Coaton 1958) and *Coptotermes lacteus* (Evans and Gleeson 2001) depend on air and soil temperatures.

To some extent, abiotic factors might also rule termite diversity patterns indirectly, via their impact on biotic factors such as plant biomass and plant diversity. For example, Jones et al. (2003) revealed a strong dependence of termite diversity on vegetation characteristics such as woody plant basal area, canopy height and the amount of dead wood.

Additionally, anthropogenic alteration of habitats within an ecosystem will often modify termite species richness and their abundance and activity. Most studies showed declining species richness and abundance with increasing land-use intensification (see review in Jones et al. 2003, Vasconcellos et al. 2010). However, the response of termite species to land-use changes will differ according to their feeding and nesting habits (Black and Okwakol 1997).

For example, Eggleton et al. (2002) revealed a decline in the species diversity of soil feeding termites, but an increase in wood feeding termite species diversity along a gradient of increasing anthropogenic disturbance.

Our study was part of a large, interdisciplinary research program, "BIOTA Southern Africa", which established standardised study sites along rainfall gradients at locations with

different land-use patterns in Namibia and South Africa. The project aimed to assess and monitor the biodiversity at these sites and to reveal the drivers and processes that are responsible for the observed patterns. The first objective of the present study was to compile an inventory of the termite taxa occurring on 13 different study sites of the BIOTA Southern Africa project in Namibia. The second aim was to test the hypotheses that termite diversity decreases with decreasing rainfall, decreasing vegetation cover and increasing anthropogenic land-use.

Methods

Study sites

Sampling took place at 13 BIOTA Southern Africa "Observatories", standardised study sites of 1 km² (Schmiedel and Jürgens 2005), in Namibia. The sites were located along two transects, both characterised by strong rainfall gradients. The first transect leads from northern Namibia close to the Angolan border to southern Namibia (Fig. 1, Table 1).

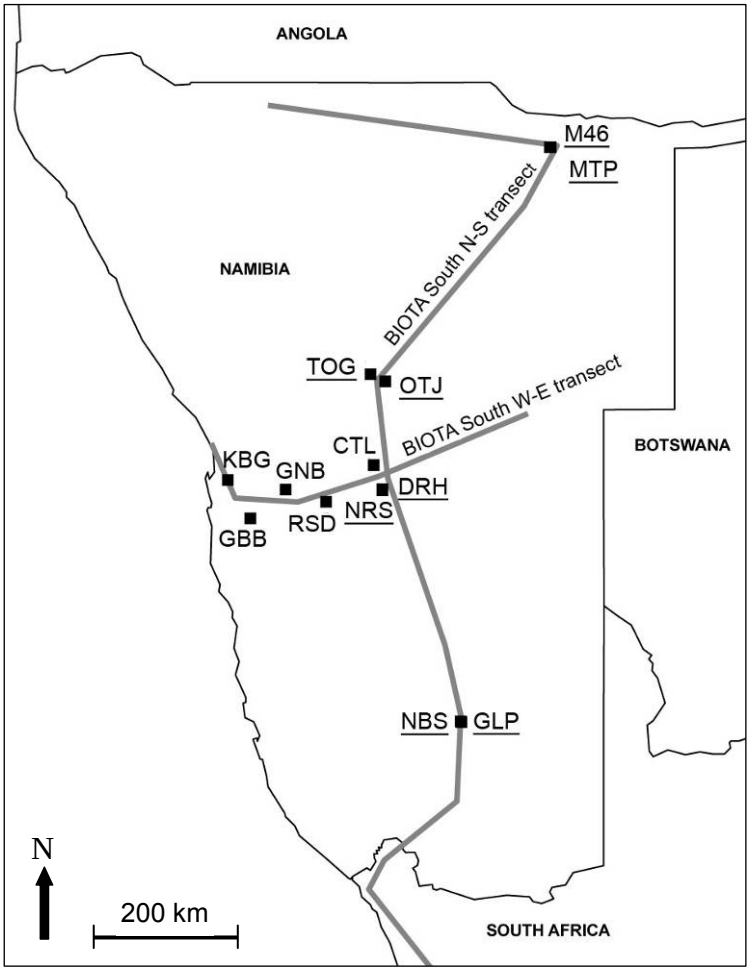

Fig. 1: Map of Namibia showing the location of the study sites along the BIOTA Southern Africa transects. Sites which are underlined belong to the twin-Observatories located along the north-south transect.

Table 1: Main characteristics of the BIOTA Observatories included in this study. Data follow Jürgens et al. (2010).

Tran-sect	BIOTA-Number and Name of Observatory	Abbre-viation	Lat. Long.	Biome	Altitude [m a.s.l.]	Mean annual temp. [°C][1]	Mean annual temp. range [°C][1,2]	Mean annual precipitat. [mm][1]	Precipitat. seasonality [%][1,3]	Simpson index (vascular plants)	Type and history of land use	Relative intensity of land use
N	01 Mile 46	M46	18.30 S 19.25 E	Woodland Savanna	1180	22.2	9.6	536	106	0.92	Research farming for cattle breeding	Low
	02 Mutompo	MTP	18.30 S 19.26 E	Woodland Savanna	1180	22.2	9.7	536	106	0.90	Cattle grazing	High
	04 Toggekry	TOG	21.50 S 16.73 E	Thornbush Savanna	1519	19.1	9.8	394	110	0.77	Farming with game for hunting	Medium
	05 Otjiamongombe	OTJ	21.60 S 16.94 E	Thornbush Savanna	1495	19.3	9.8	396	106	0.85	Farming with cattle and game for hunting	Medium
	39 Narais	NRS	23.12 S 16.90 E	Nama Karoo	1624	18.6	10.8	289	108	0.79	Farming with cattle	Low
	40 Duruchaus	DRS	23.13 S 16.90 E	Nama Karoo	1614	18.6	10.9	287	112	0.76	Farming with cattle and goats	Medium
	10 Gellap Ost	GLP	26.40 S 18.00 E	Nama Karoo	1099	20.5	12.9	153	106	0.67	Farming with sheep, cattle and horses	Medium
S	11 Nabaos	NBS	26.39 S 18.00 E	Nama Karoo	1045	20.8	12.9	146	103	0.62	Farming with goats, sheep and donkeys	High
W	34 Kleinberg	KBG	22.99 S 14.73 E	Namib Desert	188	17.6	5.6	16	90	NA	Conservation area	None
	35 Gobabeb	GBB	22.53 S 15.05 E	Namib Desert	419	20.9	6.6	21	84	NA	Conservation area	None
	36 Ganab	GNB	23.12 S 15.54 E	Namib Desert	995	19.5	7.0	129	130	0.60	Conservation area	None
	37 Rooisand	RSD	23.29 S 16.10 E	Thornbush Savanna	1160	19.5	8.5	200	125	0.77	Conservation area	Medium
E	38 Claratal	CTL	22.78 S 16.78 E	Thornbush Savanna	1865	17.9	10.1	335	110	0.90	Farming with cattle and game for hunting	Medium

[1] Data are based on global interpolations, mostly from WorldClim (Hijmans et al. 2005; see http://www.worldclim.org) for the period 1950–2000.
[2] Difference in the mean temperature between the coldest and the warmest month.
[3] Variability of the precipitation among the means of the 12 months, expressed as coefficient of variation.

Precipitation decreases along this transect southwards, from roughly 540 mm per year at Mile 46 (M46) and Mutompo (MTP) in the north to 150 mm at Gellap Ost (GLP) and Nabaos (NBS) in the south (Jürgens et al. 2010). The mean annual temperatures at these northern- and southernmost Observatories are only slightly higher, with 22.2°C at M46 (range in the mean temperature between the coldest and the warmest month: 9.6°C) and 20.5°C (range: 12.9°C) at GLP, respectively.

The west-east transect leads from the South Atlantic coast, through the Namib Desert up the escarpment to the highlands. The westernmost Observatory, Kleinberg (KBG), is located only 21 km inland from the coast and is characterised by hyper-arid conditions. Although the mean annual precipitation is less than 16 mm at this Observatory, it is characterised by high humidity as this site is exposed to frequent fogs approaching from a southwesterly direction. The mean annual temperature at KBG is 17.6°C (range: 5.6°C). The easternmost Observatory of the west-east transect is Claratal (CTL). It is situated in the "Khomas Hochland" 1865 m above sea level. The mean annual precipitation at this site is 387 mm and the mean annual temperature of 17.9°C (range: 10.1°C) is similar to KBG.

At all sites, the variation in rainfall between years is large and increases with decreasing rainfall. The standard deviation of annual total rainfall amounts given in percentage of the mean annual rainfall is 30−40% at M46 and MTP but reaches 60−70% at GLP and NBS in the south. This rainfall variation coefficient is even higher close to the coast at KBG (>100%) but decreases in an easterly direction to 40−50% at CTL (Mendelsohn et al. 2003).

All of the study sites show pronounced seasons, with rainfall occurring mainly during the summer months of January, February and March. The differences in precipitation between summer and winter are marked, ranging between as little as 8%−14% winter precipitation (proportion of precipitation from April to September relative to the annual precipitation) at the Observatories along the north-south transect and 11%−29% winter rainfall along the west-east transect (Jürgens et al. 2010).

Along the north-south transect, in each case two of the Observatories are located close to each other but are characterised by different land-use intensity or different kinds of land-use. Otjiamongombe (OTJ) is situated 24 km southeast of its sister site Toggekry (TOG), but all other pairs of Observatories are situated only a few tens of metres apart from one another. In this paper, we refer to these pairs of Observatories as "twin-Observatories".

Sampling protocol

Sampling took place at the twin-Observatories along the north-south transect in February/March 2005, April/May 2005, September 2006, April/May 2007 and April/May 2009. At the Observatories along the west-east transect, we sampled in February/March 2005, April/May 2005 and September 2006. In each of the sampling periods, we used the following methods at each Observatory to collect the termites:

i) Direct sampling: We searched for two person-hours for termites over the whole Observatory area, looking beneath suitable habitat structures such as stones, logs and bark.
ii) Baiting: We distributed a total of 28 toilet paper rolls and 28 pieces of wood across two different subplots at each Observatory. We checked these bait stations for termites after 1–2 weeks and once more after 2–3 months.
iii) Section sampling: In each section sized 2 x 5 m, we sampled for 15 person-minutes. At each Observatory, two to three sections were distributed each in four different 1-ha^2 plots, so that in total ten sections that covered the most important habitat types of the

Observatory were sampled. At the twin-Observatories, we sampled seven additional sections in September 2006 and April/May 2007.

iv) Scrapes: In each of a total of ten sections, we dug out eight soil scrapes and searched for termites in these scrapes. Each scrape consisted of a 10 x 10 x 12 cm block of topsoil that we excavated with a shovel. We did the scraping only during the September 2006 sampling period at the twin-Observatories.

v) Pitfall traps: We filled ten pitfall traps (opening diameter: 7.2 cm) with 67% ethanol and left them in the field for 48 hours. Pitfall trapping was undertaken at the twin-Observatories only, and only in September 2006 and April/May 2007.

vi) Additional sampling: This category comprises the sampling of specimens beyond the standardised scheme. It includes encounters beyond the standardised sampling periods and collections at the bait stations at additional points in time.

Storage and identification of material

We stored the specimens in 80% ethanol and classified them according to identification keys developed by Coaton and Sheasby (1972) and Uys (2002). We only attempted to identify soldiers, except in the case of *Hodotermes mossambicus*, the workers of which can easily be distinguished from other species.

Termite abundance index

We developed an index of termite abundance to establish how many termites were present at a site. This termite abundance index counts in how many single collection events a termite was found, irrespective of its cast or taxon. In other words, it counts in how many of the direct sampling events, at bait stations, sections, scrapes and pitfall traps a termite specimen was encountered. In contrast to the relative species abundance index that is often calculated in ecological studies, the termite abundance index does not refer to the abundance relative to other taxa but counts the absolute number of encounters with termites irrespective of their taxon or cast. As a result of the smaller sampling effort at the Observatories along the west-east transect in comparison to the twin-Observatories (see sampling protocol above), no direct comparison between the Observatories of the two transects is possible. Similarly, the termite abundance index cannot be compared between the twin-Observatories M46 and MTP on the one hand and further Observatories of this transect on the other hand. The reason for this is again the sampling effort: we checked the baits at M46 and MTP only once, but twice at the other Observatories along this transect. Summing up all sampling periods, the maximum theoretical value of the abundance index is 225 for M46 and MTP, 281 for the other twin-Observatories and 155 for the Observatories along the west-east transect.

Relationship between number of taxa and environmental variables

The number of taxa at Observatory CTL was recorded as zero, as we encountered no soldiers here. In comparison, we found six taxa at the Observatories Narais (NRS) and Duruchaus (DRH), although these Observatories were as little as 40 km distant from CTL and showed similar climatic patterns (Table 2). As the reason for the low abundance of termites at CTL can most likely be attributed to soil characteristics (see “Discussion”), we excluded CTL from further analyses.

We used linear hierarchical partitioning to identify those environmental predictor variables whose independent correlation with the total number of taxa was strong. As predictor variables, we included latitude, altitude, mean annual temperature, mean annual temperature range, mean annual precipitation and precipitation seasonality. The mean annual temperature range refers to the difference in the mean temperature between the coldest and the warmest month, whereas the precipitation seasonality constitutes the variability of the precipitation among the means of the 12 months, expressed as a coefficient of variation. The corresponding values for each Observatory were taken from Jürgens et al. (2010). In the method of hierarchical partitioning, the improvement of the fit of all possible models with a particular predictor variable is compared to the equivalent model without that predictor variable (Chevan and Sutherland 1991). We used a randomisation routine to reveal the predictor variables that independently explained a larger proportion of the variance than expected by chance. If the z-score obtained from observed and predicted values based on 100 randomisations was larger than or equal to 1.65, the proportion of the variance which could be independently explained by the predictor variable was significantly ($p \leq 0.05$) larger than expected by chance (Walsh and Mac Nally 2008). The relationships between number of taxa and those variables that independently explained the distribution of termite taxa significantly were analysed with linear regressions. Similarly, we ran a linear regression for the number of termite taxa against the Simpson diversity index for vascular plants obtained from Jürgens et al. (2010). For this variable, no data were available for the Observatories KBG and Gobabeb (GBB). Therefore, we calculated a second regression of the number of termite taxa against mean annual precipitation, this time excluding KBG and GBB to achieve comparability with the regression of the Simpson index.

All calculations were done with the software R (v. 2.10.1; R Development Core Team, 2009). For the hierarchical partitioning, we used the package *hier.part* (v. 1.0-3; Walsh and Mac Nally 2008).

Results

In total, we collected roughly 650 samples and allocated the termites of these samples to 17 different taxa in 15 different genera (Table 2). Apart from *Hodotermes mossambicus* and *Psammotermes allocerus*, all belonged to the family Termitidae. We encountered the highest number of taxa at the northernmost twin-Observatories M46 and MTP (Fig. 2). No termites were encountered at KBG, the Observatory with the lowest annual precipitation. At CTL we encountered termite workers on only two occasions. These workers could not be determined.

Hodotermes mossambicus was distributed widely along the two transects and was collected from ten of the 13 Observatories (Table 3). This species occurred most frequently at Observatory DRH in central Namibia. *Psammotermes allocerus* occurred most frequently at M46, but we also encountered this species frequently at other Observatories with the exception of TOG and OTJ. At TOG and OTJ, we encountered fungus growing Macrotermitinae taxa frequently, especially the genus *Macrotermes*. Although we encountered *Fulleritermes* (belonging to the family Nasutitermitinae) only at M46 and MTP, this species was relatively common there. Similarly to *H. mossambicus* and *P. allocerus*, we found the genus *Trinervitermes* to be distributed widely at many Observatories along the transects.

Table 2: List of all species encountered. The names are grouped according to their family (subfamily). The classification of feeding groups is derived from Zeidler (1997).

Taxon	Author	Feeding group
Hodotermitidae		
Hodotermes mossambicus	(Hagen, 1853)	g
Rhinotermitidae		
Psammotermes allocerus	Silvestri, 1908	w, l
Termitidae (Macrotermitinae)		
Allodontermes sp.	Silvestri, 1914	f
Macrotermes michaelseni	(Sjöstedt, 1914)	f
Microtermes sp.	Wasmann, 1902	f
Odontotermes okahandjae	Fuller, 1922	f
Odontotermes sp. 1	Holmgren, 1912	f
Odontotermes sp. 2	Holmgren, 1912	f
Termitidae (Termitinae)		
Amitermes sp.	Silvestri, 1901	w, l
Angulitermes sp.	Sjöstedt, 1924	w/s
Lepidotermes sp.	Sjöstedt, 1924	h
Microcerotermes sp.	Silvestri, 1901	w, l
Promirotermes sp.	Silvestri, 1914	w/s
Termitidae (Nasutitermitinae)		
Baucaliotermes hainesi	(Fuller, 1922)	l, d
Fulleritermes sp.	Coaton, 1963	h
Rhadinotermes coarctatus	(Sjöstedt, 1902)	w, l
Trinervitermes sp.	Holmgren, 1912	g

f: fungus grower; g: grass feeder; h: humus feeder; l, d: litter and dung feeder; w, l: wood and litter feeder; w/s: wood/soil interface feeder.

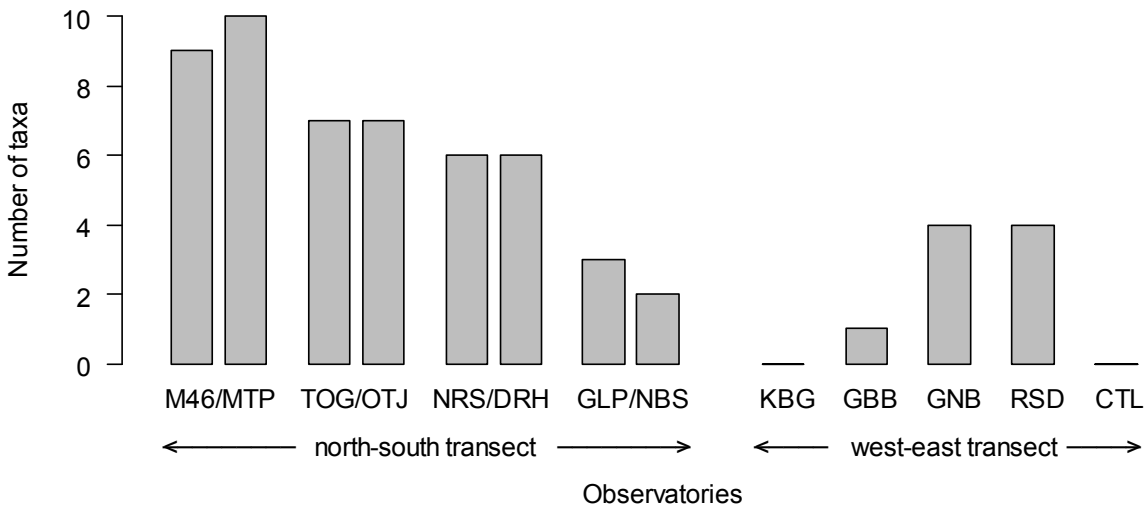

Fig. 2: Number of taxa at the Observatories.

Table 3: Occurrence of termite taxa at the Observatories.

Taxon	Observatories along the N-S transect								Observatories along the W-E transect					Total no. of Observatories with this taxon
	M46	MTP	TOG	OTJ	NRS	DRH	GLP	NBS	KBG	GBB	GNB	RSD	CTL	
Hodotermes mossambicus	√	√	√	√	√	√	√	r	-	-	√	√	-	10
Psammotermes allocerus	√	√	-	-	√	√	√	√	-	√	√	√	-	9
Allodontermes sp.	√	√	-	√	-	-	-	-	-	-	-	-	-	3
Macrotermes sp.	-	-	√	√	-	-	-	-	-	-	-	-	-	2
Microtermes sp.	√	r	√	√	-	-	-	-	-	-	-	-	-	4
Odontotermes okahandjae	-	-	-	√	-	-	-	-	-	-	-	-	-	1
Odontotermes sp. 1	-	-	√	√	√	√	-	-	-	-	-	-	-	4
Odontotermes sp. 2	r	√	-	-	-	-	-	-	-	-	-	-	-	2
Amitermes sp.	-	√	-	-	√	√	-	-	-	-	√	-	-	4
Angulitermes sp.	-	-	r	-	√	r	-	-	-	-	-	-	-	3
Lepidotermes sp.	-	-	-	-	-	-	-	-	-	-	-	√	-	1
Microcerotermes sp.	r	√	-	-	-	-	-	-	-	-	-	-	-	2
Promirotermes sp.	√	√	-	-	-	-	-	-	-	-	-	-	-	2
Baucaliotermes hainesi	-	-	-	-	-	-	√	-	-	-	-	-	-	1
Fulleritermes sp.	√	√	-	-	-	-	-	-	-	-	-	-	-	2
Rhadinotermes sp.	-	-	√	-	-	-	-	-	-	-	-	-	-	1
Trinervitermes sp.	√	√	√	√	√	r	-	-	-	-	√	√	-	8

r: rare occurrence of the taxon at the Observatory; i.e. the taxon was not found during the standardized sampling, but during additional sampling.

The total number of taxa did not differ greatly within the Observatories with different land-use systems. We encountered *Amitermes* at MTP, but this species was absent at M46. *Angulitermes* and *Rhadinotermes* were among the species we detected at TOG, but not at its twin-Observatory OTJ. At OTJ on the other hand, *Allodontermes* and *Odontotermes okahandjae* occurred, both being absent at TOG. The Observatories NRS and DRH displayed the same taxa, while the termite fauna of GLP and NRS differed in the occurrence of *Baucaliotermes hainesi* at GLP.

The termite abundance index showed a distinct pattern (Fig. 3). The abundance of soldiers and workers irrespective of their taxon differed largely between the twin-Observatories NRS and DRH, the abundance index being much higher at DRH. Although GLP showed a remarkably high frequency of *H. mossambicus*, the abundance at this Observatory was slightly lower than at NBS. The abundance index appeared not to correspond to the rainfall gradient along the north-south transect.

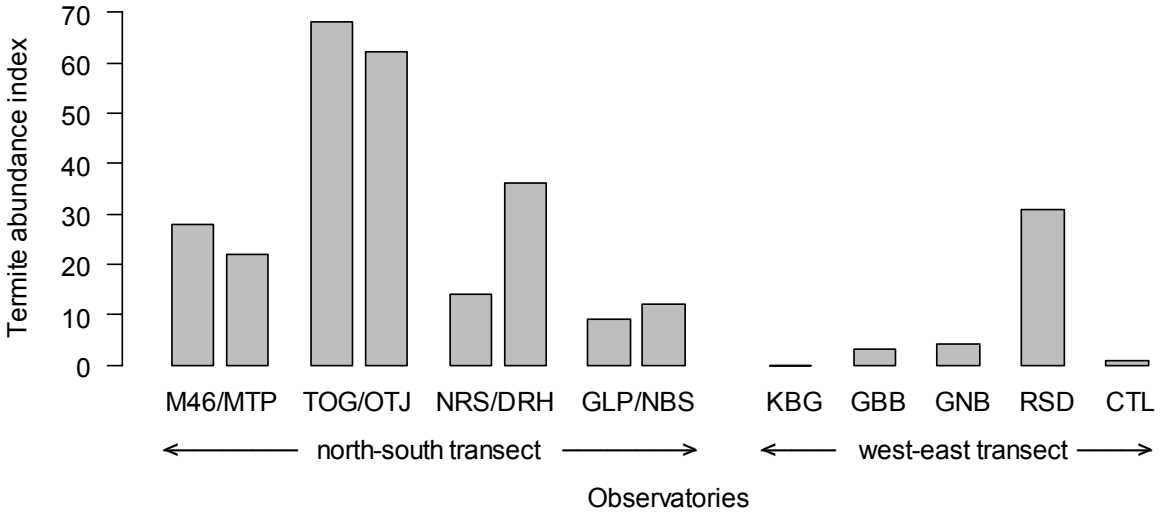

Fig. 3: Termite abundance index of the Observatories. This index is the number of samples in which a termite worker or soldier was sampled. Note that the sample size was smaller at the Observatories along the west-east transect compared to the north-south transect. Within the north-south transect the bait stations at the Observatories M46 and MTP were checked only once, compared to twice at the other Observatories.

With the exception of Observatory CTL where there were only two encounters with termite workers, the number of taxa and the termite abundance index roughly increased with increasing rainfall at the Observatories along the west-east transect. We excluded the data from CTL from further analyses, as the near-absence of termites at this Observatory was most probably a result of the rocky substrate rather than other factors.

We analysed the dependence of termite taxa on different geographical and climatic patterns along the transects in more detail using the hierarchical partitioning procedure (Fig. 4). Latitude, altitude and mean annual precipitation were correlated independently with the total number of taxa more strongly than expected by chance. In contrast, the seasonality of precipitation (variability of the precipitation among the means of the twelve month), the

mean annual temperature and the mean annual temperature range (difference in the mean temperature between the coldest and the warmest month) displayed weak independent correlation with the number of taxa.

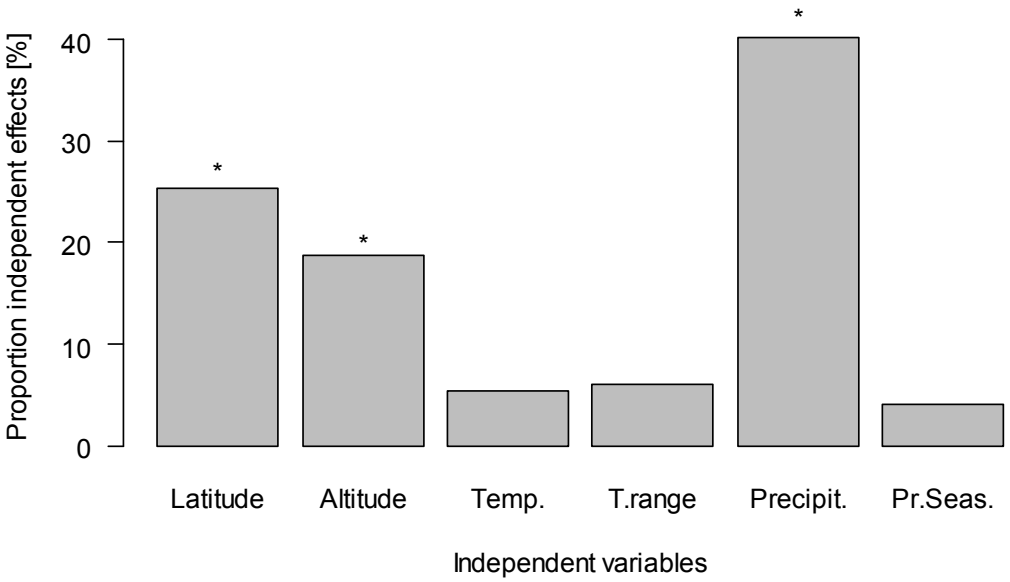

Fig. 4: Percentage of variance in the total number of taxa explained by each of the eight geographical and climatic variables independently, determined by hierarchical partitioning. Variables marked with an asterisk were identified as independently explaining a significantly larger proportion of the variance than expected by chance. Data from Observatory CTL were excluded. Temp.: Mean annual temperature; T.range: Mean annual temperature range; Precipit.: Mean annual precipitation; Pr.Seas.: Precipitation seasonality.

The slopes of the linear regression models for latitude, altitude and mean annual precipitation for all Observatories excluding CTL differed significantly from zero (Table 4). The squared correlation coefficient was largest for mean annual precipitation (0.957), indicating that rainfall explains 96% of the variation in termite taxa diversity. Excluding Observatories KBG and GBB as well, the slopes of the regressions of the Simpson index and precipitation both differed significantly from zero ($p < 0.001$). Rainfall still explained more variation (94%) in the number of termite taxa than did the Simpson index (81%; see also Fig. 5).

Table 4: Results for the slopes of linear regression models to environmental variables against total number of termite taxa.

	n	Estimate	Std. error	*t*-value	*p*-value	R^2
Latitude	12[(1)]	-0.963	0.244	-3.948	0.003	0.609
Altitude	12[(1)]	0.005	0.002	3.218	0.009	0.509
Mean annual precipitation	12[(1)]	0.017	0.001	14.827	<0.001	0.957
Mean annual precipitation	10[(2)]	0.016	0.002	10.823	<0.001	0.936
Simpson index (vascular plants)	10[(3)]	21.236	3.616	5.873	<0.001	0.812

[(1)] CTL was excluded due to its rocky substrate.
[(2)] CTL was excluded due to its rocky substrate; GBB and GNB were excluded to achieve comparability to the Simpson index.
[(3)] CTL was excluded; no data were available for KBG and GBB.

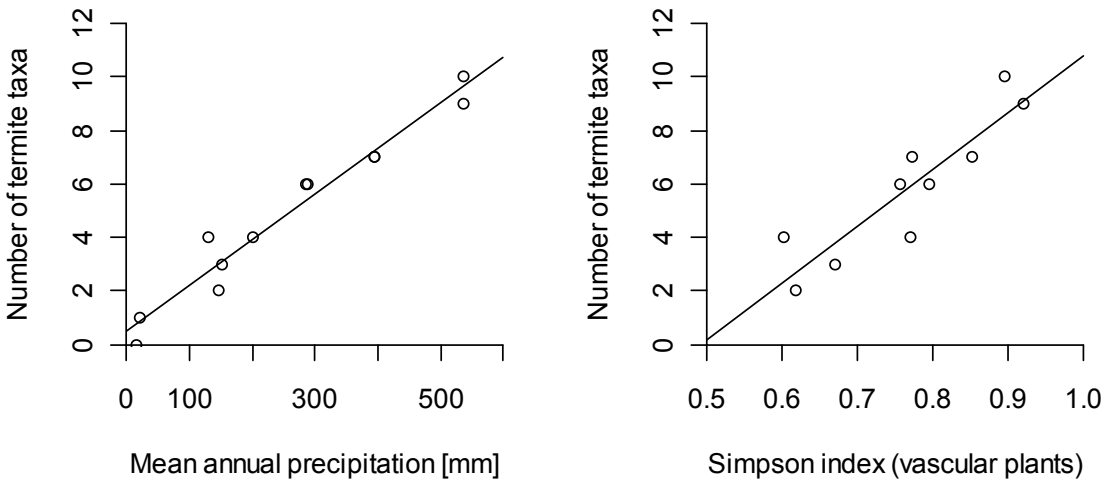

Fig. 5 Relationships between mean annual precipitation (left), Simpson diversity index for vascular plant taxa (right) and number of termite taxa. Data from Observatory CTL were excluded; no data were available for the Simpson index for Observatories KBG and GBB.

Discussion

Taxa encountered at the Observatories

In total, we encountered 17 different taxa of 15 genera at the 13 Observatories sampled (Tables 2, 3). According to Uys (2002), 54 genera comprising 165 species are described from southern Africa. In their "National Survey", an extensive survey of termites in southern Africa, Coaton and Sheasby (1972) found 33 of these genera in Namibia. The total number of species in Namibia remains unclear, as at least a third of the genera (e.g. *Odontotermes*, *Microtermes* and *Microcerotermes*) need taxonomic revision (Uys 2002). In the present study, we encountered less than half of the genera sampled during the National Survey. The far more exhaustive sampling effort and the extensive spatial scale of the latter study explain this difference. During the National Survey, sampling took place over the whole of Namibia, along the major roads at points 16 km apart. In total, samples were taken from more than 9,000 colonies at 790 localities.

In an attempt to gauge the completeness of the present study, we compared the genera found at the Observatories with those one would expect based on the results of the National survey. For this purpose, we examined the genera encountered by Coaton and Sheasby (1972) at localities that were closest to our study sites. When comparing this data, one should bear in mind that our study was restricted to Observatories of a 1-km² area whereas the data from the National Survey was extensively collected.

During our study, we encountered nine and ten genera respectively at the northern-most Observatories M46 and MTP. According to Coaton and Sheasby (1972), many more genera occur in this region, namely *Cubitermes, Epicalotermes*, *Macrotermes*, *Noditermes*, *Ovambotermes*, *Spatulitermes*, *Termes* and the *Anoplotermes* group. On rare occasions, *Lepidotermes*, *Neotermes*, *Schedorhinotermes* and *Unguitermes* were also found in this area during the National Survey. Adjacent to Observatories TOG and OTJ, *Amitermes*, *Epicalotermes* and *Microcerotermes* were encountered by the National Survey in addition to the genera that were found by us. Only rarely present in the National Survey at sites close to TOG and OTJ were *Allodontermes*, *Angulitermes* and *Rhadinotermes*. At NRS and DRH, one would expect *Allodontermes*, *Lepidotermes*, *Microcerotermes*, *Microtermes* and *Promirotermes* in addition to the genera listed in Table 3 for these Observatories. According to the National Survey, additional to the three genera we sampled at GLP and NBS, *Amitermes* and *Microcerotermes* are distributed widely in that region. Besides these two genera, some more but sparsely distributed genera occur in this southern region as *Angulitermes*, *Lepidotermes*, *Microtermes* and *Promirotermes*.

We encountered no termites at the easternmost and driest Observatory KBG. However, *P. allocerus* and *H. mossambicus* were detected by the National Survey in this area. They are presumably restricted to habitats characterised by more vegetation cover than KBG. Only four vascular plants occur at KBG (Jürgens et al. 2010) which could provide food for the wood and litter feeding *P. allocerus*. Grasses occur only after good rainfall events, but their sparse coverage and the absence of grasses during years with meagre rainfall seem to be responsible for the lack of *H. mossambicus* at this Observatory. We attribute the lack of *H. mossambicus* at GBB during our study to the small sample size, as we encountered this species on several occasions around the research station Gobabeb that is located only two kilometres from the Observatory. In contrast to the National Survey, we did not find *Epicalotermes* at GBB, a genus that nests mostly in dead branches and stump of living trees, but also in exposed dead wood. We explain this as being due to the absence of

large trees at this site, although they do grow in dense stands on the banks of the nearby Kuiseb River. In addition to the four taxa encountered at both Ganab (GNB) and Rooisand (RSD), according to the National Survey one would expect *Epicalotermes* and *Microtermes* at GNB, and both these taxa as well as *Angulitermes* and *Promirotermes* at RSD. We encountered termites on only two occasions at CTL, and at both times only workers, of which classification is demanding. The lack of further termites at CTL is appears remarkable as *Amitermes*, *Angulitermes*, *Cubitermes*, *Hodotermes*, *Lepidotermes*, *Microcerotermes*, *Odontotermes*, *Promirotermes* and *Trinervitermes* were detected at neighbouring sites during the National Survey. However, the landscape at CTL is rocky and mountainous with steep slopes and shallow soil. These soils seem to be too shallow to allow termite colonies to build nests.

In contrast to the remarkably large difference compared to the National Survey, the distribution of taxa encountered in the present study deviate little from the results of Vohland and Deckert (2005) at the twin-Observatories M46/MTP, OMT/ERF and GLP/NBS. However, in contrast to Vohland and Deckert (2005), we did not encounter *Schedorhinotermes* at M46/MTP, although we did sample *Trinervitermes* and *Fulleritermes* which they did not encounter. The present survey revealed more genera, e.g. *Allodontermes*, *Microtermes* and *Rhadinotermes*, at OMT/ERF compared to Vohland and Deckert (2005). No deviations remain when regarding GLP and NBS together, however, in contrast to our study Vohland and Deckert (2005) did encounter *Baucaliotermes* not only at GLP but also at NBS.

In conclusion, the present study underestimates the diversity of termite taxa, especially at the northerly Observatories. We see the reason for this in the combination of the limited size of an Observatory and the small sample size of our study. However, since we encountered the similar genera to Vohland and Deckert (2005), we assumed that we detected the most common taxa occurring at the sites.

The differences in taxa richness between sites with different land-use systems most probably do not represent the real differences between taxa occurring at the sites. For example, there is no apparent reason for the absence of *Amitermes* at M46 although it occurs at the related site MTP. *Odontotermes okahandjae*, which we encountered at OTJ but not as its twin-Observatory TOG, is associated with the heavier soils found e.g. on river floodplains and riverbanks (Coaton and Sheasby 1971). As such features are not present at TOG, we assume that the absence of *O. okahandjae* at TOG is a consequence of differences in habitat structures. We sampled *Baucaliotermes hainesi* at GLP but not at its twin-Observatory NBS, while Vohland and Deckert (2005) encountered this species at both sites. According to Uys (2002), *B. hainesi* forages mainly at night. We saw this species at GLP approximately one hour before sunset. Consequently, the absence of this species at NBS might not only be a result of the sparser grass and litter cover at this site, but also a question of the sampling effort and time. In general, apart from the sampling effort, differences in geological and pedological properties might prevail over the land-use differences as, for example, at TOG/OTJ.

Termite abundance index

In order to understand the effects of varying land-use on termite communities, it might be more informative to include the frequencies and densities of termite encounters at a site. Such data might reflect the faunal responses in a more telling way, as species negatively affected by a certain land-use system might still occur at the site, but at low densities or in special and rare habitats only. When analysing the termite abundance index, one should bear in mind that the index does not discriminate between termite taxa, although the eco-

logical demands of termites and their impact on their ecosystem does depend on the taxon being considered.

The termite abundance index within the twin-Observatories M46/MTP, TOG/OTJ and GLP/NBS did not differ remarkably. (Fig. 3). In contrast, the site DRH had a much higher index compared to its twin-Observatory NRS that was characterised by less intensive land-use. These differences occurred for section sampling (ten termite encounters at DRH compared to six at NRS), as well as for the bait stations (twenty termite encounters at DRH compared to two at NRS). Section sampling at DRH mainly detected *H. mossambicus* and unidentified workers, while baiting attracted *P. allocerus* and to a lesser extent unidentified workers. Founding colonies of *H. mossambicus* establish most successfully on overgrazed areas that are denuded of grass cover during the time when swarming flights take place (Coaton 1958). The higher stocking rate with cattle, horses and formerly goats at DRH compared to the much lower stocking rate with cattle at NRS might be responsible for the prevalence of *H. mossambicus* at DRH. No similar pattern is described for *P. allocerus*. The frequent acceptance of bait by this species at DRH in contrast to NRS might be an effect of the sparser vegetation at the former site, leading to a higher rate of utilisation of the available food items.

At the Observatories M46 and MTP, we checked baits only once and not twice as at the other sites (see "Methods"). Hence, the termite abundance index at M46/MTP is lower compared to TOG/OTJ. Further sampling at the bait stations would have led to a rise in the abundance index up to a possible maximum of 82 for M46 and 77 for MTP. Indeed, examination of the few remaining bait stations revealed heavy use during later sampling periods. We therefore assume that a further sampling procedure at the bait stations at M46 and MTP would have raised the termite abundance index of these sites up to a level higher than that of TOG and OTJ.

Regarding the Observatories along the west-east transect, the termite abundance index is extraordinarily high at RSD. At this site, the bait stations were utilised heavily while at GNB only one bait station was utilised by termites in February 2005. At RSD, termites were sampled from 14 baits in February 2005 and from 15 baits in May 2005. With the exception of CTL and the twin-Observatories M46/MTP, the termite abundance index along the two transects roughly increases with increasing mean annual precipitation.

Relationship between number of taxa and environmental variables

Of the eight variables tested, mean annual precipitation, latitude and altitude independently explained a significantly larger proportion of the variance in termite diversity than expected by chance (Fig. 4). The significant effect of altitude appears to result from a correlation of this variable with rainfall and vegetation patterns at the west-east transect. Along this transect, rainfall increases with altitude and we assume that rainfall and the related vegetation patterns are more influential for termite taxa diversity than altitude.

On a global scale, decrease in species diversity with increasing latitude is a widely recognized pattern. This pattern also holds for the generic richness of termites (Eggleton 2000). However, in southern Africa, with increasing latitude towards the Cape region in South Africa, the generic richness of termites again increases (Eggleton et al. 1994). The effect of latitude on species diversity is indirect, as many essential climatic variables are correlated with latitude. Bignell and Eggleton (2000) speculate that a drop in insolation or rainfall causes the decrease of termite genera with increasing latitude. In the present study, latitude was indeed correlated significantly with mean annual precipitation (Pearson's product-moment correlation, $t = -3.972$, $df = 10$, $p < 0.01$).

Rainfall showed the highest proportion of independent effects on the variation in number of taxa and a close positive relationship to the number of taxa (Fig. 5). A strong relationship between rainfall and termite diversity was also found e.g. by Buxton (1981) and Zeidler (1997). The latter author analysed the data of the National Survey (Coaton and Sheasby 1972) and revealed a significant positive relationship between most termite genera and rainfall in Namibia. However, some genera such as *Angulitermes*, *Baucaliotermes* and *Psammotermes* showed a negative relationship with rainfall in the study of Zeidler (1997), while the pattern of *Rhadinotermes* was insignificant. In our study, we encountered *Angulitermes* at Observatories with moderate precipitation only, i.e. TOG, NRS and DRH. We sampled *Baucaliotermes* at GLP. This genus occurs in the more arid regions of southern Namibia, where it replaces *Trinervitermes*, which occurs in the more grassy areas with higher rainfall (Coaton and Sheasby 1972). We encountered *Psammotermes* at almost all of the Observatories and hence can draw no conclusions as to the relationship between this species and annual precipitation. The same holds true for *Rhadinotermes*, which we sampled at TOG only.

Relationship between number of termite taxa and Simpson index for vascular plant taxa

Mean annual precipitation itself might not directly be the main factor ruling termite taxa richness, rather, vegetation patterns may play the most decisive role. Rainfall in general is related positively to primary productivity (Rosenzweig 1968) and botanical diversity (O'Brian et al. 1998). On a global scale, Eggleton et al. (1994) showed a positive response of termite diversity to increasing net primary production. In our study, the number of termite taxa increased with increasing diversity of vascular plants (Fig. 5). The corresponding squared correlation coefficient was large, indicating that the Simpson index for vascular plants explains as much as 81% of the variation in termite taxa diversity.

In our study, the mean annual precipitation explained still a slightly higher proportion of the variation in termite taxa than did the Simpson index for vascular plant taxa. However, no general conclusions can be drawn from this fact as our study was not extensive enough to answer this question. Most probably, not one single factor but a combination of rainfall, plant biomass, plant diversity and soil characteristics rule termite diversity. Additionally, the precision of the variables measured play a role. In our study, data for mean annual precipitation covers the years 1950 to 2000. However, the Simpson index was ascertained during only one year at the sites GNB and RSD, and over six to nine years at the other Observatories. Hence, site-specific deviations from the long-term mean during the years of investigation influence the Simpson index to a larger extent than the precipitation.

Conclusion

In total, we encountered 17 termite taxa belonging to 15 different genera. This is far less diversity than expected, especially at Observatories with relative high rainfall (M46/MTP, TOG/OTJ). However, we assume that we successfully sampled the most abundant taxa at all Observatories.

We revealed a strong positive relationship between termite taxa diversity and mean annual precipitation. Hence, a decline in annual precipitation, as predicted in the course of global climate change for Namibia (Solomon et al. 2007), will in general – directly or indirectly via changes in vegetation patterns – lead to a decline in termite taxa diversity. On the

scale of a 1 km² Observatory, termite community composition and abundances of certain termite taxa might change. As most termite species fulfil important task in ecosystem functioning, it is desirable to establish how the reaction of termites to environmental changes will affect ecosystem processes (Zeidler 1997).

We can draw no conclusions as to the effect of anthropogenic land-use on the termite fauna from our data. The number of termite taxa and the abundance of termites were too low to soundly answer this question. To tackle this task, a sampling protocol that is adapted to arid regions should be developed and tested. This protocol should be designed in a way that allows the comparison of the abundance of different termite taxa at the study sites. In addition, the difficulties in the identification of termite workers need to be addressed to enhance the sampling success in areas with low termite densities.

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Chapter III

Macrotermes michaelseni mounds enhance the spatial heterogeneity of nitrogen distribution

Abstract

Recently published papers underline the importance of mound building by termites for maintaining habitat heterogeneity, thereby affecting species richness and ecosystem functioning. For example, it has been shown that the composition and abundance of plant and animal species vary with distance from termite mounds. However, studies addressing the underlying factors that govern these patterns are sparse in the literature. In this paper, we investigate the soil properties of *Macrotermes* mounds in central Namibia, quantify the amount of soil eroding from them and compare the composition of mound material with that of soil samples at different distances from the mounds. We firstly review the pertinent literature and then compare the findings with own results from *Macrotermes* mounds. Contrary to the expectations based on the review, the nitrogen contents of the Namibian mounds were much higher compared to the adjacent subsoil. The high nitrate contents can be attributed to nitrogen, which is transported by water more easily in the less loamy soils of the central Namibian mounds and accumulates via evaporation processes on the mound surface. The soil composition differed substantially between the central Namibian mounds and adjacent topsoils. Although roughly 245 kg ha^{-1} $year^{-1}$ of soil eroded from the mounds, no differences were detected between samples collected at 1, 5 and 25 m distances from the mounds. The amount of soil eroded from an average sized inhabited mound theoretically covers a 1 m wide circular ring around the pediment of this mound up to a height of 2.4 mm per year, although this calculation contains a considerable error probability. Through building activities, such as the construction of foraging galleries and sheetings, termites mix different soil layers. It seems as if through such activities, surface soil is mixed with deeper soil layers at a rate that does not allow the eroding soil to alter the composition of the adjacent topsoil substantially.

Keywords
Isoptera, Mound erosion, Namibia, Soil nutrient distribution, Termite mound

Introduction

Habitat heterogeneity is important in generating species diversity in an ecosystem (Tews et al. 2004, McClain and Barry 2010). Species richness in turn has been found to be correlated positively with biomass production (Zhu et al. 2010) and positively affects ecosystem services (Naeem et al. 1994, Balvanera et al. 2006). In the same context, Tylianakis et al. (2008) showed that the correlation between biodiversity and ecosystem functioning is greatest in those ecosystems in which limiting resources are spatially heterogeneously distributed.

Recent studies demonstrate that termite mounds in African savannas generate the spatially heterogeneous distribution of e.g. plant species, atmospheric N fixation rates and animal abundances (Traoré et al. 2008, Moe et al. 2009, Brody et al. 2010, Fox-Dobbs et al. 2010, Pringle et al. 2010). To understand the mechanisms responsible for these patterns, it is essential to identify the underlying factors. Most probably, the causal factors of these patterns are soil properties that differ between mound and off-mound sites.

In general, it has been found that termite mounds have higher organic matter content, total N and C contents and exchangeable Ca, Mg, K and Na contents compared to adjacent soils. For reviews on the differences between the physical and chemical properties of termite mounds and adjacent soils, see Lee and Wood (1971), Wood and Sands (1978), Lobry de Bruyn and Conacher (1990), Holt and Lepage (2000) and Sileshi et al. (2010). However, differences have been found between regions, termite taxa (Lobry de Bruyn and Conacher 1990) and based on the primary food source of the termites (Black and Okwakol 1997). Hence, when comparing mound properties across different studies, attention has to be paid to the termite taxon which has built the mound. This has been largely neglected in the past. Additionally, the control samples have to be chosen with care. Mounds of Macrotermitinae are commonly built of subsoil (Wood 1988) and should be compared with samples from adjacent subsoil to reveal modifications to soil characteristics. Most termite mounds have higher organic matter contents than subsoils and this might be attributed to the saliva used to cement the soil particles. The chemical properties of mound materials might vary over time. Soluble ions for example, might be dissolved and subsequently washed from the mounds during rainfall.

The mound soil is gradually eroded by rain and wind and thereby re-distributed to the surrounding terrain. At a site with 1,100 mm precipitation per year, Lepage (1984) calculated the erosion from *Macrotermes bellicosus* mounds to be 0.37 m^3 $mound^{-1}$ $year^{-1}$ extrapolated to 9.4 m^3 ha^{-1} $year^{-1}$. This represents an average soil thickness of 0.75–1 mm over one year. Further data on soil erosion from *Macrotermes* mounds and termite mounds in general are sparse. To characterise the spatial extent of the habitat heterogeneity evoked by termite mounds, it is not sufficient to know the amount of soil eroding from mounds. It is also important to assess how far this soil is distributed from the mound. In this context, Arshad (1982) found the percent of fine particles such as clay and silt to decrease over increasing distance from the mound. However, to our knowledge, other literature concentrates only on vegetation patterns dependent on the distance from the mound, but does not examine underlying factors such as the patterns of the soil properties which might lead to the respective vegetation pattern.

In this paper, we aim to characterise soil heterogeneity generated by the fungus growing termite genus *Macrotermes*. To begin with, we summarise current knowledge of the soil characteristics of termite mounds compared to adjacent top- and subsoils. We hypothesise that similar patterns to those found for *Macrotermes* mounds in east, west and central

African savannas hold for *Macrotermes* mounds in a semi-arid savanna in Namibia. We then concentrate on the temporal alteration of the soil on the mound surface and presume that mound material, recently brought to the mound surface by termites, contains more soluble ions than older mound material exposed to rain. We also focus on the question up to which distance the adjacent soil in a mound's vicinity is recognisably modified by mound material. We investigate how much mound material is eroded from the mounds by rain and hypothesise that the continuous erosion of mound material has a significant effect on the topsoil up to at least 1 m distance from the mound.

Methods

Current knowledge of *Macrotermes* mound characteristics

To review studies which analysed *Macrotermes* mound material we focused on the papers included in the reviews of Sileshi et al. (2010) and Lobry de Bruyn and Conacher (1990). We also searched for further papers comparing *Macrotermes* mound soils with adjacent soils using several keywords in Google Scholar, Web of Science and the cited reference search at Web of Science. We included papers that analysed

i) mounds build by *Macrotermes* species larger than 1 m high (thereby excluding young, undeveloped mounds that feature different shapes and maybe also different soil characteristics than mature mounds),
ii) the surface of the mound chimney (excluding those papers that mixed samples of the surface and the inner structures),
iii) topsoil and subsoil (deeper than 50 cm) samples of the adjacent soil and
iv) inhabited or only recently abandoned mounds.

In all studies meeting the above-given requirements, the original values of the soil characteristics were listed for each sample. We compared the mound soils with the lowest soil stratum given in the papers. An exception was made for Nye (1955), where only the pH was analysed in the lowest stratum. Here, we included the second lowest stratum in the analyses. Data on the C/N ratio were available from four different publications (see supplementary Table S1). The C/N ratio given in Abe et al. (2009) refers to the ratio of total C to total N (C_t/N_t), while the ratios given in Arshad (1981), Boyer (1973) and Hernández and Febres (1989) refer to the ratios of organic C to total N (C_{org}/N_t). We assumed that inorganic C comprises only a negligible proportion of the total C content and did not differentiate between the C_t/N_t and C_{org}/N_t ratio.

To account for methodological differences between the studies, we calculated the natural logarithm of the ratio of mound soil values to adjacent subsoil values. This procedure is similar to the log response ratio used in common meta-analyses (Hedges et al. 1999).

Study site

The following studies were undertaken at the BIOTA Observatory Toggekry, a 1 km^2 site located in the central Namibian Thornbush Savanna (21.51°S, 16.73°E) at an altitude of 1,519 m a.s.l. (Jürgens et al. 2010). During the period from 1950 to 2000, mean annual temperature was 19.1°C and the range between the mean temperatures of the coldest and the warmest month was 9.8°C. Rainfall occurs mainly during the summer months from

January to March with an annual mean of 394 mm, although this can vary considerably between years (Hijmans et al. 2005, Jürgens et al. 2010).

Characteristics of *Macrotermes* mounds in central Namibia

We randomly chose 26 mounds inhabited by *Macrotermes michaelseni* and took soil samples from the chimney of the mounds at breast height. The samples were collected in equal quantities from mound surface to 10 cm below it. As a control for each mound, we included analyses from soil profiles published in Petersen (2008). The distance between each profile and its mound varied between 10 and 50 m. We compared the mound soils with three different strata from this soil profile:

i) topsoil: 0–10 cm depth,
ii) upper subsoil: the soil horizon located below the topsoil; the lower boundary of this stratum was at 35 cm depth averaged for all profiles, with a maximum depth of 65 cm,
iii) lower subsoil: the soil horizon that includes the depth of 75 cm (mean range: 50–113 cm).

We analysed the pH value, total C, N and P contents, C_{org}/N_t ratio and EC values of the samples. As is usual in the literature, we subsequently refer to the C_{org}/N_t ratio as the C/N ratio. For a description of the analytical methods see supplementary Table S2.

We did not analyse the soil texture. However, as some elements are known to be strongly correlated with clay concentration in the soil we ran a multiple regression with data obtained from a total of 1,139 soil samples of different depths from the same study site. Using the programme ORIGIN, we included the total contents of Al, Na, K, Ca, Mg, P, Ti, Fe and Mn (analysed with X-ray fluorescence) as independent variables and clay as the dependent variable. The regression revealed that 78% of the overall variation in the clay content can be explained by the total contents of Al, Mg, Ti, Fe and Mn. We used the equation obtained by the multiple regressions to calculate a clay index “clayMR” that represents the clay content of the samples:

$$\text{clayMR} = -7.0 + 6.4\,\text{Al} - 0.8\,\text{Mg} - 11.0\,\text{Ti} + 1.3\,\text{Fe} - 3.9\,\text{Mn} \qquad \text{(eqn 1)}$$

where clayMR = clay content [weight per cent] (approximated via the multiple regression), Al = total Aluminium, Mg = total Magnesium, Ti = total Titanium, Fe = total Iron, Mn = total Manganese, each in g kg^{-1}.

We compared the mound samples with those of the adjacent soil profiles using a linear mixed effects model. The plot numbers of the paired samples, each of the latter comprising one mound and its corresponding reference soil profile, were included as a random factor. Differences between the soil types were analysed with Tukey’s multiplicity-adjusted pairwise comparisons. We ran the linear mixed effects model with the software R (v. 2.10.1; R Development Core Team 2009) using the *lmer* function implemented in the package *lme4* (Bates and Maechler 2010). Post-hoc comparisons were performed with the *glht* function of the package *multcomp* (Hothorn et al. 2008).

Temporal alteration of *Macrotermes* mound surface material

To reveal how mound material changes in the course of its exposure to rain, wind and sunlight, we initially collected material from the surface (0–10 cm) of twelve mounds which showed no sign of recent construction. We then excavated a hole of 30–50 cm in diameter in

the outer wall of the mound until an internal channel was exposed. The following day, we sampled the material with which the openings had been repaired by termites. Analyses comprised the texture, pH- and EC values (see supplementary Table S2). We compared the characteristics of new vs. old mound material with repeated measures ANOVAs using R (v. 2.10.1; R Development Core Team 2009). Prior to the test, EC values were transformed to their natural logarithm to distribute the variances of the residuals homogeneously.

Magnitude of soil eroding from *Macrotermes* mounds

We determined the amount of soil that was washed from 14 termite mounds by rain. To this end we chose seven inhabited and seven uninhabited mounds that represented the size spectrum of all mounds.

At the base of each mound we clamped four strong plastic bags aligned north, south, east and west to collect the eroding mound material. We used nails to attach the 65 cm wide opening of the bags flush to the soil surface and used wire to keep the bags open 10–15 cm above the soil level. Metal droppers positioned on each side of the bags stabilised the construction. On rare occasions, when larger pieces of the mound chimney broke from the mound, soil accumulated on top of the bags. This material was disregarded.

We collected the soil that eroded during five different rainfall events separately. The amount of precipitation during each of these events was measured with a manual rain gauge. We oven-dried the soil that had accumulated in each bag at 105°C until a constant weight was reached and weighted the samples. For each mound and each rainfall event, we estimated the amount of soil eroded from the entire mound. For each mound, the ratio of the mound perimeter to the width of all four bags was calculated. This value was then multiplied by the amount of soil that eroded into the four bags of the mound being considered.

Influence of soil eroding from *Macrotermes* mounds on the characteristics of adjacent topsoil

Within each of four major habitats at the site (Jürgens et al. 2010), we randomly chose one termite mound built by *Macrotermes michaelseni*. From these mounds, we took soil samples along four transects that were oriented to the four cardinal points of the compass and leading outwards from the mounds. Sample positions were the chimney of the mound, the mound's base, its pediment and distances of 1, 5 and 25 m from the outer margin of the pediment. Each sample comprised a block of topsoil of 0–10 cm depth and was analysed with regard to its pH value, total C and N content, C/N ratio and EC value. Additionally, for each sample the index ClayMR was determined from the total contents of Al, Mg, Ti, Fe and Mn as described by eqn 1 (see supplementary Table S2 for the analytical methods). We displayed the differences in sample composition in a NMDS plot.

Prior to analyses, the values of total C, N P and the EC value were $\log_e$-transformed and each variable was normalised (according to the term's usage in PRIMER, Clarke and Gorley 2006), so that the mean of each variable was 0 and its standard deviation equal to 1. The resemblance matrix was generated based on Euclidean distances. We excluded one sample with missing values and two samples with extreme outliers. Each of these samples originated from the mound's base. Based on the same resemblance matrix, we subsequently ran an ANOSIM with 999 simulations to validate the differences in the samples displayed in the NMDS ordination. We present no *p* values for the pairwise comparison as they depend heavily on the sample size, whereas the *R* statistics are a more absolute measure (Clarke and Gorley 2006). Both NMDS and ANOSIM were carried out with PRIMER (Plymouth Routines in

Multivariate Ecological Research, version 6). Additionally, for one of the four mounds, we analysed the nitrate contents of the 24 samples taken from the different mound features and the corresponding transects.

Results

Current knowledge of *Macrotermes* mound characteristics

We found five published studies that compared mound material of *Macrotermes* species with adjacent subsoil and fulfilled the requirements mentioned in the methods (see Table 1). From these, we extracted data concerning 13 *Macrotermes* mounds and the corresponding reference soils. The range of physical and chemical soil properties presented differed between the studies (supplementary Table S1).

Table 1: Details of studies which compared soil properties of *Macrotermes* mounds with adjacent subsoil.

Author(s) and year of publication	No. of mounds included in this review	Country	Annual precipitation [mm]	Species	Depth of lower subsoil sample [cm]
Abe et al. 2009	3	Nigeria	1100	*M. bellicosus*	58–120
Arshad 1981	6	Kenya	460–470	*M. subhyalinus* and *M. michaelseni*	80–120
Boyer 1973	1	Central African Republic	1600	*M. bellicosus*	100
Hernández and Febres 1989	1	Ivory Coast	1300	*M. bellicosus*	40–100
Nye 1955	2	Nigeria	1230[(1)]	*M. nigeriensis*	30–76

[(1)] precipitation was not specified in Nye (1955), but taken from Nye (1954).

Mound soils contain much higher clay and less sand and silt fractions compared to the adjacent topsoils (Fig. 1). However, clay and sand proportions of the mounds did not differ from those of the adjacent subsoils. The pH values of the mound soils were only slightly higher compared to the top- and subsoils. Organic C, total N, total P values and the C/N ratio of the mound soils were much lower compared to topsoils, but slightly higher compared to the subsoil. No clear trends were found for exchangeable Ca, Mg, K and Na of the mound soils compared to topsoils, while the levels of Ca and K were greater in the mounds compared to subsoils. The standard deviation of the C/N ratio was small, although this ratio was given as a C_t/N_t ratio in the case of Abe et al. (2009) and a C_{org}/N_t ratio in the cases of Arshad (1981), Boyer (1973) and Hernández and Febres (1989).

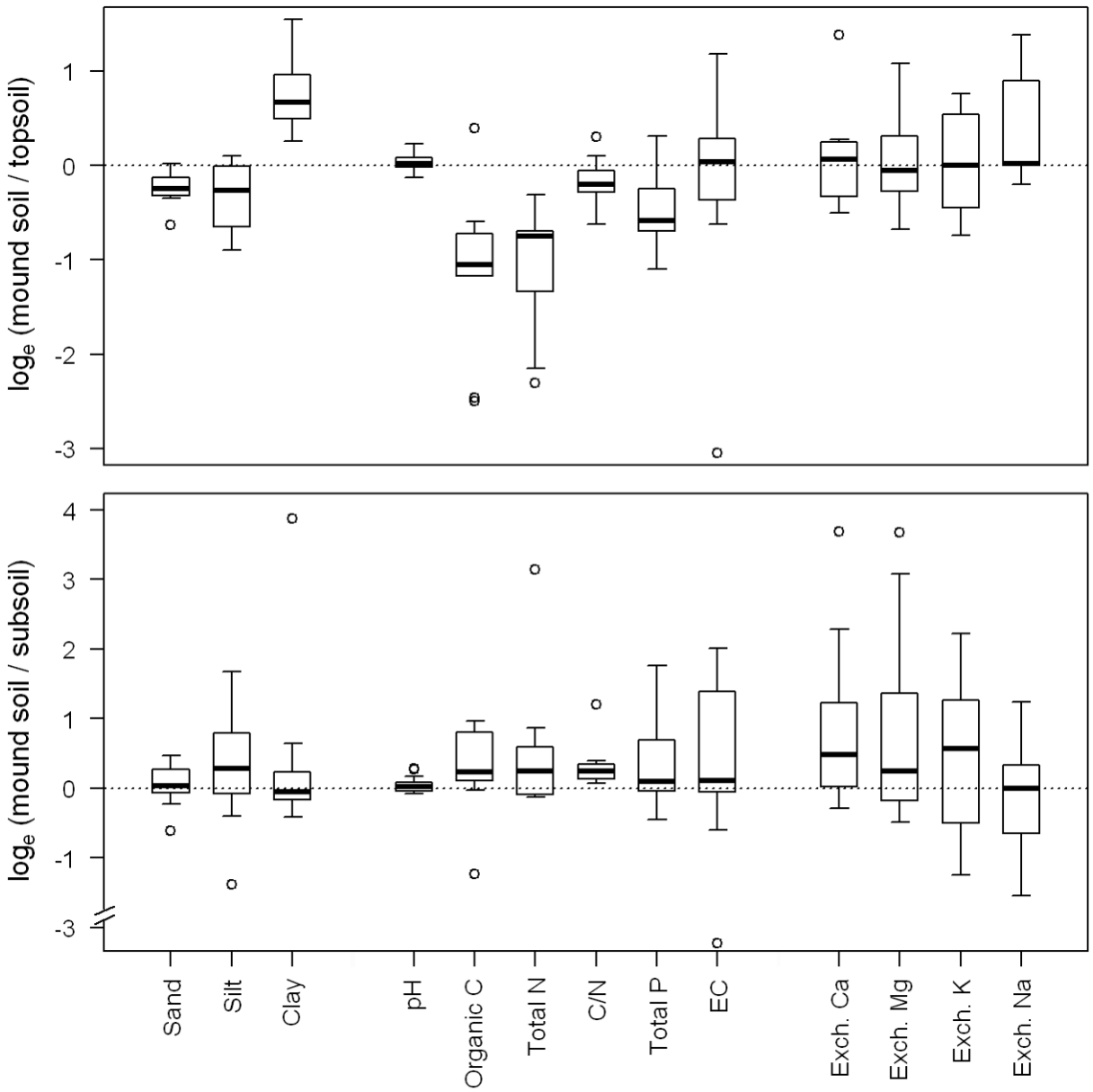

Fig. 1: Log response ratio of soil properties of *Macrotermes* mounds compared to adjacent topsoils (above) and subsoils (below). Data were taken from the papers listed in Table 1. Values >0 indicate that the value of the respective characteristic was higher in the mound soils compared to the adjacent soils. For Abe et al. (2009), the C/N ratio refers to C_t/N_t, for Arshad (1981), Boyer (1973) and Hernández and Febres (1989) it refers to C_{org}/N_t. Sample size ranges between 9 and 13 mounds, see supplementary Table S1.

Characteristics of *Macrotermes* mounds in central Namibia

The clay contents of all mounds were greater than the adjacent topsoil. In comparison to the subsoil, the mounds of the studies reviewed contained similar clay proportions, but those in central Namibia were significantly greater.

While the pH value of the mounds was significantly higher compared to all the strata of the adjacent soil profile, the total C content was only higher in comparison to the lowest stratum (Fig. 3). The level of inorganic C was below the detection limit for most samples. Mounds in central Namibia featured unexpectedly high total N contents, 3.0 times that of the adjacent topsoil and 2.7 times that of the lowest soil stratum of the soil profile. In accordance with this, mounds featured a significantly lower C/N ratio compared to the top- and subsoil. This contrasts strongly with the findings of the studies reviewed which revealed an increase in the C/N ratio of mounds compared to the subsoil. The total P contents of the different soils showed no significant patterns. Lastly, the EC values of the samples showed similar patterns to those of the total N contents.

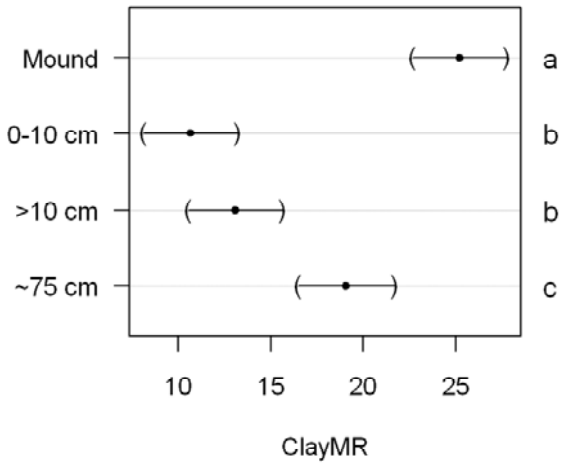

Fig. 2: Estimates and 95% confidence intervals obtained from the linear mixed effects model for a clay index derived from a multiple regression of total micronutrient content. Results of Tukey's pairwise *post hoc* comparisons are displayed on the right side of each graph: Pairwise comparisons differed significantly at $p < 0.05$ if they do not share the same letter.

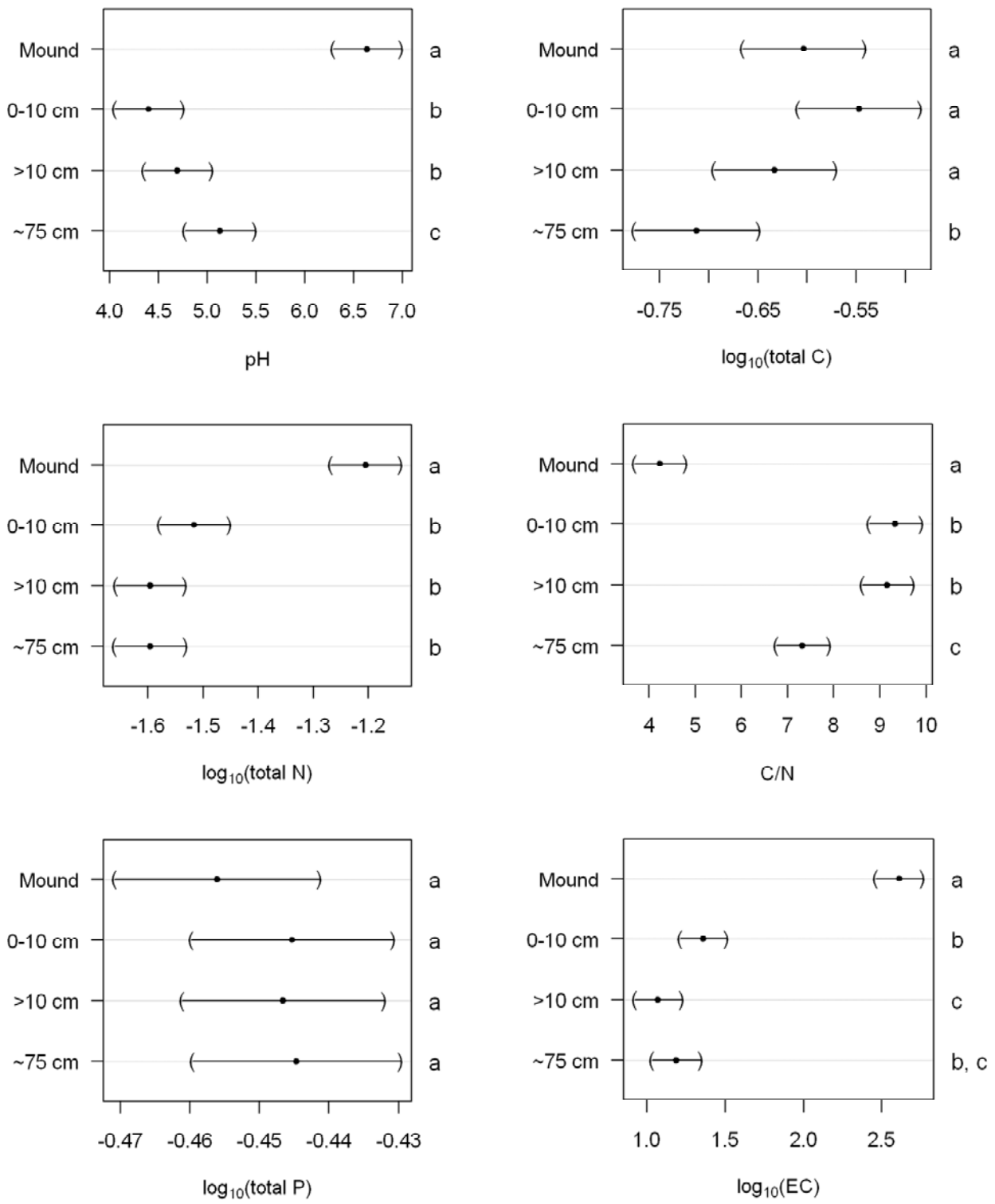

Fig. 3: Estimates and 95% confidence intervals obtained from the linear mixed effects model for different soil characteristics. Results of Tukey's pairwise *post hoc* comparisons are displayed on the right hand side of each graph: Pairwise comparisons differed significantly at $p < 0.05$ if they do not share the same letter.

Temporal alteration of *Macrotermes* mound surface material

Soil material used by termites for recent mound construction did not differ in its texture and pH value from material which had been exposed to sunlight, wind and rain for some time (Table 2). However, the EC values of older material were significantly greater than that of newer mound material.

Table 2: Mean (standard deviation) of the soil characteristics of new and old mound material derived from twelve mounds.

	New material	Old material	*p*-value
Sand [%]	59.6 (3.5)	59.4 (4.0)	0.88
Silt [%]	10.6 (1.7)	10.9 (1.3)	0.64
Clay [%]	29.8 (3.3)	29.7 (4.1)	0.97
pH	6.5 (0.5)	6.5 (0.6)	0.84
EC [µS cm^{-1}]	80.0 (103)	264.7 (429)	0.01

The *p*-values are obtained from repeated measures ANOVAs. EC values were transformed by the natural logarithm before running the ANOVA.

Magnitude of soil eroding from *Macrotermes* mounds

The mean quantity of soil collected during the five rainfall events from each of the 14 mounds was 5 kg (interquartile range: 4–8 kg). Extrapolated to the whole mound, this becomes 13 kg (IQR: 8–19 kg) per mound. More soil eroded from inhabited mounds than from uninhabited ones (Table 3).

According to Petersen (2008), the bulk density of the soils is about 1.6 g cm^{-3} and this figure was used to help calculate how much soil is deposited within a 1 m wide ring around the edge of the mound pediment. Firstly, imagine an annulus with the inner radius being the outer margin of the pediment of a mound and the outer radius being 1 m larger than the inner one. Secondly, the amount of soil eroded during the five rainfall events summed up to 0.70 mm (IQR: 0.22–1.01 mm) for the total surface of an inhabited mound. Thirdly, the total rainfall during the period in which eroding mound material was collected amounted to 114 mm, less than a third of the mean annual precipitation at this site (394 mm per year). Therefore, if one accounts for the actual annual rainfall then the amount of soil eroded per inhabited mound will fill a 1 m wide ring around the mound with a 2.4 mm (IQR: 0.8–3.5 mm) layer of soil per year. For uninhabited mounds, the height of this soil layer would be 1.0 mm (IQR: 0.8–1.3 mm).

Table 3: Amount of soil eroded from seven inhabited and seven uninhabited termite mounds during five rainfall events.

Date	Rainfall [mm]	Median (interquartile range) of soil eroded from inhabited termite mounds [kg][(1)]	Median (interquartile range) of soil eroded from uninhabited termite mounds [kg][(1)]
23.–24.3.2005	20	0.8 (0.6–2.7)	0.7 (0.5–1.2)
13.2.2006	20	9.0 (2.5–19.9)	6.4 (3.5–8.7)
15.2.2006	16	2.2 (0.7–2.9)	1.0 (0.6–1.1)
21.–22.2.2006	20	1.7 (0.5–2.5)	0.6 (0.4–0.9)
1.–17.3.2006	38	4.4 (1.8–12.0)	2.4 (1.0–3.2)
Sum	114	18.8 (9.5–45.1)[(2)]	11.6 (8.1–13.7)

[(1)] calculated from four subsamples per mound.
[(2)] the sum of all rain events was calculated separately for each mound.

Influence of soil eroding from *Macrotermes* mounds on the characteristics of adjacent topsoil

The NMDS-ordination of soil characteristics analysed from samples taken from the chimney, base and pediment of the mounds as well as from 1, 5 and 25 m distances from the pediment revealed strong differences between the samples taken from the mound soil and the off-mound topsoil (Fig. 4). These differences were less pronounced but still apparent in mound number 1.

The NMDS did not reveal strong differences between the three sample locations on the mounds. Similarly, the samples taken at the three distances from the mounds did not differ largely in their characteristics. The same trends held when analysing the data with a two way crossed ANOSIM. The global test for differences between the four mounds across the six sample positions confirmed significant differences between mounds (R = 0.649, $p < 0.001$). The differences between sample positions across all mounds were significant as well (R = 0.643, $p < 0.001$). Pairwise comparisons revealed strong differences between the three mound and the three off-mound samples (Table 4). Within the mounds, soil characteristics did not differ between the mound chimney and base, but between chimney and pediment, as well as between base and pediment (R = 0.456 and R = 0.578 respectively). The ANOSIM also confirmed the similarity of the samples taken at a distance of 1, 5 and 25 m from the pediment. Nitrate concentrations of mound number 2 were 456-fold higher compared to the adjacent topsoil (Fig. 5).

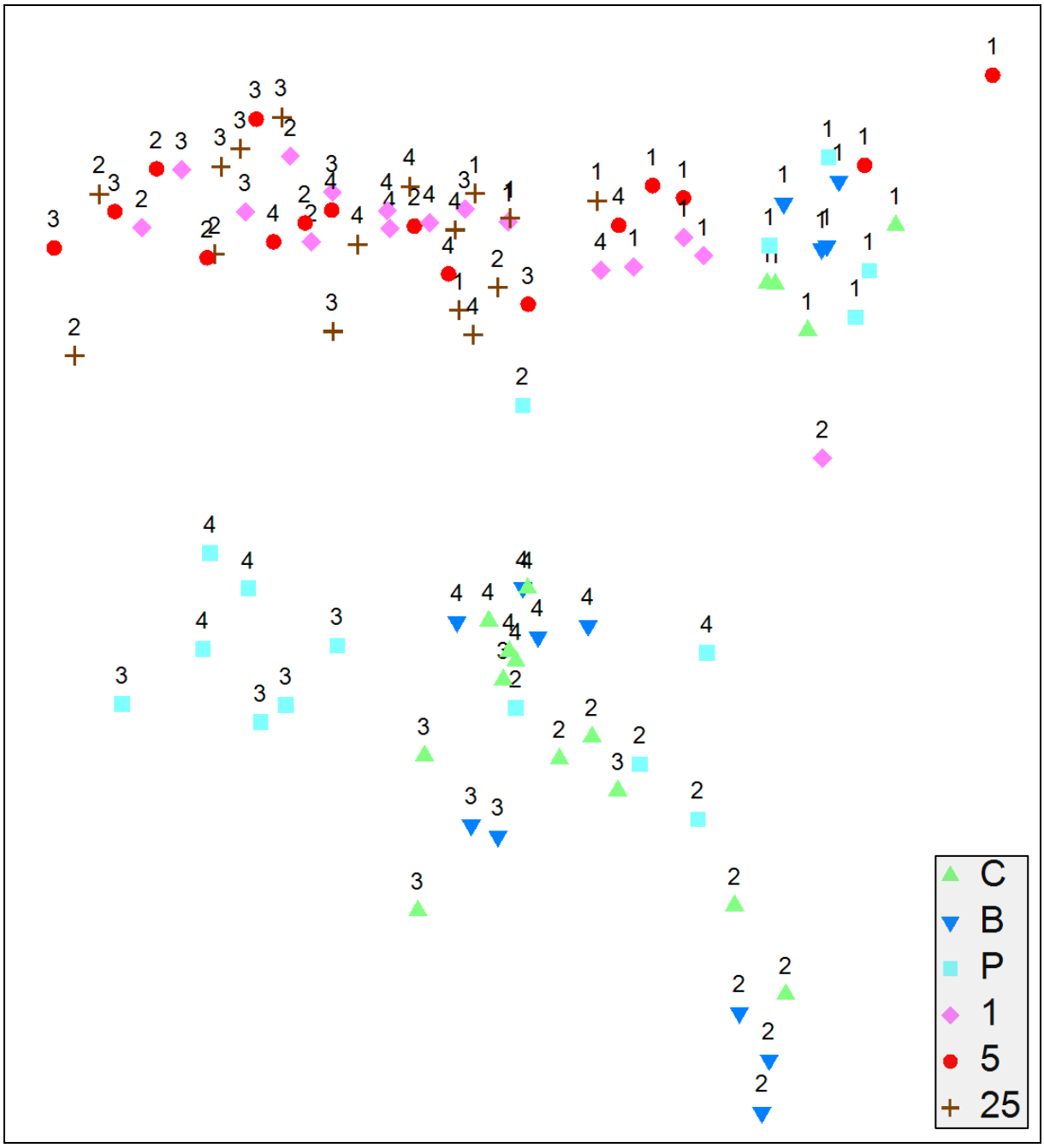

Fig. 4: Two-dimensional NMDS-ordination of soil properties analysed from 93 soil samples taken from transects leading from four different mounds (numbers 1–4) to the surrounding substrate. Four transects were sampled per mound, aligned to the four cardinal points of the compass. Soil properties included pH value, total contents of C, N and P, EC value and the clay index ClayMR. C, N, P and EC values were $\log_e$-transformed. All variables were normalised before calculating the resemblance matrix based on Euclidean distances. Note that in this plot, the horizontal axis does not represent the highest variance among samples as it was rotated to optimise the readability of the numbers. Axes were not drawn as they have no meaningful absolute scales. Stress: 0.11. Green triangle: mound chimney; blue triangle: mound base; light blue square: pediment; pink rhomb: 1 m distance from outer margin of the pediment; red circle: 5 m distance; brown cross: 25 m distance.

Table 4: Pairwise comparisons of similarities in soil characteristics of samples taken along transects leading from four mounds to the surrounding substrate. Four transects were sampled per mound, aligned to the four cardinal points of the compass.

	C	B	P	1	5	25
C						
B	0.132					
P	0.456	0.578				
1	0.943	0.940	0.747			
5	0.940	0.944	0.839	0.180		
25	0.997	0.997	0.844	0.049	0.234	

The *R* statistics of the two-way crossed ANOSIM are displayed.
C: mound chimney; B: mound base; P: mound pediment; 1, 5, 25: 1, 5 and 25 m distance from the outer margin of the pediment respectively.

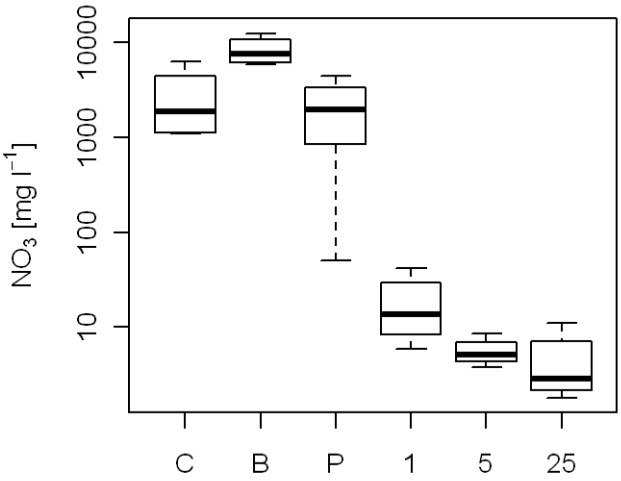

Fig. 5: Nitrate concentrations in different parts of and in the vicinity of mound number 2, measured along the four transects. C: mound chimney; B: mound base; P: mound pediment; 1, 5, 25: 1 m, 5 m and 25 m distance from outer margin of the pediment respectively.

Discussion

Characteristics of *Macrotermes* mounds as revealed by the literature review and the study of mounds in central Namibia

The review and the results from sampling in central Namibia strongly underline the necessity of differentiating between top- and subsoil when comparing mound soils with adjacent soils (Fig 1). This is most apparent in the total C contents, which were higher in the mound soils compared to the topsoil, but lower compared to the subsoil.

According to the literature review, mound soils contained much higher clay proportions than adjacent topsoil but similar proportions when compared to the adjacent subsoil. In contrast, the proportion of clay (indicated by the clay index "clayMR") in the mounds of the central Namibian savanna was significantly higher than that of the subsoil (Fig. 2). This clay-enrichment seems to be a result of the selection of clay particles by termites within the stratum of the subsoil analysed. Such active selection has been described by Jouquet et al. (2002). Termites might ensure the optimized texture of their mounds via such particle selection, especially if the clay contents of the subsoils are low (Pomeroy 1983). Indeed, central Namibian mounds were composed of only 25(±4)% clay while the mounds of the studies reviewed were composed of 38(±14)% clay (mean ± standard deviation).

The review showed that total N contents of *Macrotermes* mounds were much lower compared to the adjacent topsoils, see Holt and Lepage (2000), but higher than in the subsoils (Fig. 1). In contrast, mounds in Namibia possessed a remarkably high total N content compared to the adjacent soil at all depths. These high N contents can be attributed to extraordinarily high nitrate contents found in mound material (Fig. 5). High nitrate contents might also be responsible for the high EC values of the mounds investigated (Fig. 3).

The fact that old mound material showed much higher EC values than fresh material (Table 2) also indicates that nitrogen or other soluble ions become concentrated in mound soils rather than being washed out from the mound by rain. To our knowledge, such differences between the EC values of old and fresh mound material have not been described before. Pomeroy (1983) stated that new and old materials vary only slightly while authors of other studies did not pay attention to this issue. To exclude the possibility that the low EC values of the fresh mound material are a characteristic of a particular soil that termites might use to repair large holes (30–50 cm in diameter), we also analysed the soil that termites used to fill gaps of only a few centimetres in diameter. We did not find any significant differences between the soils used in these two instances.

We assume that nitrate accumulates in termite mounds through evaporation processes. Via evaporation, the readily soluble nitrate is transported by water and accumulates on the mound surface. Similarly, Hesse (1955) attributed high contents of $CaCO_3$ in mound soils, which he found especially at the base of older mounds, to the greater evaporation from termite mounds compared to adjacent soils. As the annual water deficit (evaporation – precipitation) between the sites analysed by Arshad (1981) and the present study do not differ largely (Kållberg et al. 2005), we assume that the low proportion of clay in the central Namibian mounds are responsible for their high total N contents in comparison to the mounds of the reviewed studies. The higher the sand content of a soil, the higher is the percentage of coarse and middle sized pores in the total soil-pore volume. In consequence, water moves more easily in sandier soils and the transport of nitrates to the mound surface by water can occur at higher rates than in clayey soils. There is a further effect which might additionally be responsible for the high N contents of mounds with low clay contents. Holt

and Lepage (2000) state that N-fixating micro-organisms have been found in termite mounds. If oxygen is lacking, these denitrifying bacteria use nitrates as a substitute for oxygen and produce N_2. Sandy soils are better aerated than clayey soils and therefore less nitrogen might be lost by denitrification.

Magnitude of soil eroding from *Macrotermes* mounds

We extrapolated that the amount of soil eroding per year from an inhabited mound fills a 1 m wide ring around the mound with a 2.4 mm thick layer of soil. Considering the lifespan of a *Macrotermes michaelseni* queen to be 18 years (R.H. Leuthold, pers. comm., also cited in Keller 1998), then this sedimentation will increase to approximately 44 mm during this time. At the study site, a hectare includes a mean number of 2.6 inhabited and 1.9 uninhabited mounds (Grohmann et al. 2010). From this it follows that projected for the rainfall of a year 245 kg of soil were eroded from termite mounds per hectare.

However, one should bear in mind that these are only rough estimates and the severity of erosion depends on rainfall intensity (Bonell et al. 1986), the size of raindrops (Parsons and Gardian 2000), soil texture (Grohmann, unpublished data) and time within the rainy season. We assume that our data underestimate the amount of erosion from termite mounds as sometimes large pieces were observed to break off from the chimneys and fell on top of or between the bags. This material was disregarded as it could not be analysed in a standardised way.

Influence of soil eroding from *Macrotermes* mounds on the characteristics of adjacent topsoil

As expected from the comparison of mound soil characteristics with those of adjacent top- and subsoil (Fig. 2, 3), strong differences between mound and off-mound soil appeared. As shown by Fig. 4 and Table 4, the soil eroded does not have an influence on the composition of the soil in the direct vicinity of the termite mound and the soil at 1 m distant is similar to that at 25 m distant from the mound. This is in contrast to the findings of Arshad (1982) and Sileshi et al. (2010) who found strong dependencies between the properties of soils and their distance from termite mounds. However, the nitrate concentration at 1 m distance from mound number 2 differed from those concentrations found at 5 and 25 m distances (Fig. 5). As these data originate from only one mound, further samples are needed to validate this finding.

We assume that in the central Namibian savanna, a combination of three factors is responsible for the findings of this study. First of all, the amount of soil eroded might not be sufficient enough to raise the nutrient levels of the topsoil. Secondly, nitrate and other soluble ions might be dissolved by rain and leached from the topsoil to deeper soil layers. A third factor might be the activity of the termites themselves. Through the construction of soil sheetings with which they cover their food items and the construction of tunnels through which they reach their food items, termites continuously mix soil from different depths. The amount of soil that erodes from a termite mound might be mixed with the adjacent subsoil at a rate that is too rapid to alter the composition of the topsoil.

Even though soil texture and soil chemical characteristics did not differ with distance from termite mounds, differences in vegetation patterns and arthropod distribution dependent on distance from termite mounds, as described by Arshad (1982), Pomeroy (1983) and Pringle et al. (2010), can be explained by physical soil characteristics. The density of macropores built by the termites for their foraging activities might decrease with increasing

distance from the mound. Macropores in general are known to positively influence the rooting success of plants, allowing for easier root penetration and a better oxygen supply. Additionally, even if no differences in the physical and chemical characteristics of soil occur between sites close to the mounds and those further apart, the vegetation patterns at these sites might differ if the plants' roots reach the mound.

The present study revealed that in the focal study site in central Namibia, *Macrotermes* mounds enhance the spatial heterogeneity of nitrogen distribution considerably. Termite mounds can be seen as nutrient hotspots (Grant and Scholes 2006) and are often used by mammals as licks (Klaus and Schmid 1998). Thus, they form an important dietary supplement for wildlife and livestock (Mills et al. 2009).

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Supplementary Material

Table S1: Number of mounds which were included in the literature review with regard to different soil properties.

Author(s) and year of publication	Sand	Silt	Clay	pH	Organic C	Total N	C/N	Total P	EC	Exch. Ca	Exch. Mg.	Exch. K	Exch. Na
Abe et al. 2009	3	3	3	3	-	3	3	3	3	3	3	3	3
Arshad 1981	6	6	6	6	6	6	6	6	6	6	6	6	6
Boyer 1973	1	1	1	1	-	-	1	1	-	1	1	1	-/1
Hernández and Febres 1989	1	1	1	1	1	1	1	-	-	1	1	1	1
Nye 1955	-	-	2	2	2	-	-	-	-	2/1	2/1	2/1	2/1
Sum	11	11	13	13	9	10	11	10	9	13/12	13/12	13/12	12

The slash separates different numbers of mounds that were compared with topsoil and subsoil respectively.
The hyphen indicates that the no data on the soil characteristic were available from the study.

Table S2: Laboratory methods for soil analyses.

Parameter	Description	Reference
Particle size distribution (soil texture) sand: 63–2000 µm silt: 2–63 µm clay: <2 µm.	With a dried sample of fine earth, a pre-test on the particle size distribution is conducted: If the top layer of a soil/water suspension is clear, the analysis is done using only a). Otherwise samples are analysed using a) and b). Procedures of pre-treatment include: - Addition of HCl to remove carbonates (in case of pH in H_2O being larger than 7.4) - Addition of $Na_4P_2O_7$ to improve dispersion of particles - Ultrasonic treatment a) 300 g of pre-treated fine earth is washed from fine-grained particles by repeated addition of $Na_4P_2O_7$ and ultrasonic treatment until the supernatant is clear. The dried sample is sieved through a set of sieves (2000, 630, 200, 125, 63 µm). The weight of each fraction is measured on an electronic scale b) 30 g of pre-treated fine earth is diluted in a 1 l sedimentation cylinder with $Na_4P_2O_7$ solution. The suspension is shaken overnight. After predetermined intervals, aliquots of 10 ml are removed with a pipette, with depth and time being based on Stokes' law. The aliquots (representing particle sizes <63, <20, <6.3, <2 µm) are dried at 105°C and weighed on an electronic scale	van Reeuwijk 2002 Petersen 2008

Continued on next page

Table S2: *Continued*

Parameter	Description	Reference
pH value	Measured with a pH-electrode in a 1:2.5 mixture of soil and 0.01 M $CaCl_2$, after the suspension was repeatedly stirred for 1 hour	van Reeuwijk 2002 ISO 10390
Total amount of carbon (C_t)	Analysed by oxidising a fine-ground sample at 900°C. The CO_2 in the combustion gases is measured by thermal conductivity (vario MAX, Elementar Analysensysteme GmbH)	Burt 2004 (6A2e)
Amount of inorganic carbon (C_{inorg})	A fine-ground sample is heated and treated with 5% HCl in a closed system. The released CO_2 is introduced into diluted NaOH where the amount of carbon is measured by determining the change in electrical conductivity (Wösthoff-Apparatur)	Petersen 2008
Amount of organic carbon (C_{org})	Calculated by C_t - C_{inorg}	-
Total amount of nitrogen (N_t)	Analysed by oxidising a fine-ground sample at 900°C. The NO_x in the combustion gases is reduced to N_2 that is measured by thermal conductivity (vario MAX, Elementar Analysensysteme GmbH)	Burt 2004 (6B4a)
Electrical conductivity (EC)	Measured in a 1:5 solution of soil with demineralised water with a conductivity sensor	-
Total contents of Al, Na, K, Ca, Mg, P, Ti, Fe, Mn	A mixture of 8 g fine-ground sample and 1.6 g of HWC-wax is placed into a die of 20 mm diameter and pressed into a tablet at 200 kN. The tablet is inserted into an X-ray fluorescence spectrometer (Philips PW-1404). The total concentrations of the elements Al, Na, K, Ca, Mg, P, Ti, Fe and Mn are determined by X-ray spectroscopy	Kikkert 1983 Petersen 2008

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Chapter IV

Impact of *Macrotermes michaelseni* on soil fertility and plant growth

Abstract

As principal decomposers, termites fulfil important tasks in nutrient cycling in arid and semi-arid ecosystems. Mound building species in particular enhance soil turbation rates and are considered to be especially important ecosystem engineers. The aim of this study was to investigate if and how bioturbation resulting from the building activities of *Macrotermes michaelseni* affects soil fertility and thus plant growth in the thornbush savanna of Namibia. To determine this, plant density and biomass were assessed *in situ* at the base of mounds and on adjacent plots. In planting bag experiments, growth of radish (*Raphanus sativus* subsp. s*ativus*) and of sorghum (*Sorghum* sp.) on soil from *M. michaelseni* mounds and sheetings (soil constructions built by the termites to protect themselves while foraging) was measured and compared with specimens grown on adjacent topsoil without visible signs of termite activity. Fewer plant individuals but higher biomass was found *in situ* at the mound bases compared to adjacent soils. We ascribe this to the mounds smooth surface that impedes the adhesion of seeds and the mounds' hardness that inhibits penetration by plant roots. In the planting bag experiments, weaker growth on the mound soil compared to adjacent soil was observed. Mound soil was characterised by significantly higher clay proportions compared to adjacent soil. In addition, the soil structure was disturbed during the potting process and we assume that the weaker growth on mound soil was a result of the absence of soil pores. Depending on their size, such pores are essential for aeration of plant roots and water infiltration and storage. Sorghum and radish growth on sheeting material and on adjacent soil did not differ significantly. In contrast to the mound soil, the soil texture of sheetings was similar to the adjacent soil. The direct influence of sheetings on vegetation is presumably less important than the effect of the termites' burrowing activities to reach their food items.

Keywords
Isoptera, Namibia, Savanna, Soil pores, Termite mound

Introduction

In savanna ecosystems, water availability, disturbance (e.g. fire, grazing) and nutrient availability are considered to be the three major factors determining ecosystem structure and productivity (Scholes and Walker 1993). In this context, termites as decomposers fulfil important tasks in the nutrient cycles of these ecosystems. They decompose plant material and contribute to carbon and nitrogen mineralization and the recirculation of nutrients to the soil (see reviews by Wood and Sands 1978, Lobry de Bruyn and Conacher 1990, Bignell and Eggleton 2000).

In arid and semi-arid ecosystems where microbial and fungal decomposition is often limited by lack of moisture, termites are especially essential for ecosystem functioning (Dangerfield and Schuurman 2000). In tropical ecosystems, they constitute up to 25% of individuals of the soil macrofauna, up to 10% of soil animal biomass and as much as 95% of soil insect biomass (Abe and Higashi 1997, Bignell and Eggleton 2000). Among termite taxa, *Macrotermes* species are particularly abundant in semi-arid savannas (Dangerfield et al. 1998). In their construction of massive mounds, they process considerable quantities of soil and dramatically alter its properties compared to the surrounding topsoil (see e.g. Arshad 1982, Abet et al. 2009, Mills et al. 2009). Amongst all termites, the Macrotermitinae especially construct their mounds primarily with clay-rich sub-soils (Wood 1988, Jouquet et al. 2002). These clays have a high cation exchange capacity (CEC) due to their large specific surface area and have high potential to absorb and desorb nutrients (Lobry de Bruyn and Conacher 1990). Additionally, the soil properties are modified by the application of saliva whilst building the mound (Fall et al. 2001, Jouquet et al. 2004b). The termite induced spatial heterogeneity of the soil is often mirrored in vegetation patterns (Moe et al. 2009, Fox-Dobbes 2010, Sileshi et al. 2010, Levick, in press) and persists when the termite colony is extinct and the mound is eroding (Glover et al. 1964, Kang 1978).

However, detailed analyses of the interactions within the termite-soil-vegetation system are lacking and often show inconsistent results. To our knowledge, the only studies which focused on *Macrotermes* mound material and combined plant growth experiments in pots with physical and chemical soil analyses were done by Watson (1977) and Kang (1978) and showed conflicting results. Watson (1977) demonstrated that increased plant growth in potted mound soil is correlated with higher nutrient levels and better soil water storage capacity of the mound material compared to adjacent topsoil. His results are consistent with *in situ* studies on plant growth at the mounds (Arshad 1982, Pomeroy 1983, Konaté et al. 1999, Jouquet et al. 2004a). However, Kang (1978) observed poorer plant growth in potted mound soil compared to adjacent topsoil. This is regarded as being a direct effect of the hardness of the mound soil due to the high clay content, preventing infiltration of water and hampering root growth (see Rogers et al. 1999).

Besides the mound, Macrotermitinae construct further structures, the soil sheetings. These sheetings are built around their food items to protect foragers to a certain extent from predators and maintain a favourable micro-climate (Wood and Sands 1978, Rouland et al. 2003). As is the case with the mounds, the soil particles of the sheetings are cemented together solely with saliva (Bagine 1984, Wood 1988). However, in contrast to the mounds which are constructed with subsoil material, the soil particles used for the sheetings are selected from the topsoil (Jouquet et al. 2002). The fragile sheeting structures are redistributed over the surrounding soil surface by rain, wind and trampling by larger animals (Wood and Sands 1978, Bagine 1984, Wood 1988, Holt and Lepage 2000). Especially after heavy rains, sheetings can be re-built within a very short period of time in extremely large

quantities (Bagine 1984, Ferrar 1982, Rouland et al. 2003) and it has been suggested that the sheetings could have a more important influence on soil turbation than the mounds (Holt and Lepage 2000, Rouland et al. 2003). All studies of recent decades show that the sheetings of Macrotermitinae contain more nutrients, particularly carbon and exchangeable cations, than the adjacent topsoil (Mando 1997a, Jouquet et al. 2002). Therefore, sheetings create spatial heterogeneity in soil nutrient distribution on the soil surface (Sileshi et al. 2010). Moreover, sheeting building activities enhance soil porosity via the termites extensive burrowing activity and therewith the soil's capacity for water absorption and water storage (Mando 1997a, D. Kaiser, unpublished data). However, to our knowledge there is no study which has focussed directly on the influence of soil sheetings on plant growth.

The first main objective of this study was to compare growth patterns of plants grown in samples of mound or sheeting soil to those grown in samples of adjacent soils. The second main objective was to reveal those soil properties which are responsible for the observed differences in plant growth on termite modified soils (mound soil and sheetings) compared to adjacent soil without visible termite activity.

Methods

Study area

The study was conducted on the cattle farm Erichsfelde, located in central Namibia (21.61°S, 16.92°E) approximately 100 km north of Windhoek in the Otjozondjupa region. The farm covers an area of roughly 13,000 ha and has a mean altitude of 1495 m a.s.l. (Jürgens et al. 2010). The unconsolidated substrates consist of loamy soils beneath which a patchy calcrete layer is found. The dominant soil types are Luvisols and Calcisols.

Between 1986 and 2007 Erichsfelde received an average of 350 ± 150 mm of rain annually over the one distinct rainy season (September – April/May). However, the rainfall is very variable in space and time and during the rainy season of 2007/2008 rainfall amounted to 511 mm from December to March (R. Scheidt, pers. comm.). The average annual temperature is 20°C with a variation ranging from an average maximum temperature of 36°C during the hottest month to an average minimum temperature of 4°C during the coldest month. In the dry season the temperature falls below 0°C for 10 to 20 nights per year (Mendelsohn et al. 2002).

The natural vegetation is thornbush savanna with several *Acacia* species (*A. erioloba*, *A. hebeclada*, *A. tortilis*, *A. mellifera* etc.) as the main woody components. Additionally, *Boscia albitrunca* is common in some localities. Various grasses such as *Stipagrostis uniplumis* dominate the herbaceous layer (Giess 1971).

Plant growth *in situ*

To study the influence of *M. michaelseni* mounds on the vegetation, we measured *in situ* the density and biomass of plants growing on the base of mounds and compared these data with plants growing on corresponding adjacent soils without visible termite activity. The number of grass (Poaceae) and other herbaceous plant individuals were counted separately on 50 x 30 cm plots at six inhabited, as well as at six uninhabited mounds and their adjacent soils. Moreover the plants on these plots were collected, air-dried and weighed to obtain the dry biomass per plot.

There was no significant difference between the influence of soil from inhabited and uninhabited mounds on the vegetation, neither in the number of plant individuals nor in their biomass (Wilcoxon rank sum test; number of grass individuals: $W = 7$, $p = 0.093$, $n_1 = 6$, $n_2 = 6$; number of herb individuals: $W = 8$, $p = 0.132$, $n_1 = 6$, $n_2 = 6$; biomass: $W = 14$, $p = 0.589$, $n_1 = 6$, $n_2 = 6$). Therefore, the data on the inhabited and uninhabited mounds were merged. The same applies to the adjacent soils for the two different mound types.

Plant nutrient content analyses

At the aforementioned *in situ* growth sites, the herb *Nelsia quadrangula* was sampled and its nutrient content was analysed for each plot. To study the indirect influence of termite activity on the plants, the dried shoots of *N. quadrangula* were analysed for macronutrients (nitrogen, phosphorus, potassium, calcium and magnesium). Analysis of the plants was carried out by dry ashing of the plant leaf tissue (Richards 1993, Mills and Jones 1996) in the laboratory (Agricultural Laboratory; Ministry of Agriculture, Water and Forestry; Windhoek; Namibia). There was no significant difference between the influence of soil from inhabited and uninhabited mounds on the macronutrient content of *N. quadrangula*. Calculations and procedures were similar to the planting bag experiments (Wilcoxon rank sum test; nitrogen: $W = 5$, $p = 0.486$, $n_1 = 4$, $n_2 = 4$; phosphorus: $W = 4.5$, $p = 0.343$, $n_1 = 4$, $n_2 = 4$; potassium: $W = 5$, $p = 0.486$, $n_1 = 4$, $n_2 = 4$; calcium: $W = 6$, $p = 0.686$, $n_1 = 4$, $n_2 = 4$; magnesium: $W = 6$, $p = 0.685$, $n_1 = 4$, $n_2 = 4$).

Growth experiments

Plant growth experiments were conducted using commercially obtained sorghum (*Sorghum* sp., variety Superdan; Poaceae) and radish (*Raphanus sativus* subsp. *sativus*, variety Comet; Brassicaceae) seeds to compare growth of these plants in soils differently affected and unaffected by *M. michaelseni*.

Soil samples and analyses

Paired samples of soil were collected from six inhabited *M. michaelseni* mounds and from adjacent topsoil without visible trace of termite activity. In addition, paired soil samples were taken from six uninhabited *M. michaelseni* mounds and their adjacent topsoil as well as from numerous *M. michaelseni* sheetings within six different plots and their adjacent topsoil. Furthermore, 1:1 ratio mixtures were made from each category of termite modified soil and its adjacent topsoil.

At each mound, samples were collected from various parts of the mound walls (0–10 cm soil depth). From inhabited mounds, only newly-constructed parts were collected from the mound surface as structures of different age can possess very different nutrient contents (Mando and Miedema 1997). Mounds were deemed uninhabited if a) no termites were visible after digging a hole into the mound's gallery system and b) the damage was not repaired after one week. The corresponding adjacent topsoil (0–10 cm soil depth) was randomly sampled at a distance of 10 m from the out-wash pediment of each mound, because at this distance the direct influence of the termite colony is negligible (Arshad 1982; C. Grohmann, unpublished data). Any leaf litter was removed. Sheetings were sampled from the soil surface as well as from the surface of woody material such as dead branches and twigs lying on the ground. This sheeting material was preferably taken from small patches (max. 25 x 18 m) to avoid differences in the composition of nutrients and grain size of the

samples. As for the mound soils, only newly-constructed sheetings were collected to exclude changes in the nutrient contents due to different ages. The corresponding adjacent topsoil (0–10 cm soil depth) without visible termite activity was sampled in the direct vicinity of the sheetings.

All soil samples were air-dried and analysed for the amount of organic carbon ($C_{organic}$), total amount of nitrogen (N_{total}), plant available phosphorus (P_2O_5) and plant available exchangeable cations such as potassium, sodium, magnesium and calcium (ISO 13878, Burt 2004 (6A2e), Burt 2004 (6B4e), Helmke and Sparks 1996). Additionally the pH value was measured in a 1:2.5 suspension of soil and 0.01M $CaCl_2$ (ISO 10390) and the electrical conductivity (EC) in a 1:2.5 suspension of soil and aquademin (van Reeuwijk 2002, Blume et al. 2003). Grain size distribution was measured in three fractions: sand 63–2000 µm, silt 2–63 µm and clay <2 µm (van Reeuwijk 2002).

Experimental set-up and procedure

The randomized experimental set-up was located outdoors in direct sunlight on a plastic tarpaulin to avoid contact between the plant roots and the natural soil surface. Six soil samples from inhabited mounds, a sample of their adjacent soil and a 1:1 ratio mixture for each of these paired samples were used and the same procedure was employed for uninhabited mound soils and for termite sheetings. In all growth experiments, each of the paired soil samples and mixtures of paired samples were divided into ten separate polythene planting bags (8.5 x 10.0 x 11.5 cm) for radish and ten identical planting bags for sorghum resulting in a total of 1,080 planting bags.

Approximately 1 kg of moist soil was used per planting bag and six seeds of each species were sowed in each. Four days after sowing, small or stunted seedlings were removed, leaving only one radish and one sorghum plant to grow in each bag. The plants were watered once a day with bore-hole water.

The length of the longest leaf of the plant in each planting bag was measured once a week. After 40 days, the experiment was stopped because Red-billed Francolins (*Francolinus adspersus*) massively damaged the leaves of the radish plants. Therefore, for the statistical analyses, we analysed the length of the longest sorghum leaf at day 35 and for the radish plants the longest leaf at day 21 was analysed, because at this time the damage was minimal and the remaining sample size adequate for a sound statistical analysis. However, the radish tubers were harvested at day 40 and their diameters and fresh and dry weights were measured.

Growth differences between inhabited and uninhabited mound soil were compared using the Wilcoxon rank sum test and no significant differences could be detected for sorghum ($W = 14$, $p = 0.59$, $n_1 = 4$, $n_2 = 6$) or radish ($W = 3$, $p = 0.07$, $n_1 = 6$, $n_2 = 6$). Therefore, results from soils of inhabited and uninhabited mounds were combined and we refer to both types as mound soil. Equally, no significant differences in growth could be determined when using the different adjacent soils and the results from these soils were also combined as were, for the same reason, the results from the mixtures.

Statistical analyses

All data were analysed using the software R (R Development Core Team 2009). The numbers of grass and herb individuals, biomass, nutrient content of *N. quadrangula* as well as the results of the soil analysis of the mounds were compared to their corresponding reference

soils using a paired Wilcoxon signed rank test. Where necessary, a log transformation was applied to the data to achieve a symmetrical distribution of the differences of the pairs.

To analyse plant growth on the different soil types we used a linear mixed model as implemented in the R package *lme4* (Bates and Maechler 2010). The twelve plots, each comprising one mound (M), its adjacent soil (R_M) and the associated mixture (M&R_M) were used as a random factor into which the soil type (M, R_M, M&R_M) is nested. The same procedure was applied to the sheeting material (S) with its adjacent soil (R_S) and its associated mixtures (S&R_S). Plant growth differences were analysed with pairwise comparisons with multiplicity-adjustments as implemented in the R package *multcomp* (Hothorn et al. 2008). The correlation of the length of the longest radish leaf with diameter, fresh weight and dry weight of the radish tuber was tested using Kendall's rank correlation *tau*.

Results

Plant growth *in situ*

The steep central part of the mound was always bare of grass and herbs, but vegetation was observed to spread onto the base of the mound after a long period of wet weather with heavy rainfall. Although fewer grass and herb individuals grew on the base of mounds compared to the adjacent soils (Figs. 1(a), (b)), their total biomass was significantly higher (Fig. 1(c)).

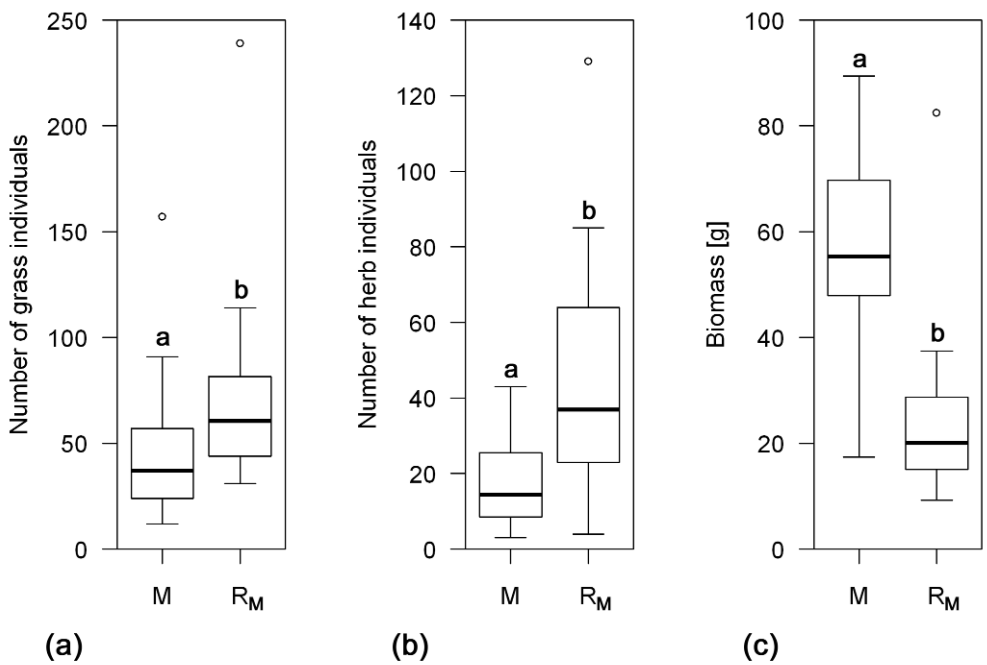

Fig. 1: **(a)** Number of grass individuals, **(b)** number of herb individuals and **(c)** biomass of the plants growing on the mounds (M: $n = 12$) compared to their adjacent soil (R_M: $n = 12$). Horizontal line: median; box: interquartile range; whiskers: 1.5x of interquartile range; circles: outliers. Data of boxplots indicated by dissimilar letters are significantly different at $p < 0.05$ (paired Wilcoxon signed rank test).

Nutrient content of *N. quadrangula*

The nitrogen, potassium, calcium and magnesium content of *N. quadrangula* did not differ significantly between the plants growing on the base of mounds and the adjacent soil (Table 1). However, the phosphorus content of *N. quadrangula* growing on the base of mounds was significantly higher than from those growing on the adjacent soil (Table 1).

Table 1: Median (interquartile range) of the macronutrient content of *N. quadrangula* growing on the base of mounds (M: $n = 8$) compared to those growing on adjacent soils (R_M: $n = 8$).

	M	R_M	*V*	*p*
N [%]	3.18 (0.41)	3.09 (0.72)	25	0.383
P [%]	**0.29** (0.26)	0.07 (0.13)	33	0.039
K [%]	**4.61** (2.25)	2.81 (1.93)	34	0.023
Ca [%]	0.61 (0.48)	1.07 (1.02)	12	0.461
Mg [%]	0.56 (0.33)	0.47 (0.51)	15	0.742

Bold letters indicate the growth site with higher values where the differences between the growth sites (M vs. R_M) were significant at $p < 0.05$ (paired Wilcoxon signed rank test).

Growth experiments

Sorghum and radish plants differed in the length of their longest leaf between the mound materials, the adjacent soils and the mixtures of both of these soil types (Table 2). Sorghum and radish plants grown in soils from mounds had significantly smaller leaves than sorghum and radish plants grown in the adjacent soils (Figs. 2(a), (c)).

The same held true for plants grown on mixtures of mound material and the adjacent soil compared to plants grown in pure adjacent soil. When comparing pure mound soil with the mixtures, the latter soil type provided better growing conditions for the sorghum and radish plants (Table 2, Figs. 2(a), (c)). In contrast, concerning the sheeting material, no significant differences in the length of the longest sorghum or radish leaf could be detected between plants growing on sheeting material, adjacent soils or mixtures of these soil types (Table 2, Figs. 2(b), (d)).

The length of the longest radish leaf was significantly correlated with diameter (*tau* = 0.31, $p < 0.001$, $n = 474$), fresh weight (*tau* = 0.35, $p < 0.001$, $n = 474$) and dry weight (*tau* = 0.34, $p < 0.001$, $n = 474$) of the radish tuber.

Table 2: Estimates for the length of the longest sorghum and radish leaves grown on the different soil types obtained by a linear mixed model.

Soil type	Sorghum length [cm] after 35 days			Radish length [cm] after 21 days		
	Estimate	Std. error	*n*	Estimate	Std. error	*n*
M	11.04[a]	0.61	99	6.28[a]	0.30	93
R_M	15.77[b]	0.62	102	8.54[b]	0.30	112
M&R_M	13.36[c]	0.61	106	7.46[c]	0.30	114
S	14.07[a]	1.50	56	8.73[a]	0.59	50
R_S	14.33[a]	1.50	54	9.09[a]	0.59	52
S&R_S	14.79[a]	1.50	56	8.81[a]	0.58	55

M: mound soil, R_M: adjacent soil, M&R_M: mixture of both soil types, S: sheeting soil, R_S: adjacent soil, S&R_S: mixture of both soil types. Results marked with the same letter do not differ significantly at $p < 0.05$.

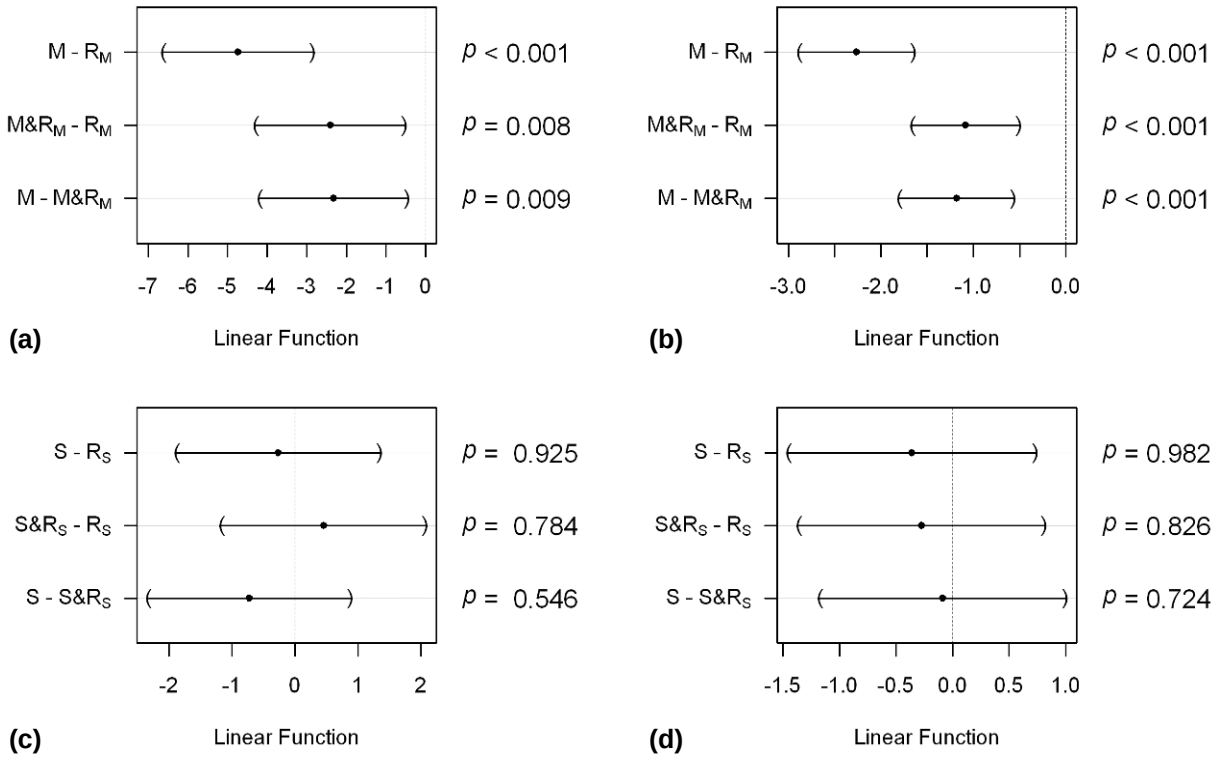

Fig. 2: Linear mixed model with *post hoc* performance of **(a)** the length of the longest leaf at day 35 of the sorghum plants growing on mound soil (M: $n = 99$), adjacent soil (R_M: $n = 102$) or a mixture of both soil types (M&R_M: $n = 106$), **(b)** on sheeting soil (S: $n = 56$), adjacent soil (R_S: $n = 54$) or a mixture of both soil types (S&R_S: $n = 56$), **(c)** the length of the longest radish leaf at day 21 on mound soil (M: $n = 93$), adjacent soil (R_M: $n = 112$) or a mixture of both soil types (M&R_M: $n = 114$) and **(d)** on sheeting soil (S: $n = 50$), adjacent soil (R_S: $n = 52$) or a mixture of both soil types (S&R_S: $n = 55$). The estimators and the confidence intervals of Tukey's all-pair comparisons are given. The corresponding *p*-values are displayed on the right hand side of each plot. If the confidence interval lies completely to

the left (right) side of the zero line, the plants growing on the soil type given first are significantly smaller (larger) compared to those growing on the soil type mentioned second.

Soil characteristics

Most of the nutrients, the pH-value and the soil texture differed between the mound soils and the adjacent soils (Table 3). Whereas the organic carbon content was greater in the adjacent soils than in the termite mound soil, there was no significant difference in the total nitrogen content and the amount of plant available phosphorus oxide. Soil pH was more alkaline in soils from mounds than in adjacent soils. Furthermore, the EC of the mound soil was significantly higher than in adjacent soils. The level of exchangeable sodium, magnesium and calcium was greater in termite mound soil compared to the adjacent soils. The levels of potassium ions did not differ significantly. The particle size distribution of mound soils was different from those of adjacent soils, with a trend to greater content of fine material in mounds. The termite mound soil was enriched with clay compared to the adjacent soil. Conversely, the adjacent soil had more sand than the termite mound soil.

The soil analyses of the *M. michaelseni* sheeting material revealed that there were fewer differences between sheeting material and adjacent soil compared to the mound soil and adjacent soil (Table 3). The amount of organic carbon was significantly higher in the sheeting material than in the adjacent soil, but there was no difference in total nitrogen, plant available phosphorus and pH-value. EC values were significantly higher in sheeting material than in adjacent soil. Higher values of exchangeable magnesium and calcium were found in the sheeting material compared to the adjacent soils, but there was no significant difference in values of exchangeable sodium and potassium between the two soil types. The soil texture of sheetings and adjacent soil differed less than the texture of mound soil in comparison to adjacent soil (Table 3). However, the sand proportion was significantly lower in the sheeting material compared to the adjacent soil.

Table 3: Median (interquartile range) chemical and physical properties of the mound soil (M: $n = 12$) compared to its adjacent soil (R_M: $n = 12$) as well as of the sheeting soil (S: $n = 6$) compared to its adjacent soil (R_S: $n = 6$).

	M	R_M	*V*	*p*	S	R_S	*V*	*p*
$C_{organic}$ [%]	0.41 (0.07)	**0.63** (0.16)	0	<0.001	**0.65** (0.26)	0.51 (0.08)	21	0.031
N_{total} [%]	0.05 (0.01)	0.07 (0.02)	14	0.100	0.06 (0.02)	0.05 (0.01)	20	0.063
P_2O_5 [mg $100g^{-1}$]	1.20 (1.80)	0.63 (1.40)	32.5	0.260	1.29 (1.36)	1.30 (1.36)	6	0.787
pH ($CaCl_2$)	**7.25** (0.58)	5.85 (0.83)	77	0.003	6.75 (0.63)	6.05 (0.45)	15	0.059
EC [µS cm^{-1}]	**104.00** (127.25)	24.50 (21.25)	78	0.003	**61.00** (23.00)	21.00 (8.75)	21	0.031
Na [$mmol_c$ kg^{-1}]	**3.50** (1.05)	1.95 (0.23)	78	<0.001	2.05 (0.25)	1.90 (0.08)	17	0.203
Mg [$mmol_c$ kg^{-1}]	**67.00** (53.80)	28.70 (22.75)	78	<0.001	**25.45** (5.50)	22.75 (5.68)	21	0.036
Ca [$mmol_c$ kg^{-1}]	**164.70** (104.13)	64.55 (37.73)	78	<0.001	**115.10** (136.43)	62.95 (37.08)	21	0.031
K [$mmol_c$ kg^{-1}]	8.75 (3.65)	9.35 (4.50)	35	0.791	6.75 (1.48)	6.95 (1.23)	11	0.419
Clay [%]	**35.90** (14.04)	22.46 (7.78)	74	0.003	18.98 (11.09)	15.23 (5.64)	19	0.094
Silt [%]	11.30 (2.22)	13.60 (1.48)	17	0.092	10.61 (0.88)	11.73 (1.73)	7	0.563
Sand [%]	50.83 (9.05)	**63.76** (7.57)	0	<0.001	69.89 (8.63)	**71.93** (5.77)	0	0.031

Bold letters indicate the soil type with higher values where the differences between the soil pairs (M vs. R_M respectively S vs. R_S) were significant at $p < 0.05$ (paired Wilcoxon signed rank test).

Discussion

The survey of *in situ* plant growth at the base of *M. michaelseni* mounds showed that although fewer plant individuals grew on the mounds, they produced considerably higher total biomass than plants on adjacent soils. Arshad (1982) reported that the primary production of grass growing on *M. michaelseni* mounds was twice as high as that on corresponding ambient reference soils. Pomeroy (1983) and Loveridge and Moe (2004) also found a higher plant biomass on *Macrotermes* mounds compared to adjacent areas.

Two main reasons could be responsible for the establishment of fewer plant individuals on mounds compared to the adjacent soil. Firstly, the hardness and relative smoothness of the mound surface prevents seed lodgement. Secondly, in case that a seed was able to adhere at the mound surface, its seedling withers due to the strong surface crusting in dry years (Rogers et al. 1999). Furthermore, fewer seeds might persist at the mounds because

the bareness of the mound may increase seed mortality due to exposure to the elements (e.g. wind and running rain water) and predators (e.g. granivorous birds and ants). Additionally, even in wet conditions, many plant species are not able to establish themselves on the mound before the surface has once again hardened and root penetration is again inhibited. As a consequence of these factors, a plant that does manage to establish itself on a mound could assimilate more light and nutrients and out-compete later germinating plants. The high individual plant biomass at termite mounds might therefore be a function of the less competitive circumstances, compared to a reference plot with significantly more plant individuals (Konaté et al. 1999).

In addition, we detected more grass than herb individuals at mounds. This observation conforms to the findings of Rogers et al. (1999) who also found more grass than herb individuals at *Coptotermes lacteus* mounds in Australia. Grasses, especially early colonizing species, have relatively shallow roots and are fast growing (Chapman and Peat 1992). It is likely that faster growing grasses are more capable of establishing themselves on a mound because they are able to benefit from the brief windows of time when the mound surface is more easily penetrable, such as after heavy rainfalls. In addition, the infructescences of some grasses possess spikes and hairs which can attach more easily to difficult substrates such as the relatively steep sides of mounds. Most of the grasses and herbs (e.g. *Setaria verticillata, Erucastrum arabicum*) found at the mounds were species which depend on nutrient rich soils and were never encountered on the ambient savanna soil. Due to the fact that plants at the mounds possessed high nutrient contents, especially phosphorous (Table 1; Grant and Scholes 2006), the grasses and herbs on the termitaria are beneficial dietary supplements for ungulates in this savanna ecosystem. In fact, in numerous African savannas favoured browsing and grazing by large herbivores on termite mound vegetation has been observed (Loveridge and Moe 2004, Mobæk et al. 2005).

In contrast to the higher biomass recorded for plants growing *in situ* on the mounds, the sorghum and radish plants showed poorer and weaker growth in potted *M. michaelseni* mound soil compared to adjacent soil. However, similarly to the *in situ* results, the plants in the planting bag experiments had generally higher nutrient contents if they succeeded in growing on mound material.

For the comparison of termite treated soil with adjacent soil without visible signs of termite activity, it is important to keep in mind that over any longer time period it is likely that all soils in this savanna ecosystem are influenced by bioturbation by termites of different genera, thus constituting a true “termitosphere” (Brauman 2000). Therefore, the observed differences in plant growth between directly termite affected soil and adjacent soil must be regarded as reflecting relatively short-term effects of termite activity.

The observation of weaker plant growth in potted mound soil compared to adjacent soil is in accordance with the findings of Kang (1978), but in contrast to our results he found that maize plants grown in *Macrotermes* sp. mound soil in Nigeria contained lower nutrient contents than maize plants grown in adjacent soil. These differences are probably due to the fact that we found generally higher CEC in the mound soils compared to the adjacent soil than did Kang (1978). In contrast, Watson (1977) reported that in pot experiments in Zimbabwe, *Macrotermes falciger* mound soil increased yields of ryegrass (*Lolium perenne*) over those of the adjacent soil. In accordance with our results, he showed that mound material has greater CEC and EC than the adjacent soil. Additionally, he found higher values of mineral nitrogen and plant available phosphorus compared to the adjacent soil. However, the soils of *M. michaelseni* mounds in Namibia analysed in the course of this study showed

no significant differences in nitrogen and phosphorus between mound and adjacent soil. These results suggest that the effect of termite activities on nutrient content of mounds and the resulting vegetation patterns may differ between eco-climatic regions and perhaps also between termite species.

In accordance with our results, all former studies found an increased clay proportion in mounds of *Macrotermes* species (e.g. Abe et al. 2009, Mills et al. 2009, Sileshi et al. 2010). The relative proportions of sand, silt and clay influence the stability and size of soil pores. The presence of pores enhances the soil's absorption and storage capacity of water and air and makes them available to the plant roots. Loam, consisting of relatively equal proportions of sand and silt but a distinctly lower clay proportion is considered to be ideal for agricultural use (Oades 1984). In contrast to the adjacent soil, the termite mound materials in the present study were mainly composed of sand (51%), some silt (11%) and had a clay content of 36%. Increasing the clay proportion causes a decrease in soil pore size and increases the soils impermeability. Rain water falling on termite mounds rapidly runs off, leaving the mound soil relatively dry. The runoff water accumulates at the base of the mound and could enhance plant growth there as indicated by our *in situ* results. However, on the other hand, the high clay content of these soils leads to shrink-swell dynamics that can shear plant roots and retard plant growth (Darlington 2005). The weak growth of sorghum and radish plants observed in this study was probably caused by the aggregation and compaction of mound soils due to the high clay fraction.

Furthermore, an increased clay proportion is directly related to an increase of the CEC (Jouquet et al. 2004b, Mills et al. 2009). The higher calcium, sodium and magnesium exchange capacities and the higher EC of the mound material can accordingly be seen as a result of the mound soils' enrichment with cation-rich clay and indicate high salt concentrations in the termite mounds. Due to the high CEC and EC in the mound soil, the radish and sorghum plants might have undergone stress due to osmotic water retention which could additionally explain their retarded growth in the mound soil. In addition, the accumulation of salts, especially calcium carbonate and sodium carbonate, could lead to the observed higher pH-value of the mound material compared to the adjacent soil. Watson (1962; 1977), Wood and Sands (1978), Arshad et al. (1988) and Mills et al. (2009) also reported that the activity of the termites generally increases the pH-value of the mound soil.

In our experiments, as found by Potineni and Veeresh (1989), the simple mixture of equal proportions of mound material and adjacent soil resulted in better plant growth compared to pure mound material, but was still weaker when compared to the adjacent soil. In view of this, experiments with different ratios of mound soil mixed with adjacent soil could reveal more about the effect of the high clay content of mound soil on plant growth.

The contradictory growth results of the planting bag and *in situ* experiments might have resulted from the disturbance to soil structure that occurred during the potting process. Conduits and channels, which pervade the mounds, can be found as little as 3 cm below the mound surface (Turner 2000) and are presumably beneficial for plant growth. In combination with other macropores and voids in the mounds they increase the aeration of the soil and might store plant available water after long periods of wet weather, favouring plant root growth.

The sorghum and radish growth on sheeting material did not differ significantly from the growth on adjacent soil or mixtures of both soil types. The sheeting material was composed of a significantly lower sand fraction, but only a slightly higher clay fraction compared to the adjacent soil. This implies that the material used to construct the sheetings is mostly taken

from the topsoil. The difference in the clay/sand ratio might be a result of particle selection by the termites or the addition of some soil from deeper layers.

It is known from the literature that sheetings of different termite species can contain considerable quantities of nutrients and can enrich the surface soil with nutrients useful to plants (Bagine 1984, Mando 1997a, Jouquet et al. 2002, Ndiaye et al. 2004). This is in accordance with our results which show that the sheeting material of *M. michaelseni* had a higher EC and contained more organic carbon and exchangeable magnesium and calcium than the adjacent soils. Higher carbon content influences both water-retention capacity and CEC in a positive way and contributes to the availability of nutrients (Tate 1987). However, as termite sheetings did not promote plant growth compared to the adjacent soil, the value of the sheetings for the vegetation is presumably less than that of the termites' soil tunnelling behaviour. Through the construction of foraging tunnels and their openings at the soil surface, termites create macropores that enhance the infiltration of rainwater considerably (D. Kaiser, unpublished data).

In summary, our data show that termites play a major role in modifying African savanna ecosystems and that termite-induced change to surface soil properties, vegetation structure and productivity are beneficial to the functioning of this rangeland ecosystem.

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Chapter V

Multi-scale pattern analysis of *Macrotermes* mounds

Abstract

Termite mounds are a widespread feature in most African savannas. These structures exhibit high nutrient contents and often host a special vegetation composition. In this study, we analysed mound distribution patterns of a fungus-growing termite species, *Macrotermes michaelseni*, an important ecosystem engineer in the savannas of Namibia. Inhabited mounds taller than 0.7 m were regularly distributed. We view this pattern as a result of intraspecific competition. The heights of mounds taller than 0.7 m were correlated positively with their distance, such that mounds closer together, i.e. up to inter-mound distances of approximately 50 m, tended to be smaller than average. This indicates that intraspecific competition for foraging areas controls mound distribution pattern and colony size. Differences between mound heights increased on the spatial scale up to inter-mound distances of 80 m. We assume that the foundation of new colonies is only possible in unoccupied patches. In such patches, young colonies are able to occur close together as they have a relatively low foraging demand and therefore a low spatial demand. In contrast, their critical distance to taller colonies with higher foraging demands is rather large, which leads to the observed increasing difference of mound heights with increasing distances between them.

Keywords
Isoptera, Namibia, Point pattern, Savanna, Second-order statistics

Introduction

The phenomenon of scale is one of the most discussed topics in the ecological literature. This is due to the fact that most ecological patterns and their related processes as well as their perceptibility vary with the observational scale (Dungan et al. 2002, Haines-Young 2005). Patterns are not only generated by certain ecosystem processes, but each pattern also has retroactive consequences onto the processes of its ecosystem (Levin 1992).

The arrangement of objects that are irregularly or randomly distributed in the plane can be described by mathematical models, the so-called spatial point processes (e.g. Illian et al. 2008). These models help to deduce rules of causality from the observed distribution. Many ecological studies have dealt with dispersion patterns of plants (see Perry et al. 2006, Wiegand et al. 2007), but point patterns are also common for analysing the intra- and inter-specific behaviour of animals. Burrows or mounds are often used as spatial reference for the distribution of specimens or colonies of the target species. For example, Fisher et al. (2007) investigated the spatial clustering of burrows of a ground-living owl, Schooley and Wiens (2001), analysed kangaroo rat mounds in New Mexico and Crist and Wiens (1996) deduced, from the distribution of ant colonies, implications for ecosystem processes.

Globally, arid and semi-arid regions comprise more than 25% of the terrestrial surface and are inhabited by almost 30% of the human population (Millennium Ecosystem Assessment 2005). In this biome, termites are most important for ecosystem functioning (Wood and Sands 1978, Whitford 1991). The fungus-growing Macrotermitinae play an especially prominent role across a range of spatial scales, e.g. from the modification of local water infiltration rates to the creation of regional landscape mosaics (Dangerfield et al. 1998). They enhance decomposition processes and alter nutrient content, texture and hydrological properties of soils through their foraging and building activities. Mounds built by *Macrotermes* species above their nests are common in most African savannas. These termitaria supply a critical resource of scarce micro-nutrients to wildlife (Mills et al. 2009) and host a special vegetation composition (Moe et al. 2009).

So far, studies on the spatial distribution patterns of *Macrotermes* mounds have yielded contradictory results. For example, an aggregation of mounds was found by Meyer et al. (1999) whereas a random pattern was determined by Collins (1981). Most studies have revealed a regularity of mound distribution and attributed this to intra- and inter-specific competition (Wood and Lee 1971, Lepage 1984, Levings and Adams 1984, Pomeroy 2005). Concerning mounds of *Macrotermes michaelseni* (Sjöstedt, 1914) in eastern Africa, regular distributions were described by Darlington (1982), Kaib et al. (1997) and Pomeroy (2005). However, in southern Africa, only two studies considered the spatial distribution of *M. michaelseni* and neither of them found significant deviations from a random pattern for active mounds (Schuurman and Dangerfield 1997, Turner 2000).

In most cases, only the distance to the nearest neighbour was analysed, not taking into account that further neighbours might also play a role in competition pressure. However, more complete information, namely that on the effects of multiple neighbours can be derived by methods that use second-order characteristics such as Ripley's *K*-function, the pair correlation function and related techniques (Illian et al. 2008). They offer the great advantage of providing information on various scales and have been applied successfully in different fields of ecology. Concerning termite mounds, corresponding analyses were done by Spain et al. (1986) and Barot et al. (1999) for Australian and West African species, respectively, both finding regular distributions. Fisher (1993) revealed that termite mounds in Brazil, which were randomly distributed according to Clark-Evans nearest neighbour analy-

ses, showed a clustered distribution with a minimum spacing between close neighbours when applying second-order statistics. However, no comparable data are available for *M. michaelseni*.

In this study, we analysed the spatial distribution patterns of termite mounds built by *M. michaelseni* in a multi-scale approach based on second-order characteristics. Mound height was used as a surrogate for colony size, based upon findings that for this species, mound height is correlated positively with colony size (Darlington and Dransfield 1987) as well as with the number of eggs (Kaib et al. 2001).

Firstly, the distribution patterns of different mound categories defined by their height and status (inhabited vs. uninhabited) were investigated. Although only random patterns have been reported for *M. michaelseni* mounds in southern Africa to date, a regular distribution of inhabited mounds was expected as documented for many other *Macrotermes* species. Indeed, if intraspecific competition forces mound patterns, it should regulate the size and density of termite colonies. Hence, we secondly hypothesised that the height of a mound increases with its distance to further mounds. It is known from the literature that new mounds appear in certain years only. As we assume that such small, young mounds can occur close together (see 2nd hypothesis), we thirdly test the hypothesis that the height differences of mounds increase with increasing distance between them.

Methods

Mound mapping

Fieldwork was carried out in a central Namibian thorn-bush savanna (21.51°S, 16.73°E). The average annual rainfall of approximately 300–350 mm can vary considerably from year to year and occurs mainly in summer between November and May. Mean annual temperature is around 21°C, with an average maximum temperature of roughly 35°C in December, dropping to an average minimum temperature of 5°C during July (Mendelsohn et al. 2003).

Within a square site of 1 km², the position of each termite mound built by *Macrotermes michaelseni* was located at the beginning of the 2007 dry season and its position was recorded using a GPS (Garmin III plus, accuracy approx. 3 m). Mounds were defined as being "inhabited" or "alive" when (i) *M. michaelseni* individuals were seen, (ii) fresh mound structures built by this species were present, or (iii) a hole drilled into the mound was repaired by *M. michaelseni* within one day. Otherwise, mounds were categorised as "uninhabited" or "dead"; this category also included almost entirely eroded mounds.

The total mound height and the basal diameter (both excluding the outwash pediment) were recorded. The bases of the mounds were generally asymmetrical and were therefore measured in the direction which seemed to best represent the average diameter. Mound height and mound diameter were correlated significantly (Kendalls's rank correlation, $\tau = 0.53$, $p < 0.001$, $n = 444$). We used mound height for the analysis due to the asymmetry of the bases. Inhabited mounds were divided into three height classes: A1 (0–0.7 m), A2 (0.7–2.0 m) and A3 (>2.0 m). The reasons for this classification are explained in "Discussion". Mounds larger than 0.7 m showed a similar pattern and were merged to the category A2 $\cup$ A3 for most analyses. There were no obvious trends in the density or height of mounds or the association between mounds within the study site, so that the requirement of site homogeneity for the chosen test statistics was met.

General distribution pattern

The general spatial distribution of mounds was analysed using the pair correlation function (pcf), which is known to be a valuable summary characteristic for homogeneous multi-scale point patterns (e.g. Perry et al. 2006). The function is related to the probability of finding a point at distance *r* from an arbitrary point of the pattern; see Illian et al. (2008) for further interpretation. Furthermore, there is a close relationship to the well-known *K*-function: with λ being the point density and $K(r)$ being Ripley's *K*-function, $\lambda K(r)$ reflects the mean number of points in a disc of radius *r*, centred at the typical point of the pattern. The pair correlation function $g(r)$ is given by the derivative of $K(r)$ (Wiegand and Moloney 2004, Illian et al. 2008):

$$g(r) = \frac{K'(r)}{2\pi r} \qquad \text{for } r \geq 0. \qquad \text{eqn 1}$$

The shape of the pcf can be interpreted as follows: For a random point pattern, $g(r)$ is equal to 1. For a clustered pattern, $g(r)$ has values larger than 1 for small *r* and converges towards 1 with increasing values of *r*. The cluster diameter can be estimated from that value of *r* where $g(r)$ first approaches 1. Regular distributions result in $g(r) = 0$ for small *r* values, while for larger *r*, values greater than 1 and significant fluctuations around 1 are possible (see Fig. 1 and Illian et al. 2008).

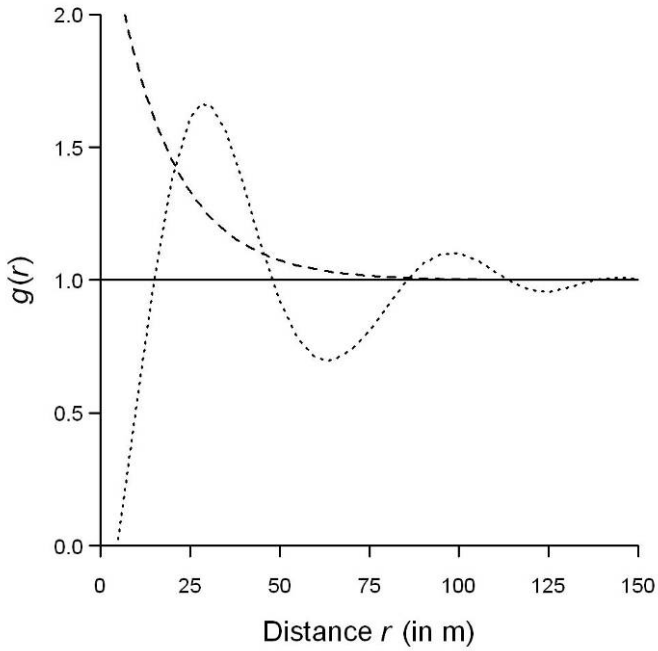

Fig. 1: Idealised theoretical pair correlation function for random (solid line), clustered (dashed line) and regular spatial pattern (dotted line).

The pcf was estimated using the method recommended in Illian et al. (2008); for edge correction, the translation method was applied. The point patterns were tested for significant ($\alpha = 0.05$) deviations from complete spatial randomness using the *L*-test (Chiu 2007, Illian et al. 2008). This test is considered as a powerful test and can be easily applied if suitable software is available. It considers the maximum absolute deviation of the empirical *L*-function

from the theoretical *L*-function of the Poisson process. If this deviation is larger than a critical value, which depends on sampling area and sample size, the hypothesis of complete spatial randomness is rejected.

Spatial relationship between small and large inhabited mounds

Small mounds may show a different type of distribution compared to larger ones (in particular, clumped versus regular distributions, see Korb and Linsenmair 2001a) and were included in this study. They are difficult to detect in the field, especially in dense vegetation. Therefore, small mounds were excluded in some studies on mound patterns (e.g. Pomeroy 1983a). According to Pomeroy (1983b), the proportion of inhabited *Macrotermes* mounds, particularly those smaller than 0.5 m, can vary strongly between different years.

For analysing the relationship between small and large mounds, the mark connection function $p_{ij}(r)$ was applied, with the respective group numbers 1 (A1) and 2 (A2 $\cup$ A3) as marks. This function was chosen because it is not cumulative as is $L_{ij}(r)$ and it does not depend on the number of mounds at a certain distance *r'* as does $g_{ij}(r)$. According to Stoyan and Stoyan (1994) and Illian et al. (2008), $p_{ij}(r)$ can be interpreted as the probability that two mounds at distance *r* have marks *i* and *j* (*i*, *j* = 1, 2). The behaviour of the mark connection function provides information on the association of marked points in point patterns (here: A1 vs. A2 $\cup$ A3). High values of $p_{ij}(r)$, compared to values of the mark connection function in the case of independence, indicate that points in pairs of points with distance *r* are frequently of different types. According to Illian et al. (2008), in the case of independence

$$p_{ij}(r) = 2 p_i p_j \qquad \text{eqn 2}$$

with

$$p_i = \frac{\lambda_i}{\lambda}, \qquad \text{eqn 3}$$

where λ_i denotes the density of points with marks *i* and λ is the density of all points irrespective of their mark.

It was tested whether the compared groups are marked independently (random labelling) using the method of random reallocation. In this procedure, the points are kept fixed, while the marks (group numbers) of these points are randomly permuted. Pointwise envelopes for 99 simulations were obtained, which can be interpreted as being appropriate for an error probability of $\alpha = 0.01$ (Illian et al. 2008). The simulations yielded estimates of the multivariate *L*-function $L_{ij}(r)$, which is related to the number of points of type *j* in a disc of radius *r* centred at an arbitrary point of type *i*. If the empirical L_{12}-function leaves the envelopes ($L_{12,\min}$ and $L_{12,\max}$), the hypothesis of random marking is rejected.

In the following analyses, only inhabited mounds larger than 0.7 m (A2 $\cup$ A3) were considered.

Correlation of mound height with distance to further mounds

We applied the mark correlation function $k_{mm}(r)$ with mound height as the continuous mark to mounds larger than 0.7 m (A2 $\cup$ A3), in order to analyse whether the heights of termite

mounds are correlated dependent on their distance to others, indicating intraspecific competition. Values of $k_{mm}(r) < 1$ occur if the product of the heights of two mounds r length units apart tends to be smaller than the square of the overall mark mean μ. If mound pairs with distance r are larger than average, in terms of the product of their heights, then $k_{mm}(r)$ is >1. After Illian et al. (2008), $k_{mm}(r)$ is defined as:

$$k_{mm}(r) = \frac{c_{mm}(r)}{\mu^2} \qquad \text{for } r > 0, \qquad \text{eqn 4}$$

with $c_{mm}(r)$ being the mean of the product of the marks of a randomly selected pair of points with inter-point distance r, and μ being the overall mark mean.

To test for significance, pointwise envelopes for 99 simulations were obtained, where the points are fixed, but the marks are randomly permuted. The simulations were run for the mark-weighted L-function $L_{mm}(r)$, which is related to the mean of the sum of the products formed by the marks of a randomly chosen point and the marks of all points in the disc of radius r centred at that point (Illian et al. 2008). If the empirical L_{mm}-function leaves the envelopes ($L_{mm,\min}$ and $L_{mm,\max}$), the hypothesis of independence of mound heights is rejected.

Similarity of mound heights

Further information on the correlations of the mound heights can be obtained by means of the mark variogram $\gamma_m(r)$ which characterises the squared differences of heights of mounds dependent on their distance from each other (Illian et al. 2008; page 344). The function has small values if the marks of mound pairs tend to be similar and large values if the mounds differ, for given distances r. If the marks are controlled by some co-variable, it is typical that $\gamma_m(r)$ has small values for small r and increases with increasing r.

Statistical remarks

An important characteristic of the introduced functions is the range of correlation r_{corr} (Illian et al. 2008), which was roughly estimated from the shape of the respective function. This is the distance up to which correlations in the marked pattern occur. Beyond this distance, the functions are theoretically constant and their statistical estimates fluctuate around certain limits. For $g(r)$ and $k_{mm}(r)$, the limit value for large distances is 1, while for $p_{12}(r)$ it is $2p_1p_2$ and for $\gamma_m(r)$ it is the variance of mound heights.

As is usual in spatial point process statistics (see Illian et al. 2008 Section 7.4 and Diggle 2003 Chapter 6), for testing the independence hypotheses, we used refined versions of the L-function, namely $L_{12}(r)$ and $L_{mm}(r)$. This is analogous to the well-known Kolmogorov-Smirnov test in classical statistics. The main difference between the functions $L_{12}(r)$ and $L_{mm}(r)$ compared to $p_{12}(r)$ and $k_{mm}(r)$ is the cumulative nature of the L-functions.

Pairwise inter-mound distances were calculated to indicate the sample size at each distance for the functions $p_{12}(r)$, $k_{mm}(r)$ and $\gamma_m(r)$. To estimate $g(r)$, $p_{12}(r)$, $L_{12}(r)$, $k_{mm}(r)$ and $\gamma_m(r)$, to determine the significance envelopes and to compute pairwise distances, the software R (vers. 2.8.1; R Development Core Team 2008) was used with the package *spatstat* (vers. 1.15-3; Baddeley and Turner 2005). The resulting values of $p_{ij}(r)$ were multiplied by two to achieve comparability with Illian et al. (2008). For the calculation of $L_{mm}(r)$, Pascal applications written by D. Stoyan were used. The bandwidth of the functions $g(r)$, $k_{mm}(r)$ and $\gamma_m(r)$ were calculated using the default method given by *spatstat*. For the computation of

$p_{ij}(r)$, the bandwidth (according to the term's usage in *spatstat*) was set to 4.4 in *spatstat* to achieve an informative plot.

Results

In the 1 km² area surveyed, a total of 444 mounds of *Macrotermes michaelseni* were identified. About 58% of them were inhabited (Table 1), reaching up to 4.4 m in height (mean 1.7 m).

Table 1: Statistical parameters and distribution types of termite mounds within the 1 km² study area.

Mound category	Mound height			Number of mounds	Deviation from random pattern
	Range [m]	Mean [m]	Standard deviation [m]		
all		1.3	0.9	444	regular
alive		1.7	0.9	256	regular
A1	0–0.7	0.5	0.1	48	n.s.
A2	>0.7–2.0	1.4	0.4	115	regular
A3	>2.0	2.6	0.5	93	regular
A2 ∪ A3	>0.7	2.0	0.7	208	regular
dead		0.8	0.5	188	n.s.

Categories A1–A3 and A2 ∪ A3 refer to inhabited mounds. Where the pattern deviated significantly from complete spatial randomness (*L*-test, *p*-value < 0.05), the kind of deviation was specified according to the shape of the pair correlation function; n.s.: not significant.

General distribution pattern

The spatial patterns for all termite mounds, as well as for the inhabited ones, showed a regular distribution (Fig. 2). For both patterns, their deviation from complete spatial randomness was significant (*L*-test, *p*-value < 0.05). The only difference appeared for inhabited small mounds (A1, Fig. 3) where there was a tendency towards a clustered pattern. Large inhabited termite mounds (A2, A3 and A2 ∪ A3) were regularly distributed. Their deviation from complete spatial randomness was significant (*L*-test, *p*-value < 0.05). Mounds of category A2 ∪ A3 showed a range of correlation of about 70 m, which is in the same order as the mean distance to the 3rd neighbour (73 m) in this group. The patterns of uninhabited mounds did not differ significantly from complete spatial randomness.

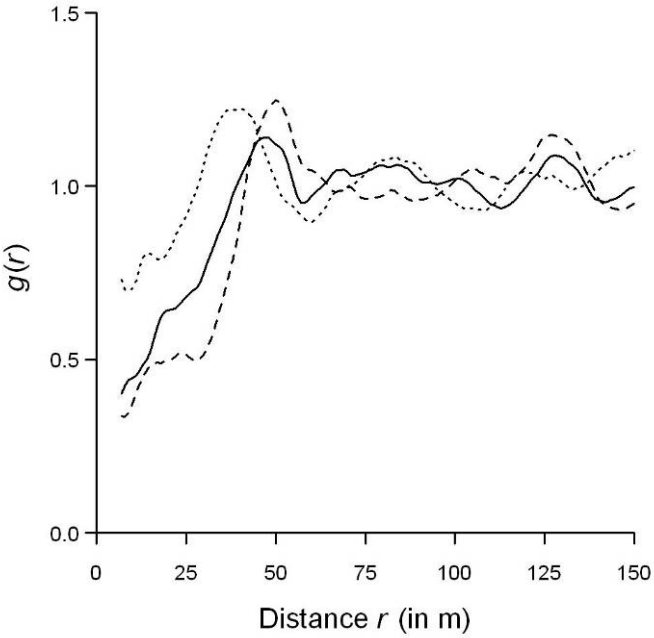

Fig. 2: Pair correlation functions for termite mounds within the study plot of 1 km² (all mounds: solid line, inhabited: dashed line, uninhabited: dotted line). All three functions indicate regularity, but that of uninhabited mounds is not significant (see Fig. 1 and Table 1).

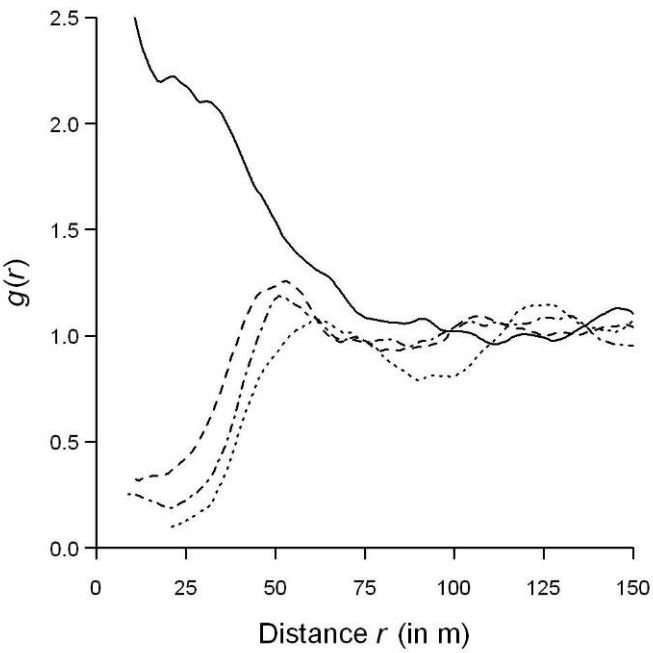

Fig. 3: Pair correlation function for inhabited mounds; A1: solid line, A2: dashed line, A3: dotted line, A2 ∪ A3: dot and dash line. The function for A1 shows a tendency towards a clustered distribution (see Fig. 1). All other functions indicate regularity; the deviation from a random pattern is significant (see Table 1).

Spatial relationship between small and large inhabited mounds

For inhabited mounds of categories A1 (mark 1) and A2 ∪ A3 (mark 2), the empirical mark connection function $p_{12}(r)$ clearly exceeds 0.30 ($2p_1p_2$ with $p_1 = 48/256 = 0.19$ and $p_2 = (115+93)/256 = 0.81$; see "Methods") which is the limit value for independent marking (Fig. 4). This means that there is a higher probability than expected from the hypothesis of independent marking that of two mounds that are less than 50 m apart, one mound belongs to the category A1 and the other one to A2 ∪ A3. According to the envelope test, the result is significant (Fig. 5) as the empirical L_{12}-function is partly outside the envelopes.

Small mounds (A1) show a different pattern than larger ones. Firstly, they are not distributed regularly, and secondly, they occur closer to larger mounds than expected by chance. Therefore, mounds smaller than 0.7 m were excluded from the following analyses; see "Discussion" for a more detailed argumentation.

Correlation of mound height with distance to further mounds

Concerning inhabited mounds larger than 0.7 m (A2 ∪ A3), the mark correlation function $k_{mm}(r)$ with mound height as continuous mark was smaller than 1 up to a range of correlation of approximately 50 m (Fig. 6). Thus, the product of the heights of two mounds with distance less than 50 m to each other is smaller than on average. The L_{mm}-function is partly outside the envelopes obtained by 99 simulations of random distribution of mound heights, indicating that the result is significant (Fig. 7).

Similarity of mound heights

The mark variogram $\gamma_m(r)$ for mounds of category A2 ∪ A3 is decreasing in r for small r (Fig. 8). In contrast, the mark variogram is increasing for r larger than 25 m until it reaches the level of the variance of the marks (0.54 m^2). The latter part of the mark variogram for r larger than 25 m resembles part of a typical geostatistical variogram, indicating that mounds less far apart are more similar in their heights compared to those further apart. However, a typical geostatistical variogram would start in the origin ($\gamma_m(0) = 0$), or at least start monotonically, but in Fig. 8 the mark variogram is not monotonic.

In searching for a cause of the unusual variogram form for small r, we analysed all mound pairs with distances less than 25 m. Only eight mound pairs showed such small inter-mound distances. At such a small sample size, even one mound pair with an extreme value for γm(r) can have a strong impact on the shape of the function. For most pairs, the differences between their heights were much less than expected by chance. However, the mound pair with the minimum distance between them (8.0 m) was characterised by an extraordinary large difference in their heights (0.8 vs. 3.1 m). To exclude the influence of this pair, we ran a second calculation of the mark variogram without the small mound of this mound pair (Fig. 8, the mound which was excluded is marked by the filled circle in Fig. 9). This time, the mark variogram is monotonically increasing in r, up to an inter-mound distance of 80 m. From there on, only random fluctuations around the variance of the marks (again, 0.54 m2) can be observed and the mark variogram can now be easily interpreted: there is some spatial correlation of the mound heights in that members of mound pairs less than 80 m apart tend to be more similar in their heights than members of randomly selected mound pairs.

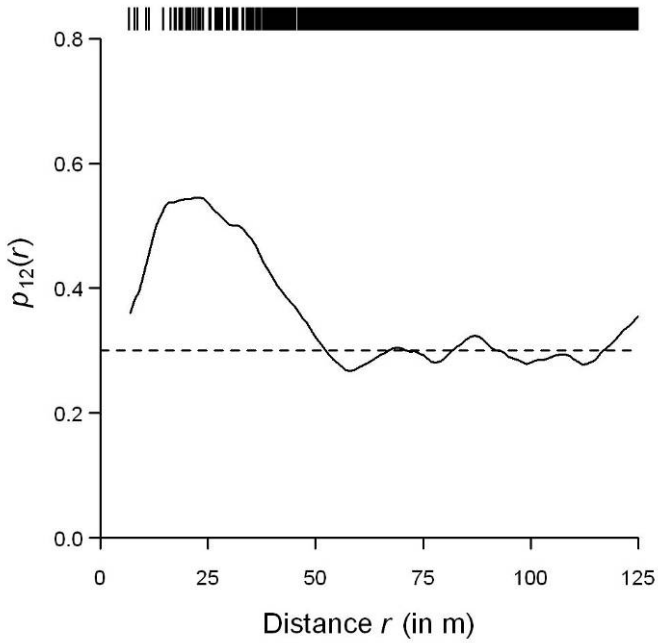

Fig. 4: Mark connection function $p_{12}(r)$ (solid line) describing interactions between termite mounds of category A1 (mark 1) and A2 ∪ A3 (mark 2). The large values of $p_{12}(r)$ in comparison to $2p_1p_2 = 0.30$ (dashed line, $p_1 = 0.19$, $p_2 = 0.81$) corresponding to independent marking indicate a tendency of points less than 50 m apart to belong to different categories. Vertical stripes above the plot indicate mound pairs exhibiting the inter-mound distance plotted beneath.

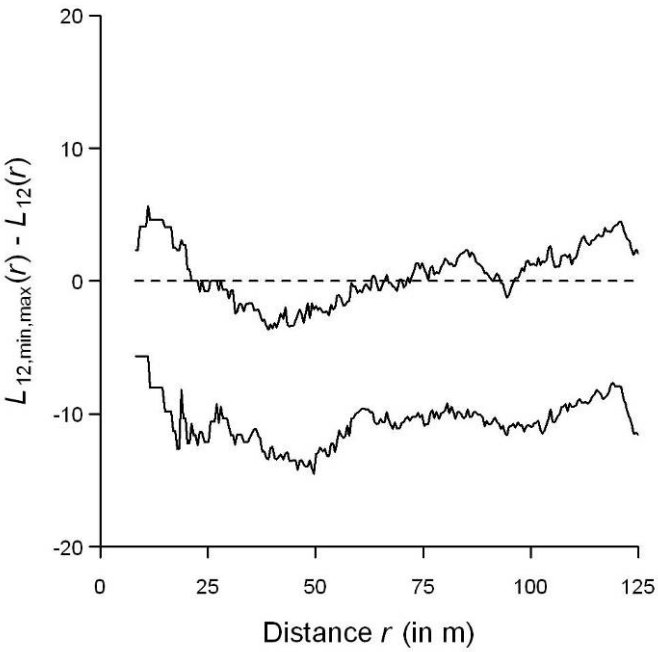

Fig. 5: Envelopes $L_{12,min}(r) - L_{12}(r)$ and $L_{12,max}(r) - L_{12}(r)$ (solid lines) for the association of termite mound categories A1 (mark 1) vs. A2 ∪ A3 (mark 2), resulting from 99 simulations obtained by random labelling. The hypothesis of independent labelling is rejected since $L_{12}(r)$ (set to 0, dashed line) is partly outside the envelopes. This shows that the deviation of $p_{12}(r)$ from 0.30 shown in Fig. 4 is significant.

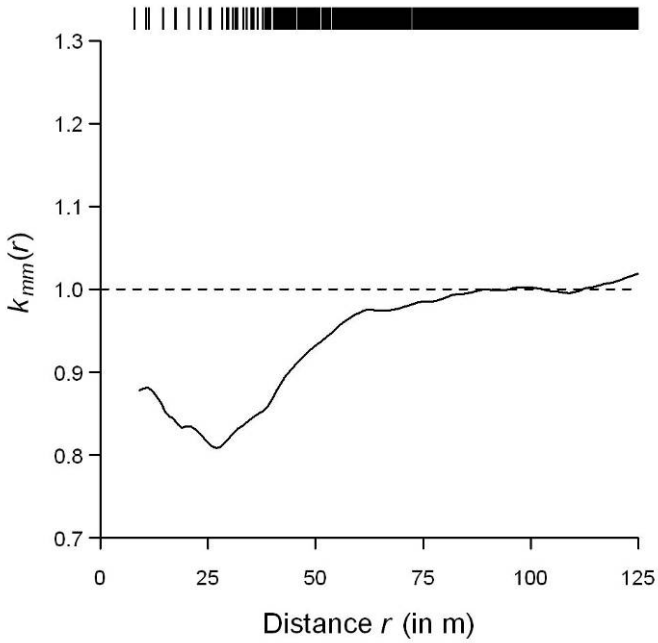

Fig. 6: Mark correlation function for heights of mounds of category A2 ∪ A3 (solid line). There is some tendency that mounds close together are smaller than average. The test of independent marking shown in Fig. 7 demonstrates that the deviation of $k_{mm}(r)$ from 1 (dashed line) is significant. Vertical stripes above the plot indicate mound pairs exhibiting the inter-mound distance plotted beneath.

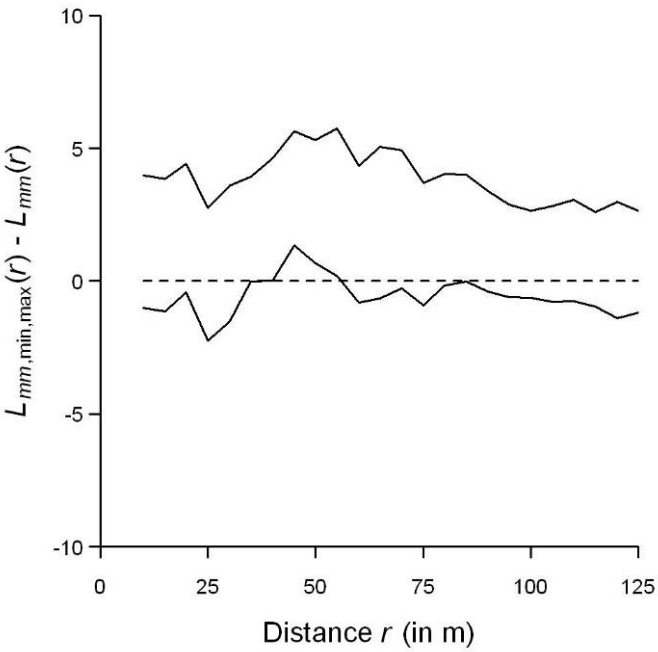

Fig. 7: Envelopes $L_{mm,\min}(r) - L_{mm}(r)$ and $L_{mm,\max}(r) - L_{mm}(r)$ (solid lines) resulting from 99 simulations for the height of larger inhabited termite mounds of category A2 ∪ A3. The hypothesis of independence of mound height from distance to further mounds is rejected since $L_{mm}(r)$ (set to 0, dashed line) is partly outside the envelopes. This shows that the deviation of $k_{mm}(r)$ from 1 in Fig. 6 is significant.

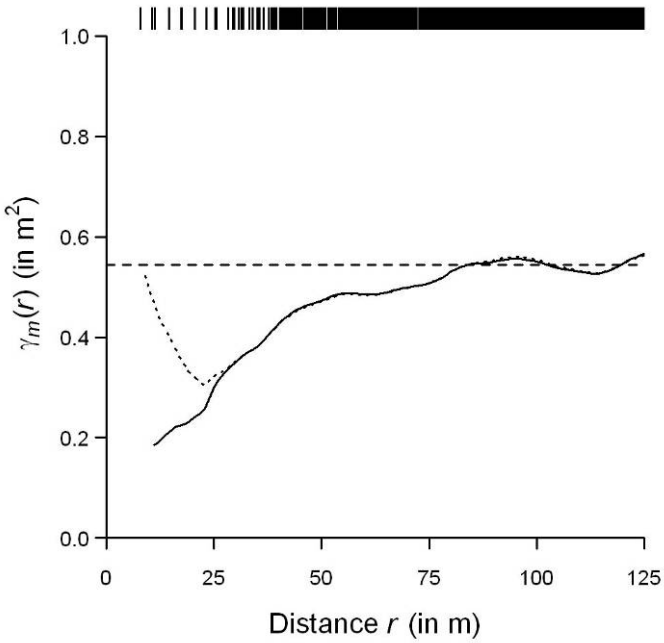

Fig. 8: Mark variograms for all heights of mounds of category A2 ∪ A3 (dotted line) and for the heights without the mound that is highlighted in Fig. 9 (solid line). The variance of the marks (0.54 m² for both calculations) is indicated by the dashed line. The latter mark variogram (solid line) indicates that mounds close together tend to be of similar heights. Each vertical stripe above the plot indicates when there is at least one mound pair exhibiting the inter-mound distance plotted beneath.

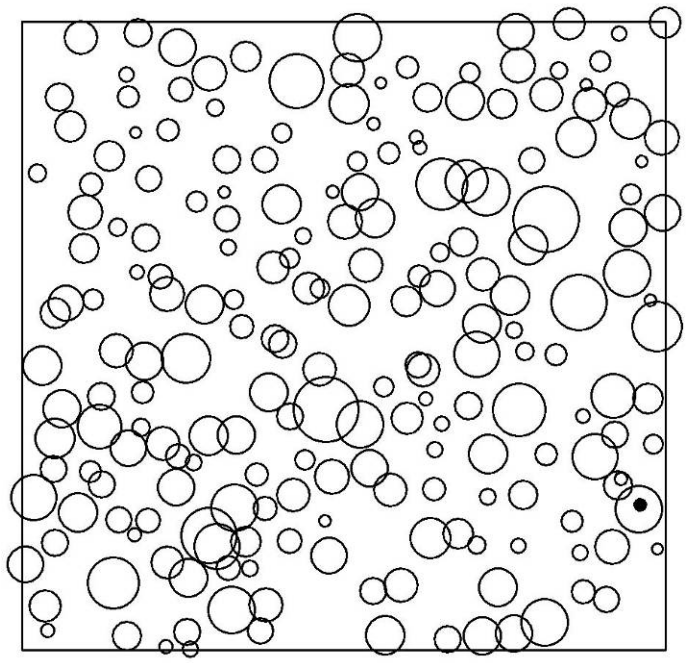

Fig. 9: Spatial distribution of mounds of category A2 ∪ A3 within the study site of 1 km². Circle diameters indicate the relative heights of mounds (0.8–4.4 m). The filled circle represents a mound which was excluded for the calculation of the mark variogram in Fig. 8. This mound, together with the nearby mound of greater height, is responsible for the strange shape of the mark variogram calculated from all mounds >0.7 m.

Discussion

General distribution pattern

The statistical analysis of the pattern of all mounds showed a significant regular spatial distribution of *Macrotermes michaelseni* mounds. This pattern is pronounced in inhabited mounds, particularly so for larger ones of the categories A2 and A3. Such regularity has been described already for several mound-building termite species and is generally interpreted to be a result of intra-specific or inter-specific competition (Wood and Lee 1971, Lepage 1984, Pomeroy 2005). In contrast, earlier investigations of *M. michaelseni* did not detect any deviations from a random dispersion in Botswana and Namibia (Schuurman and Dangerfield 1997, Turner 2000), but did do so in East Africa (Kaib et al. 1997).

Small inhabited mounds, i.e. less than or equal to 0.7 m, showed no significant deviation from a random distribution, but a tendency towards a clustered pattern. Only few data on the distribution pattern of small mounds can be found in the literature. Most authors either counted larger mounds only, because small ones were difficult to find, or differences in mound heights were not taken into account. Korb and Linsenmair (2001a) found, in two out of eight plots, a significantly aggregated distribution of *M. bellicosus* mounds less than or equal to 1.5 m in height.

In addition to intra-specific competition, the distribution of mounds might be influenced by inter-specific competition. Mounds of other termite species were sparse; only a few small mounds built by *Trinervitermes* species were observed within the study site. The genus *Odontotermes* does not build mounds in this region, but is very abundant in the study area. Literature on competition between *Macrotermes* and *Odontotermes* is rare, but indicates that *Macrotermes* outcompetes *Odontotermes* in competition for food resources (Korb and Linsenmair 2001b, Schuurman 2006). However, these reports refer to competition for food resources and no direct conclusions as to the competition pressure for establishing, enlarging or defending nests can be drawn.

Not only the distribution of termite mounds but also the proportions of different mound categories might be influenced by predators. For example, in some regions, doryline ants are important predators of termites (e.g. Bodot 1961, 1967, Collins 1981, Darlington 1985). However, while doryline ants are present in central Namibia, no evidence of them attacking termite colonies could be detected in the region. Instead, aardvarks (*Orycteropus afer*) attacks are more likely, but they affect only a small percentage of mounds. At the study site, five out of the 188 dead mounds showed signs of aardvark attacks, with destroyed fungus gardens clearly visible.

The attribution of mounds to different height classes was based on long-term field experience. Abandoned mounds less than or equal to 0.7 m in height seem to erode at a much slower rate than taller ones. If inhabited mounds survive up until a height of approximately 0.7 m, they thereupon often grow very fast. At a height greater than 2.0 m, mounds seem to be able to enlarge their chimney rapidly (within some days), but the chimney also becomes more vulnerable, with a higher risk of breaking. The above-mentioned positive correlation between the size of a colony or its egg production with mound height (Darlington and Dransfield 1987, Kaib et al. 2001) holds not only for *M. michaelseni*, but also for further *Macrotermes* species (Darlington 1990, Darlington et al. 1992, Meyer et al. 2000) and also for several different termite groups (see review by Lepage and Darlington 2000).

Spatial relationship between small and large inhabited mounds

According to the mark connection function, small mounds (A1) occur closer to larger ones (A2 ∪ A3) than expected by chance. Several reasons might cause such a pattern. If two colonies were founded in the same year but one of them had better conditions for growth, the faster growing colony may suppress the growth of the colony nearby. Another explanation could be that the small colonies are related to the large ones nearby and thus are not eliminated because the strength of competition between genetically related colonies should be less strong than among non-related colonies, as found by Kaib et al. (2004). However, Brandl et al. (2005) suggest that budding is absent in *Macrotermes michaelseni* in East Africa. Darlington (1982) proposed that the removal of nascent colonies prevents the durable establishment of younger colonies in the territories of mature ones, but according to Abe and Darlington (1985), subterranean colonies are able to survive close to mature ones in small areas into which the mature colonies do not extend their subterranean galleries. Possibly, not only subterranean but also small mound-building colonies are able to survive in the direct vicinity of large ones, for example if the large colony is stressed by interspecific competition.

Genetic analyses of colony relationships combined with long-term observations on mound growth would be useful in revealing the causes of the observed spatial distribution patterns of small mounds. Since we are not certain as to how large mounds might influence the patterns of small mounds and since small mounds are not likely to have a strong impact on large mounds and ecosystem functioning, small mounds were excluded from the following analyses.

Correlation of mound height with distance to further mounds

The mark correlation function revealed that for those colonies of category A2 ∪ A3 which are up to approximately 50 m apart, there is a tendency to be smaller than the average. We assume that the distance between colonies is determined by their foraging demand and the competition pressure. Small colonies theoretically have smaller foraging demands and hence smaller foraging zones around their mounds. In conclusion, they are characterised by lessened competition with other nearby colonies when compared to larger colonies.

Information on foraging zones is sparse in the literature. According to Darlington (1982), findings from an excavated *Macrotermes michaelseni* nest in Kenya showed that the main foraging zone has a radius of 10–35 m around the mound. In Kenya, the distance between mounds fell within double the range of the main foraging zone described, indicating that intra-colonial competition for food rules mound distribution (Kaib et al. 1997).

Our data also point to this conclusion, but experimental approaches to the size of foraging zones with regard to competition pressure, foraging demand and food availability should be undertaken to underline that competition for food resources rules mound distribution.

Similarity of mound heights

The mark variogram for mounds larger than 0.7 m in height revealed a strange pattern for small *r*, which was caused by the extraordinary difference in the heights of the single mound pair with shortest inter-mound distance. This unusual occurrence of two mounds with short distances between them, but considerable differences in their heights, might have several causes. According to our data, this is, however, a rare configuration. Possibly the large

colony was somehow weakened, e.g. by infestation of its fungus garden, intraspecific competition caused by the 2nd nearest neighbour (a 1.9 m tall mound, 48 m to the northwest) or interspecific competition.

When excluding the smaller mound of this unusual pair, the mark variogram showed that the differences in mound heights are increasing with increasing distance of the mounds (Fig. 9). Such a mark variogram shape is often observed in geostatistics when regionalised variables such as soil properties, vegetation or precipitation are investigated. They also appear for marked point patterns when the marks are correlated with environmental factors. However, this is not given in the present study since the study site is relatively homogeneous, especially at a scale up to 80 m, so that variations in the habitat characteristics are unlikely to cause the differences in the mound heights.

More likely, the foundation or growth of colonies in certain years might cause the pattern. According to Pomeroy (1983b), new mounds occur almost exclusively in years with high rainfall following drought years. Most likely, they establish themselves in unoccupied patches, for example where old colonies have died. As young colonies have a low foraging demand, they can occur closer together than large ones, the latter being able to out-compete smaller colonies within their territory. These mechanisms lead to a pattern where small mounds of the same age cohort with similar, relatively low heights stand more closely together and their distances to taller mounds increase synchronously with the height of the taller mound.

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Chapter VI

General discussion

The main goal of this study was to analyse the influence of termites on their ecosystem. Chapter II contributes to this purpose as it constitutes a baseline study on **biodiversity** patterns of termites at several sites in Namibia. The 15 identified genera correspond to roughly half of the termite genera that were found in Namibia during the "National Survey", an extensive survey of termites in southern Africa (Coaton and Sheasby 1972). However, the spatial coverage of the National Survey was much larger. In total, 9,000 termite colonies were sampled from 790 localities distributed throughout Namibia. Hence, in light of the far more exhaustive sampling effort during the National Survey, I assume that the termite taxa list I compiled includes the most abundant taxa and therewith those that are probably most important for ecosystem functioning in the study areas. I found a strong dependence of the number of termite taxa on the mean annual precipitation and the Simpson biodiversity index of vascular plants. The former result is in accordance with findings by Buxton (1981) in Kenya and Zeidler (1997) in Namibia. According to the latter result, no data are available from the literature. However, on a global scale, Eggleton et al. (1994) detected a positive response of termite diversity to increasing net primary production. It could be supposed that parallel to increasing termite diversity, the variety of feeding groups and thus the pathways through which the termites influence their surroundings also increase.

Termites were particularly abundant at the Observatories Toggekry and Otjiamongombe. Fungus growing termites such as *Macrotermes* and *Odontotermes* dominated the taxa composition. As *Macrotermes* species build large mounds that are characteristic for many African savannas, chapters III to V consequently focussed on the impact of *M. michaelseni* on ecosystem functioning at these sites. In the following part, I discuss the findings of these chapters with the help of the scheme given in Fig. 1 of the present chapter.

The soil turbation mediated by *Macrotermes* sp. through the construction of **sheetings** is dealt with in chapter IV. Sheetings contained smaller proportions of sand and higher EC (electric conductivity) values than the upper 10 cm of adjacent topsoil. In conclusion, sheetings are not exclusively built by material from the upper 10 cm of topsoil, but include — at least additionally — soil particles from deeper layers. When comparing these findings with former results given in the literature, one has to take into consideration that the definition of topsoil varies between studies. Jouquet et al. (2002) compared *Odontotermes* sheetings with soil from depths of 15–20 cm, which they named topsoil as well, and concluded that soil particles used for the construction of sheetings are selected from topsoil. Additionally, as *Odontotermes* builds its sheetings more rapidly compared to *Macrotermes* (Rouland et al. 2003), results concerning *Odontotermes* species should not be directly extrapolated to *Macrotermes* species.

According to the results of chapter IV, plant growth did not differ if the plants were raised in plantings bags filled with sheeting soil or topsoil. Similar to the sheetings construction rate, references on plant growth on *Macrotermes* sheeting material are lacking. In summary, this thesis revealed that sheetings are mainly, but not solely, built from topsoil

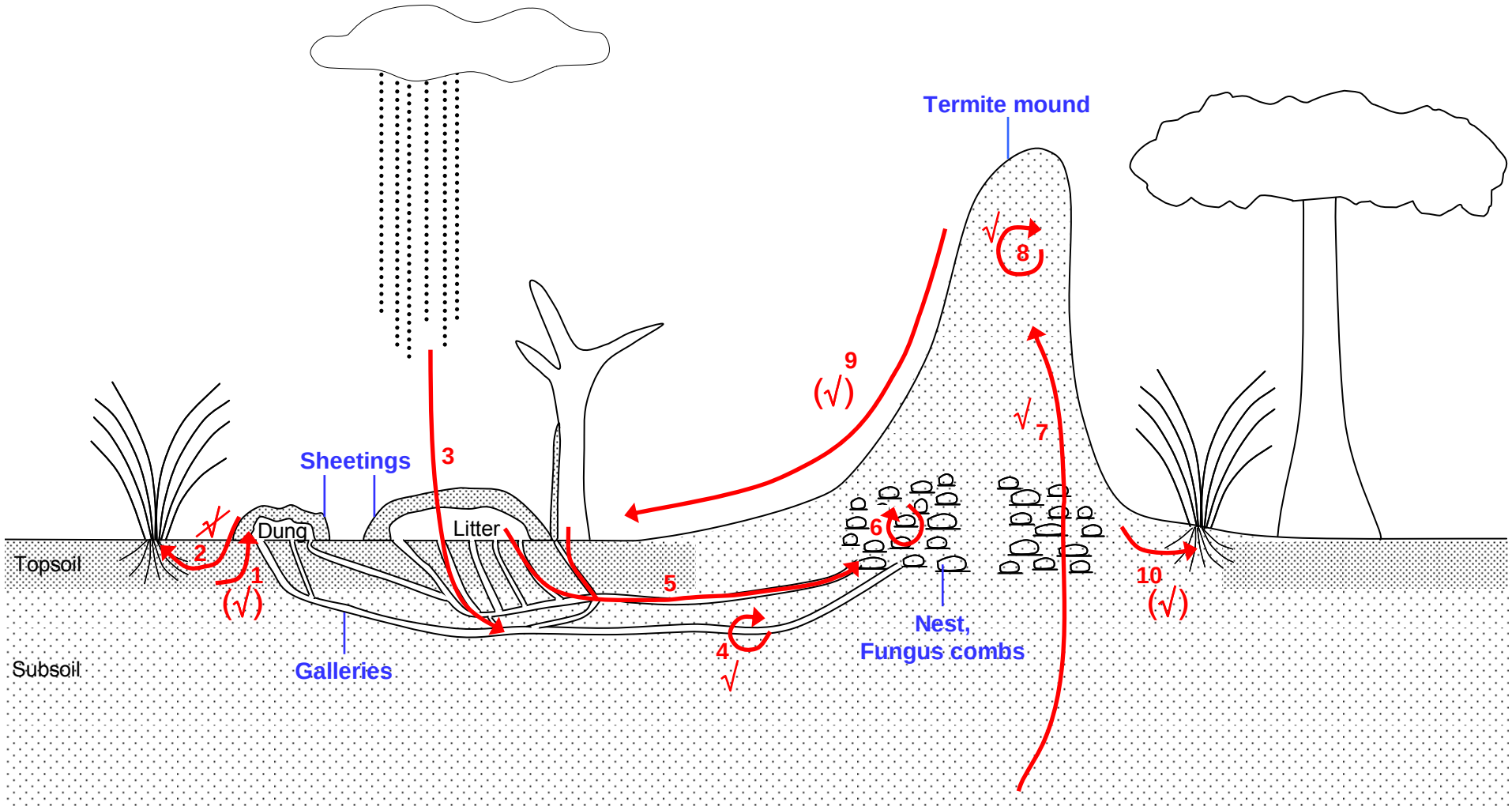

Fig. 1: Scheme of constructions (blue labels) built by *Macrotermes* species and processes (red arrows) mediated by them. Ticks (in brackets, crossed out) indicate that the process and/or its significance for ecosystem functioning is supported (partly supported, not supported) by the results of this thesis. 1: soil turbation via the construction of sheetings; 2: uptake of nutrients from the sheetings by plants; 3: increase of infiltration rates; 4: aeration of the soil; 5: relocation of organic matter (dung, litter, dead wood); 6: decomposition; 7: soil turbation via the construction of mounds with subsoil; 8: mineralisation and enrichment of nutrients; 9: erosion and redistribution of mound material; 10: uptake of nutrients from the mound material by plants.

(tick in brackets at no. 1 in Fig. 1 of this chapter). No effect of sheeting soil on plant growth was found (tick crossed out at no. 2 in Fig. 1).

The effect of subsurface **galleries** on soil characteristics and vegetation patterns (nos. 3, 4 in Fig. 1) might be larger than that of sheetings. This was not analysed directly in this thesis, but is evident from chapter IV, where it is discussed that the soil structure is essential for plant growth and soil aeration is in turn important for plant roots to penetrate the soil.

Concerning the relocation of organic matter by termites (no. 5 in Fig. 1), Schuurman (2006) revealed that the diet of *M. michaelseni* in general is broad, but the ratio of grassy to woody components in their diet depends on the availability of these resources. In the light of land use and climate change and their consequences on vegetation patterns, the question arises if *M. michaelseni* and especially its fungal partner are able to survive if the diet consists exclusively of one food type, or to what extent a mixture of both is necessary to achieve an obligate C/N ratio. The foraging patterns, transport of organic matter and decomposition processes within the mound were not considered in this thesis.

During decomposition processes within the central **nest** system (no. 6 in Fig. 1), the C/N ratio decreases. The highest C/N ratio can be found in the food items, a lesser ratio in the fungus comb and the fungus nodules feature a relatively low C/N ratio. This was demonstrated by Matsumoto (1976) for two different *Macrotermes* species. To my knowledge, no similar data are available for *M. michaelseni*. However, from such analyses one will be able to better understand the nutrition and foraging behaviour of different castes within the colony. Additionally, further studies should consider the shift in the C/N ratio from the food item through the fungus and termite's tissue and saliva to the mound material. Information on such shifts is useful to reveal the processes that lead to the largely reduced C/N ratio of the mound soil as shown in chapter III.

This thesis supports the evidence from literature (Harris 1956, Holt and Lepage 2000) that *Macrotermes* builds its **mounds** with subsoil. This is apparent as the texture of the mounds at Toggekry was rather similar to the subsoil and not to the topsoil (chapter III). However, probably due to low general clay proportions of soils in that region, *M. michaelseni* seems to select certain clay particles for their constructions so that the clay contents of the mounds were even higher than that of the subsoil. Differences between mound material and subsoil were evident in the total N (mainly nitrate) contents and the EC values which both were extraordinarily high in termite mounds. Such a manifold increase in nitrate content and EC value in mound material has hitherto not been described. In chapter III, I additionally showed that old mound material contains significantly higher EC values compared to fresh material. I address this to the relatively higher sand proportions in mounds of the central Namibian savanna compared to the sand contents of mounds from other regions described in the literature. In sandier soils, passive transport of water-soluble nitrate can occur in higher rates. Through evaporation processes, the nitrate accumulates at the soil surface. Additionally, in the better aerated sandy soils, less nitrogen is lost by denitrifying bacteria. For further evidence of such effects of mound texture on nitrogen accumulating processes, more studies are needed that focus on a defined *Macrotermes* species and analyses its mound characteristics in relation to the mound texture. Summarizing, the results on mound soil texture revealed that *M. michaelseni* builds its mounds with subsoil. The high nutrient, content of mound soil, especially the nitrate status, indicates that further processes lead to an enrichment of the mound soil with nutrients (ticks at nos. 7, 8 in Fig. 1).

I revealed that mound material erodes to the surrounding soil in rates of 249 kg ha^{-1} $year^{-1}$, which corresponds to 0.2 m^3 ha^{-1} $year^{-1}$ (chapter III). Similar data on soil **erosion** rates

from *Macrotermes* mounds are only available from Lepage (1984), who found soil eroding at a 47-fold higher rate (9.4 m^3 ha^{-1} $year^{-1}$) from *Macrotermes bellicosus* mounds in West Africa. Due to the different rainfall amounts and intensities at the two sites, the erosion rates can hardly be compared. Topsoil analyses at several distances from termite mounds presented in chapter III showed that the eroded material remains – in the short term – confined to the immediate vicinity of the respective mound, as the topsoil composition at 1 m distance to the mound did differ significantly from the mound soil composition. I assume that through the termite's burrowing activities and the construction of foraging galleries and sheetings, the soil eroding from termite mounds is quickly mixed with the adjacent soil layers which are frequently reshuffled by the foraging activities of the colony inhabitants. However, it should be considered that the erosion of material from an abandoned mound might lead to a distinct pattern in the long term, as, among other changes, no burrowing activities of the colony that once inhabited the mound occur any more. I conclude from the results that *M. michaelseni* causes a strong spatial heterogeneity in soil characteristics with sharp contrasts between mounds soil and off-mound soils. Summarizing, the amount of soil eroding from mounds was quantified in this thesis, but no significant effect on surrounding topsoil properties at 1 m distance from the mounds occurred (tick in brackets at no. 9 in Fig. 1).

The results of chapter IV demonstrated that plant biomass was higher at the base of mounds compared to adjacent soils. However, **plant growth** is hampered if the soil structure is disturbed as one fills the soil into planting bags. This holds although plants growing on mound soils featured significant higher P and K contents. Once the soil structure is disturbed, watering of the soil additionally compresses the soil. In such compact soil, plant roots can hardly penetrate the soil and suffer from lack of oxygen. In contrast, inhabited *Macrotermes* mounds are pervaded by many soil pores and can therefore provide good conditions for plant growth. The contradictory findings concerning vegetation pattern on mound soil that are discussed in the literature so far (see chapter I), might be caused by differences in soil aeration. Additionally, the mound texture might play a role, as the higher clay proportions of mound soils heavily influence their water budgets. In summary, vegetation patterns differed between mound soil and off-mound soil. However, the simple implication that plant growth is favoured by nutrient rich mound soil does not hold, as soil aeration additionally plays an important role (tick in brackets at no. 10 and tick at no. 4 in Fig. 1).

The study on spatial patterns of termite mounds presented in chapter V revealed that large inhabited mounds are regularly distributed. This indicates that intraspecific competition rules the **distribution** of *M. michaelseni* colonies in the focal area. Pringle et al. (2010) showed that, besides being hotspots for primary productivity, mounds are also local hotspots of animal abundance and productivity. For example, the abundance of several animal taxa was increased at *Odontotermes* mounds, up to distances of several ten metres from the mounds. Pringle et al. (2010) included these findings in their simulation analyses and revealed that a regular distribution of termite mounds leads to greater productivity than if the same number of mounds were randomly distributed. It should be analysed if this holds for *M. michaelseni* mounds in the central Namibian savanna. Here, soil properties did not differ significantly when they were taken at 1, 5 or 25 m distance from a mound. However, galleries seemed to have a strong effect on plant growth, and Darlington (1982) revealed the highest density of galleries to be at 10–35 m distance from a *M. michaelseni* mound in Kenya. Consequently, plant growth might not only be different at the base of a mound compared to adjacent soil as stated in this thesis, but might also differ in relation to the distances from a mound. If such an impact of mounds on the vegetation pattern at some ten metres

from a *M. michaelseni* mound occurs, the productivity of the focal site is enhanced by the regular distribution of mounds compared to a random distribution.

From the results of this thesis, I draw the conclusion that *M. michaelseni* has a significant effect on the spatial distribution of soil texture, soil nutrients and vegetation patterns in their habitats. Through their mound building activities, these termites strongly enhance the heterogeneity of their habitats. As stated in the "Biodiversity-Ecosystem Function Paradigm" (Naeem 2002), the biotic interactions between species inhabiting an ecosystem need to be considered when concluding on ecosystem function. Consequently, the question arises how further species of the central Namibian savanna do influence the functions within their ecosystem. Amongst fungus growing termites, the taxa *Allodontermes*, *Microtermes* and *Odontotermes* also occur in high densities at the focal study sites (chapter II). Species of *Odontotermes* built no epiterranean mounds in this area, but seem to occur in high abundance as their sheetings occur in high densities. All these taxa presumably play a central role in modification of soil, which is not fully understood yet due to their subterranean mode of living. Depending on the weather conditions and the season, *Hodotermes mossambicus* and *Trinervitermes* sp. were often seen foraging above the soil surface. A sound picture on the ecosystem functioning of all termite species requires elaborative techniques. However, the present thesis contributes to the understanding of processes mediated by one of the most important ecosystem engineers of the central Namibian savanna, *M. michaelseni*, and its relevance for ecosystem functioning.

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Authors' contributions

Chapter II

Biodiversity of termites along rainfall gradients in Namibia

This chapter is in preparation for publication as:

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The percentage workload carried out by the authors is distributed as follows:

K.E. Linsenmair had the idea to conduct this study. C. Grohmann designed the sampling scheme, performed the fieldwork, identified the specimens and conducted the statistical analyses. This manuscript was written by C. Grohmann and revised by K.E. Linsenmair. The language of the manuscript has been edited by a native English speaker.

C. Grohmann

K.E. Linsenmair

Chapter III

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All authors contributed to the ideas of this manuscript. C. Grohmann designed most of the sampling schemes and performed the majority of the fieldwork. A. Gröngröft and A. Petersen analysed the soil samples. C. Grohmann conducted the statistical analyses. This manuscript was written by C. Grohmann and revised mainly by K.E. Linsenmair. The language of this manuscript has been edited by a native English speaker.

C. Grohmann

A. Gröngröft

A. Petersen

K.E. Linsenmair

Chapter IV

Impact of *Macrotermes michaelseni* on soil fertility and plant growth

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C. Grohmann had the general idea of this study. It was further developed by A. Graiff and K.E. Linsenmair. The sampling design was developed by A. Graiff with the support of C. Grohmann. The fieldwork was carried out by A. Graiff. C. Grohmann conducted most of the statistical anlyses. The manuscript was written by A. Graiff and revised by C. Grohmann and K.E. Linsenmair. The language of this manuscript has been edited by a native English speaker.

A. Graiff

C. Grohmann

K.E. Linsenmair

Chapter V

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C. Grohmann and J. Oldeland had the idea to analyse mound patterns. C. Grohmann and J. Oldeland performed the fieldwork. J. Oldeland had the idea to conduct multi-scale analyses. D. Stoyan had the idea to use the functions we applied to our data and strongly supported the analyses, interpretation of the functions and mathematical formulations. C. Grohmann conducted the statistical analyses. This paper was written by C. Grohmann and revised by K.E. Linsenmair, D. Stoyan and J. Oldeland. The language of this manuscript has been edited by a native English speaker.

C. Grohmann

J. Oldeland

D. Stoyan

K.E. Linsenmair

List of publications

Grohmann C., Oldeland J., Stoyan D. and Linsenmair K.E. 2010. Multi-scale pattern analysis of a mound-building termite species. *Insectes Sociaux* **57**(4): 477-486.

Henschel J.R., Grohmann C., Siteketa V. and Linsenmair K.E. 2010. Monitoring tenebrionid beetle biodiversity in Namibia. *African Study Monographs* Suppl. **40**: 117-128.

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Book contributions

Haarmeyer D.H., Luther-Mosebach J., Dengler J., Schmiedel U., Finckh M., Berger K., Deckert J., Domptail S.E., Dreber N., Gibreel T., Grohmann C., Gröngröft A., Haensler A., Hanke W., Hoffmann A., Husted L.B., Kangombe F.N., Keil M., Krug C.B., Labitzky T., Linke T., Mager D., Mey W., Muche G., Naumann C., Pellowski M., Powrie L.W., Pröpper M., Rutherford M.C., Schneiderat U., Strohbach B.J., Vohland K., Weber B., Wesuls D., Wisch U., Zedda L., Büdel B., Darienko T., Deutschewitz K., Dojani S., Erb E., Falk T., Friedl T., Kanzler S.-E., Limpricht C., Linsenmair K.E., Mohr K., Oliver T., Petersen A., Rambold G., Zeller U., Austermühle R., Bausch J., Bösing B.M., Classen N., Dorendorf J., Dorigo W., Esler K.J., Etzold S., Graiff A., Grotehusmann L., Hecht J., Hoyer P., Kongor R.Y., Lang H., Lieckfeld L.A.B., Oldeland J., Peters J., Röwer I.U., September Z.M., Sop T.K., van Rooyen M.W., Weber J., Willer J. and Jürgens, N. 2010. The BIOTA Observatories. In: *Biodiversity in southern Africa. Volume 1: Patterns at local scale - the BIOTA Observatories* (Jürgens N., Haarmeyer D.H., Luther-Mosebach J., Dengler J., Finckh M. and Schmiedel U., Eds.). Klaus Hess Publishers, Göttingen & Windhoek. pp 6-801.

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Conference contributions

Grohmann C., Oldeland J., Stoyan D. and Linsenmair K.E. 2009. Spatial patterns of termite mounds in central Namibia. *39th Annual Conference of the Ecological Society of Germany, Switzerland and Austria (gfö)* 14.–18.9.2009, Bayreuth. Talk.

Graiff A., Grohmann C. and Linsenmair K.E. 2009. The influence of *Macrotermes michaelseni* (Isoptera, Macrotermitinae) on plant growth in the thornbush savanna of central Namibia. *39th Annual Conference of the Ecological Society of Germany, Switzerland and Austria (gfö)* 14.–18.9.2009, Bayreuth. Poster.

Grohmann C., Oldeland J., Stoyan D. and Linsenmair K.E. 2009. Multi-scale pattern analysis of a mound building termite species in central Namibia. *Joint Meeting of Association for Tropical Biology and Conservation (ATBC) & Society for Tropical Ecology (gtö)* 27.–30.7.2009, Marburg. Talk.

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Peters M.K., Brandl R., Fischer G., Grohmann C., Hausberger B., Hita G., Kagezi G., Kaib M., Kaiser D., Konaté S., Korb J., Linsenmair K.E., Reichmann S. and Wägele W. (2008): Influences of habitat degradation on African ant and termite communities. '*Biodiversity of Africa – Observation and Sustainable Management for our Future!*', International Congress 29.9.–3.10.2008, Spier, South Africa. Talk.

Grohmann C., Petersen A., Gröngröft A. and Linsenmair K.E. 2007. Termite induced soil turnover: Preliminary results from the central Namibian savanna. *20th Anniversary Conference of the Society for Tropical Ecology* 21.–25.02.2007, Bonn. Talk.

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Henschel J.R., Siteketa V., Sisamu C., Grohmann C. and Linsenmair K.E. 2005. Monitoring tenebrionid beetle biodiversity in Namibia. *BIOLOG Status Seminar* 25.–27. November 2005, Würzburg. Poster.

Grohmann C., Irmler U. and Nötzold R. 2004. Die totholzbewohnende Käferfauna (Coleoptera) in Wäldern unterschiedlichen Alters und unterschiedlicher Fläche. *Entomologentagung der DGaaE* 24.–28.03.2003, Halle. Poster.

Ehrenwörtliche Erklärung

Gemäß § 4, Absatz 3, Ziffer 3, 5 und 8 der Promotionsordnung für die Fakultät für Biologie der Bayerischen Julius-Maximilians-Universität Würzburg vom 15. März 1999, zuletzt geändert durch Satzung vom 12. August 2009, erkläre ich hiermit ehrenwörtlich, dass ich die vorliegende Dissertation selbstständig angefertigt habe und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe. Die Dissertation hat keinem anderen Prüfungsverfahren vorgelegen, weder in gleicher noch in ähnlicher Form. Die Christian-Albrechts-Universität zu Kiel hat mir am 26.05.2003 den Titel „Diplom-Biologin“ verliehen. Weitere akademische Grade habe ich weder erworben noch zu erwerben versucht.

Würzburg, 11. November 2010

Wen die Sonne Namibias einmal gebrannt hat, der kommt wieder.

Klaus-Dieter Schobel