Community ecology of African termites (Isoptera)

Dissertation

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General Introduction

Community ecology

Community ecology has become a key issue in the broad field of ecology. Understanding the mechanisms that structure species communities around the globe is of vital importance to many research questions and especially conservation schemes. Nevertheless, the processes structuring species communities are still highly debated (Chase and Leibold, 2003; Holt, 2009; Zhou & Zhang, 2008).

Today, there are two main theories trying to explain occurrence of species and community assembly. First, there is the classical *niche theory* with the associated *principle of competitive exclusion,* which has been closely associated since the concept of the 'niche' first appeared in the 1920's (Vandermeer, 1972; Alley, 1982) and was proposed as a central concept in ecology by G.E. Hutchinson more than 60 years ago, known as the Hutchinsonian niche (Hutchinson, 1957, 1978). The term '*ecological niche*' is defined as the range of environmental variation in both biotic and abiotic factors under which indivuduals of a species can engage in the activities necessary for its survival (Alley, 1982). The *principle of competitive exclusion* asserts that there can be no more than one species per niche (or per limited resource) assuming that communities exist at competitive equilibrium (reviewed in Alley, 1982). Thus, deterministic factors play an important role in the niche theory. These include interspecific competition, which was classically thought of as a major driving force in structuring communities of ecologically similar species (Diamond, 1978; Schoener, 1982), and environmental filtering, which sorts species into suitable habitats, depending on their specific traits (Fig. 1). Second, there is the unified neutral theory of biodiversity and biogeography (Hubbell, 2001), which challenged the niche theory in recent years and considered niche differences less important. The neutral theory states that trophically similar

species are demographically equivalent, meaning that all individuals of all ecologically similar species in the community have the same probability of birth, death, random migration and extinction (Zhou & Zhang, 2008). Thus, according to the neutral theory, communities are mainly structured by 'ecological drift' (Hubbel, 2001; Volkov et al. 2009). Both the niche and neutral theory can certainly explain important aspect of community assembly, but the neutral theory has brought a novel view on the processes structuring natural communities. It has been suggested to combine both theories by integrating demographic and deterministic processes into the models (Zhou & Zhang, 2007, 2008).

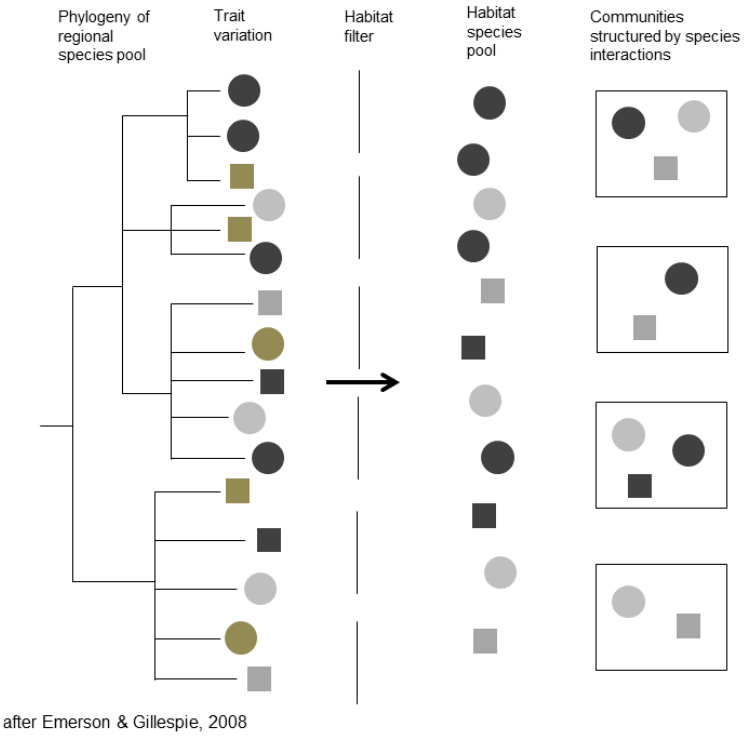

Figure 1. According to the niche theory, habitat filtering and competition (species interactions) both influence community assembly. Habitat filtering sorts species into environmentally suitable habitats (niche), according to their specific traits. Species are then sorted into communities through local species interactions. Different colors and symbols represent the trait variation of the species on the phylogenetic tree. Species with the trait 'brown' are not able to overcome the habitat filter due to unsuitable ecological traits.

Another important aspect in community ecology that has to be considered when evaluating mechanisms influencing community assembly is scale. Processes that generate and maintain species diversity vary depending on the taxonomic, spatial and temporal scale over

which they are quantified (Graham & Fine, 2008). An understanding of the importance of local versus regional processes depends on the spatial scale at which we define local and regional communities and the scale at which actual processes operate (Weiher et al. 2011). R.H. Whittaker (1975) proposed that diversity should be analyzed within a hierarchy of spatial scales. At the local scale (α niche), α-diversity represents the number of species found within a habitat. At an intermediate scale (β niche), β-diversity quantifies the turnover (change) in species composition that takes place between habitats or along environmental gradients. The regional scale is the γ niche, where γ-diversity is the species diversity of a region. At regional scales diversity gradients are influenced by evolutionary factors, such as variation in timing and rate of lineage diversification, and ecological factors, for instance current and past expanse of suitable habitats. At local scales, studies integrating community ecology and phylogenetics have shown that biotic interactions and trait evolution is crucial (reviewed in Graham & Fine, 2008).

To clarify how processes at these different scales interact and are connected, recent studies have combined phylogenetic information with distributional and ecological data, which can provide an evolutionary approach to analyse how community structure and traits of species in a community change as a result of both spatial and environmental gradients (Graham & Fine, 2008; Emerson & Gillespie, 2008; Bryant et al. 2008; Graham et al, 2009; Gómez, 2010). Phylogenetic data can provide information on the relatedness within and between species communities and can illuminate processes influencing community assembly. For one, there is phylogenetic β-diversity, which is β-diversity with a temporal dimension; it is defined as the phylogenetic distance (branch lengths) between samples of individual organisms between any two sites, which can be calculated with the PhyloSor index (Bryant et al. 2008). The ß-diversity and phylogenetic ß-diversity between two sites would be exactly the same if every species in the regional pool were equally related to every other species, but this is not a likely scenario in natural communities. Moreover, phylogenetic ß-diversity

quantifies how phylogenetic relationships among species change across space (Graham & Fine, 2008). Another useful aspect of including phylogenetic information is that it can distinguish random from non-random phylogenetic structures within a habitat (α-diversity level) by using the Net Relatedness Index (NRI). If communities are random assemblages of the regional species pool, this would be consistent with the neutral theory. Non-random patterns can result from environmental filtering on shared traits with communities being phylogenetically clustered (species co-occurring are phylogenetically more closely related than expected by chance; Fig. 2a). Biotic interactions, including competition, can result in phylogenetically overdispersed communities (species co-occurring are phylogenetically more distantly related than expected by chance; Fig. 2b) (Graham & Fine, 2008; Bryant et al. 2008; Kembel & Hubbel, 2006; Webb et al. 2002; Emerson & Gillespie, 2008). The interpretation of these results very much depends on trait lability, defined as the probability of evolutionary change in a trait (Kraft et al. 2007; Emerson & Gillespie 2008). When traits are phylogenetically conserved, habitat filtering should create clustered communities and competition should create overdispersed patterns. If traits are phylogenetically convergent, competition can cause trait divergence between close relatives (e.g. Schluter, 2000) that allow their coexistence and creates clustered communities (Cavender-Bares et al., 2009; Kraft et al. 2007; Fig. 2c) or there is environmental filtering on ecologically important labile traits which produces overdispersed communities (Fig. 2d).

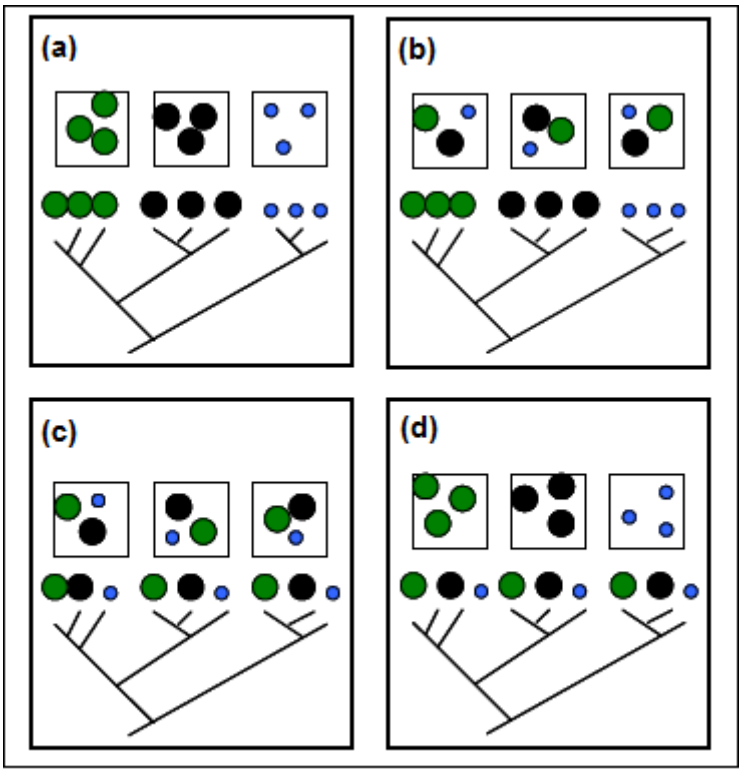

Figure 2. How environmental filters, competition and trait lability structure communities. Small squares present local communities composed of three species (circles) that are 'drawn' from a regional species pool represented by the phylogenetic tree (i.e. terminal tips are different species). Different colors represent different niche-relevant traits. (**a**) Phylogenetic and phenotypic clustering. Conserved evolution of niche traits. Strong environmental filtering. (**b**) Phylogenetic and phenotypic overdispersion. Conserved evolution of niche traits. Greater importance of species interactions over environmental filtering. (**c**) Phylogenetic clustering and phenotypic overdispersion. Consistent with evolutionary labile niche traits through interspecific competition. (**d**) Phylogenetic overdispersion and phenotypic clustering. Consistent with evolutionary labile traits and strong environmental filtering.

Phylogenetic community structure analyses can be especially useful in the light of the high species diversity in tropical ecosystems, where many species of seemingly identical niches coexist. This applies especially for insects whose sheer species richness cannot be explained by niche differences alone, which is challenging for the classical niche theory.

Termites – special social insects

A promising taxon to uncover the processes that govern the co-existence of trophically similar, potentially competing species are termites. They are frequently described as ecosystem engineers, because they are important decomposers of organic matter and

mediators of soil properties and humification processes (Abe, 1979; Eggleton et al. 1994, 1996; Holt & Lepange, 2000). They influence nutrient flux and food webs and enhance soil fertility, bioturbation and water infiltration rates (reviewed in Bignell & Eggleton, 2000; Evans et al., 2011; Dahlsjö et al., 2015). In African ecosystems one termite family, the Termitidae, dominate and within them the subfamily of the Macrotermitinae, the fungus-growers, represent a large part of the species found in African ecosystems. Many termites, and especially the fungus-growers, occupy very similar niches, with similar habitat and food requirements (Bignell & Eggleton, 2000), which is what makes termites a very interesting taxon to study community assembly processes.

Termites live on dead plant material at different stages of decomposition, from living plants to highly degraded material in the soil, which is known as a 'humification gradient'. On the non-humified end, resources are of high quality but patchily distributed (e.g. wood, grass) and at the humified end they are of low quality but very abundant (e.g. soil) (Donovan et al. 2001; Bignell & Eggleton 1995). Accordingly, termite species have been assigned to 'feeding groups' or 'functional taxonomic groups', depending on their foraging habitat, feeding habits and gut content analysis (Eggleton & Tayasu, 2001; Donovan et al. 2001; Davies et al, 2003). The widely acknowledged classification by Donovan et al. (2001) defines four different feeding groups (I-IV) and designates termite species to one of these feeding groups according to their preferred food source along the humification gradient: group I consists of dead wood-feeders, group II species are dead wood, micro-epiphytes, leaf litter and grass-feeders, group III consists of humus-feeders, and group IV termites are true soil-feeders ingesting apparently mineral soil. Within feeding group II, there are two subgroups of feeding type specialists, the fungus-growers (Macrotermitinae), which cultivate and feed on an obligate symbiotic fungus within their colony, which they provision with a variety of dead plant material (group II_f), and the specialist grass-feeding *Trinervitermes* (group II_g) that live on grass alone. In African savannah regions, the dominant feeding group is wood-litter feeders (group II), especially the

above mentioned two specialist feeding types, fungus-growers and grass-feeders. Macrotermitinae take 95% of the litter that is removed by termites, which is 23% of the annual litter production in African savannahs (Collins 1981; Hausberger et al. 2011; Hausberger & Korb, 2015). This highlights the dominance and importance of these termite species in African savannah regions.

Stable isotope methods have become a new way of analyzing and visualizing these trophic relationships in termites. Carbon and nitrogen isotopes have proven reliable to identify the trophic position of termites along the humification gradient from wood over soil-wood interface to soil-feeders (Tayasu et al. 1997; Bourguignion et al. 2009, 2011) and reveal food preferences and differences among feeding groups and genera (Tayasu et al. 1998).

Studying termites and termite communities can be constrained by the difficulty of species identification (Hausberger et al. 2011). The most commonly encountered caste is the worker caste, as they are the ones that leave the nest most frequently for foraging. Morphological identification can be difficult because workers mainly lack species-specific morphological traits. An identification, often only to the genus-level, is merely possible when collecting soldiers or winged sexuals. To resolve this problem, species-specific molecular genetic markers have been developed during the last years (Legendre et al, 2008; Hausberger et al. 2011) to identify termite species genetically from phylogenetic trees. As there are several cryptic morpho-species existent in termites (Hausberger et al. 2011), this molecular method has proven very useful to appropriately identify termite species in addition to classical morphological identification tools.

Disturbance threatens biodiversity

Anthropogenic disturbance has become a critical problem around the world, as it often leads to habitat change and loss, which frequently leads to a loss of biodiversity (Pimm & Raven, 2000; Barlow et al., 2016; Fahrig, 2003; Brooks et al., 2002). Especially habitats that are most

species-rich, the tropics, are being extensively destroyed by human activities. About two-thirds of all species occur in the tropics, largely in the tropical humid forests, which originally covered between 14 and 18 million square kilometers, but today only half of this original area remains (Pimm & Raven, 2000).

The term disturbance is often used in ecology to refer to several different phenomena, including fires, storms, earthquakes, diseases, land clearing and the like (Dornelas, 2010). As the term is used so widely, Dornelas (2010) tried to define ecological disturbance more precisely. She refers to one fundamental characteristic of disturbance, which is its discrete nature in space and time. Disturbance is temporary and localized and not to be confused with stress, which can also change biodiversity, but over a longer, permanent period (e.g, climate change). The term disturbance is often only used to refer to the above mentioned causes of disturbance, but Dornelas (2010) focuses on the consequences resulting from disturbance events. Therefore, she defines ecological disturbance as an event that causes temporary and localized shifts in demographic rates, meaning changes in mortality rates, birth rates and carrying capacity of an ecological community. This shows that it is important to look at ecological communities as a whole to reveal disturbance events and their consequences for the ecological communities. We will apply this definition of disturbance in this work.

It has become increasingly important to study African termite diversity in view of intensification of land-use and increasing population pressure, especially in West Africa (UNDP, 2010), because termites as ecosystem engineers are crucial for the preservation of savannah and forest ecosystems. It has been shown that termite diversity is strongly affected by disturbance events, as species richness can decline when forests are cleared (Davies et al., 2003; Eggleton et al. 2002) or savannahs are turned into agricultural fields which later become fallows (Hausberger & Korb, 2016; Fig. 3).

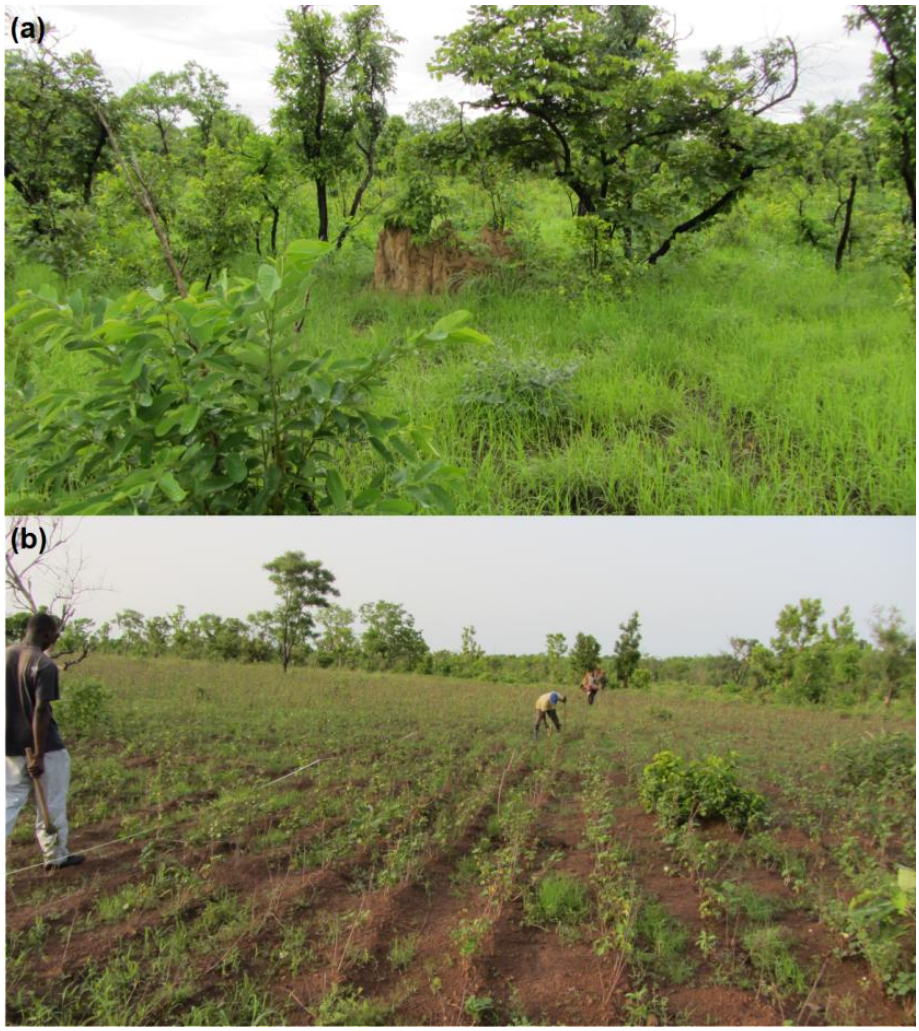

Figure 3. Savannah sampling plots in the Oti-Kéran National Park in northern Togo.**(a)** a natural, undisturbed savannah habitat with abundant vegetation and **(b)** a young fallow (1 year since last cultivation), with still clearly visible agricultural structures and remains of cotton plants.

Aims of this study

The aims of this study were as follows:

1. Analyze how anthropogenic disturbance (agriculture) affects termite species assemblages in a West African savannah region in Togo along a disturbance gradient.
2. Compare termite communities in the two major West African ecosystems, savannah and forest, both under natural settings and along a disturbance gradient.

3. Examine the stable isotope signatures of West African savannah termites to reveal possible patterns influencing community structure and thereby test existing feeding group concepts.
4. Test if local termite communities in Namibia, Southern Africa, differ from random assemblages of the regional species pool with regard to phylogenetic composition along a north/south environmental gradient.

Chapter 1

Disturbance filters termite species

Janine Schyra, Judith Korb

Abstract

Termites are important ecosystem engineers, crucial for the maintenance of tropical biodiversity and ecosystem functioning. But they are also pests which cause billions of dollars in damage annually to humans. Currently, our understanding of the mechanisms influencing species occurrences is limited and we do not know what distinguishes pest from non-pest species. We analyzed how anthropogenic disturbance (agriculture) affects species occurrences. We tested the hypothesis that strong disturbance functions as a habitat filter and selects for a subset of species which are major pests. Using a cross-sectional approach, we studied termite community composition along a disturbance gradient from fields to 12-year-old fallows in a West African savannah. We tested for ecological factors and biotic interactions associated with the co-/occurrences of species that were reliably identified using genetic means. Supporting our hypothesis, disturbance was associated with environmental filtering of termites from the regional species pool, maybe via its effect on vegetation type. The most heavily disturbed sites were characterized by a subset of termite species which are well-known pests of crop. This supports a model in which strong anthropogenic disturbance selects for termite pest species.

Introduction

Termites are major ecosystem engineers with crucial roles in decomposition, soil fertility, hydrology, and species diversity (Pringle et al. 2010; Evans et al. 2011). Concomitantly, a few species are also major pests (Rouland- Lefèvre 2011). Despite their importance, we hardly understand what determines the occurrence of different termite species and what distinguishes pest from non-pest species.

Niche overlap between different species seems to be substantial as termites are detritivores and only four major feeding types are distinguished (Donovan et al. 2001): dead wood-feeders (group I); dead wood, micro-epiphytes, leaf litter and grass-feeders (group II); humus-feeders (group III) and true soil-feeders (group IV) (reviewed in (Davies et al. 2003; Eggleton 2011). Niche overlap between termites seems to be especially pronounced in African savannahs where up to 20 higher termite species (Termitidae) of feeding group II co-exist (e.g., Dosso et al. 2010, 2013; Hausberger et al. 2011; Hausberger and Korb 2015, 2016). These group II species can be subdivided into two feeding type specialists, grass-feeding *Trinervitermes* (group II_g) and fungus-growing Macrotermitinae (group II_f). The latter cultivate an obligate symbiotic fungus within their colonies, which they provision with a broad range of dead plant material (Nobre et al. 2011). The similarity of termites' food niches implies that competitive interactions are important in shaping local savannah communities (Basu 2011; Korb and Linsenmair 2001a). However, recent analyses in Benin suggest that random processes play an important role in community assembly in an undisturbed West African savannah, with a structuring effect by one large mound building species, *Macrotermes bellicosus* (Hausberger and Korb 2015). Additionally, first evidence implies that assembly processes change to more environmental filtering with disturbance (Hausberger and Korb 2016). This suggests that disturbance can not only lead to a decline in species richness,

but also to a change of the processes that structure species communities. Few species occurred in strong anthropogenically disturbed areas and several might be pests of crop.

In the current study, we investigated termite community composition of different-aged fallows (measured as the time since they were last cultivated) in a West African savannah region in Togo. By doing this, we aimed at analysing how communities assemble over time from a strong anthropogenically disturbed habitat to a more natural setting. We expect that termite communities of younger-aged fallows are more strongly structured by environmental filters and had more pest species than older ones. To test this, we first identified all species occurring in the different communities using morphological and genetic markers. A genetic approach is necessary to unambiguously identify all termite samples. To reveal assembly processes, we then applied phylogenetic community analyses that explicitly test real, studied communities against communities that are drawn at random from the regional species pool. Finally, we investigated whether species from young-aged fallows correspond to pest species. The aims of our study therefore are (i) to determine termite community composition in a West African savannah, (ii) to test for assembly processes within these communities, and (iii) to test whether pest species are a subset of species that are more resilient to disturbance.

Materials and Methods

Termite sampling

Termites were systematically collected when they were most active, that is, during the beginning of the rainy season near the Oti-Kéran National Park in northern Togo (West Africa; 10°17’ to 10°08’ N; 0°28’ to 0°51’ E, Fig. 1). This region is a typical West African savannah lying in the center of the West Sudanian biome (mean annual precipitation: 1100 mm; Worldclim database). Termites were collected in 2012 from seven fallows of age 0, 2, 4,

6, 8, 10 and 12 years. In 2014 we added six new fallows of age 0, 0, 1, 2, 10 and 10 years. Our sampling regime was constrained by the availability of fallows with known age.

Sampling was done using a standardized belt transect protocol first developed for sampling termites in forests (Jones and Eggleton 2000) and then adapted to savannahs (Hausberger et al. 2011). In short, the protocol consists of a thorough search of dead plant material on the ground, on and in trees and mounds as well as soil sampling to assess termite diversity (Jones and Eggleton 2000). Plot size was one hectare with three transects each measuring 2 m x 50 m, divided into ten 2 m x 5 m sections, arbitrarily located within one plot. Each transect section was searched systematically for termites for 15 minutes by a trained person. Additionally, we sampled eight soil scrapes per transect section measuring 15 cm x 15 cm x 10 cm. All encountered termites were stored in 99% ethanol for subsequent molecular analyses.

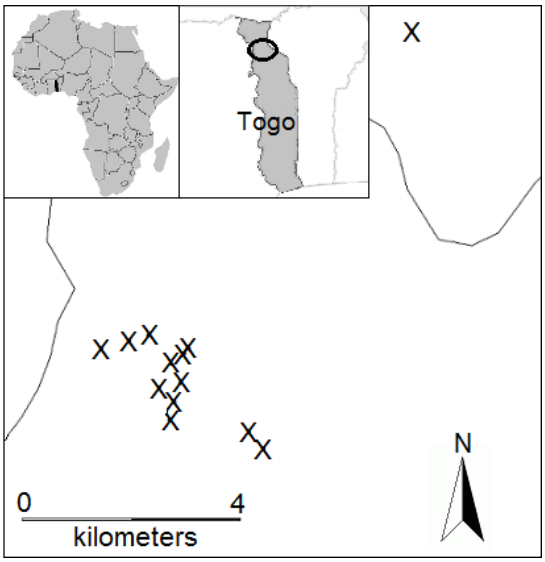

Figure 1. Map of Africa with the location of the the Oti-Kéran National Park in northern Togo (small maps) and distribution of the 13 sampled fallows in the study area (each plot is marked with X).

As in the former studies (Hausberger et al. 2011; Jones and Eggleton 2000; Korb and Linsenmair 2001 b), we chose a plot size of one hectare because the foraging ranges of termite colonies is within 100 m (Korb and Linsenmair 2001 b). Hence one hectare represents the local scale where interactions between colonies occur, i.e., it reflects the Darwin-Hutchinson-Zone, which is most relevant to study assembly of local communities (Vamosi et

al. 2009). We specifically selected plots with and without active *M. bellicosus* mounds as it is the main mound builder and an important ecosystem engineer which may influence termite communities.

All samples were identified to the species level: Samples containing soldiers were first identified using the keys by Webb (1961) and Sands (1965a), and then sequenced to obtain an unambiguous species identity (see below). Samples with workers only, were genetically analysed, as morphological identification was impossible (see below). To assign the feeding group to each sample, we followed the anatomical criteria outlined by Donovan et al. (2001). Whenever we found/encountered termites during the search within a transect section, we collected a few specimens in a vial (5-10 individuals). Then we continued searching within the section and when we encountered termites again they were placed in a separate vial. The number of all resulting vials for a study plot (i.e., the sum over all transect sections for all three replicate transects within a plot) was used as encounter rate. This is used as a surrogate of species abundance (Davies 2002). Naturally, the presence / absence of each species within each plot arose from these data as well.

During sampling, we recorded data for the environmental variable 'vegetation type' by classifying plots according to their vegetation type and vegetation density: field (recognizable cultivation and crop plants), open savannah (mainly grass land, few bushes and trees), and medium-dense savannah (many bushes and trees). The savannah was a typical West-African Sudanian savannah. The main shrub and tree species were *Afzelia africana*, *Crossopteryx febrifuga*, *Detarium microcarpum*, *Piliostigma thonningii*, *Vitellaria paradoxa*, *Combretum* spp., *Terminalia* spp. and *Gardenia* spp. All study plots had similar flat slopes and were located away (at least 1 km) from rivers or lakes. The topography of the studied plots was flat.

Genetic identification and phylogenetic analyses

To allow unambiguous species identification, we isolated DNA and sequenced fragments of three genes as described elsewhere (Hausberger et al. 2011) (additional data are given in Appendix 1, Table S1): *cytochrome oxidase subunit I* (*COI*; total length 680bp), *cytochrome oxidase subunit II* (*COII*; total length 740 bp), and *12S* (total length 350 bp). These sequences were used to re-construct phylogenetic trees using three approaches (Bayesian method, maximum-parsimony analysis, and maximum-likelihood analysis) to delimitate and identify species (for more details see Appendix 1). As in former termite studies (Legendre et al. 2008; Hausberger et al. 2011), *COII* was most useful for 'barcoding' (i.e., assigning species to samples) because it amplified well and gave appropriate resolution for species identification. All samples were identified. Species names correspond to those given in Hausberger et al. (2011) and Hausberger and Korb (2015, 2016) for Benin. *Amitermes* sp1 from the Benin studies is actually *Amitermes evuncifer*. Hence, we used the proper species name in our study. To obtain corresponding species identities, we constructed a phylogeny comprising all species occurring in Togo and Benin. Samples forming a species cluster were named identically. In total we sequenced 899 samples in the current study.

Phylogenetic community structure analyses

We analysed the local community structure with PHYLOCOM 4.2 (Webb et al. 2008). As input tree for the phylogenetic community structure analyses we used the *COII* gene tree, which was pruned prior to analysis so as to have only species of the regional species pool included and only one representative per species in the tree. This representative was the sequence with the highest quality values for each base (maximum value of 61, multiplied by ten) as defined in Chromas 2.4.4 (1998-2016, Technilysium Pty Ltd).

We calculated the net relatedness index (NRI) that measures whether locally co-occurring species are phylogenetically more / less closely related than expected by chance. It

uses phylogenetic branch length to measure the distance between each sample to every other terminal sample in the phylogenetic tree, and hence the degree of overall clustering (Webb et al. 2008). The NRI is the difference between the mean phylogenetic distance (MPD) of the tested local community and the MPD of the total community (regional) divided by the standard deviation of the latter. High positive values indicate clustering; low negative values overdispersion (Webb et al. 2002). We tested whether our data significantly deviated from 999 random communities derived from null models using the independent swap algorithm on presence / absence data (Gotelli and Entsminger 2003; Hardy 2008). The swap algorithm creates swapped versions of the sample / species matrix and constrains row (species) and column (species' presence or absence) totals to match the original matrix. The regional species pool consisted of all species from all studied localities. As suggested by Webb et al. (2008), we used two-tailed significance tests based on the ranks that describe how often the values for the observed community were lower or higher than the random communities. With 999 randomisations, ranks equal or higher than 975 or equal and lower than 25 are significant at $P \leq 0.05$ (Bryant et al. 2008).

Similarity between fallows

We quantified the compositional similarity (ß-diversity) between all localities using the Bray-Curtis sample similarity index (Magurran 1988), which was calculated in EstimateS version 8.2.0 (Colwell 2013). It ranges from 0 to 1, with low values indicating low similarity and high values the reverse. The Bray-Curtis index is quantitative; the abundance of species is taken into account when calculating the shared species statistics.

Other statistical analyses

All inferential statistics were done with the statistical package IBM SPSS 16. All tests were two-tailed. Data were tested for assumptions of parametric testing and analyses were done

accordingly. For all data, qualitatively the same results (i.e. effects were significant or non-significant) were obtained when testing parametrically or non-parametrically.

Results

Diversity

We identified a total of 19 species (regional species pool), all Termitidae (Table 1). All conducted phylogenetic analyses yielded similar topologies (Fig. 2; Appendix 1, Fig. S1, S2). As is typical for African savannahs, fungus-growing Macrotermitinae dominated with eight species (*Microtermes* sp.1, *Microtermes* sp.2, *Microtermes* sp.3, *Microtermes* sp.4, *Macrotermes bellicosus, Macrotermes subhyalinus, Ancistrotermes* sp.1, *Odontotermes* sp.1), of which all co-existed locally. The next most-species rich group were Nasutitermitinae with the grass-feeders *Trinervitermes occidentalis, Trinervitermes geminatus, Trinervitermes oeconomus, Trinervitermes togoensis* and *Fulleritermes tenebricus*. Despite occupying the same feeding niche, all four *Trinervitermes* species co-occurred locally. Further, we sampled two representatives of the soil-feeders Apicotermitinae (*Astalotermes* sp., *Adaiphrotermes* sp.1) and four species of the Termitinae (*Microcerotermes* sp.1, *Amitermes evuncifer* (both wood-litter feeders), *Procubitermes* sp.1 and *Pericapritermes* sp.1 (soil-feeders)). Surprisingly, species richness did not increase with fallow age (Spearman-rank correlation: $N = 13$, $P = 0.324$). Out of a total of 19 species that we found in the fallows, from seven to 13 species co-occurred locally. Species names are in accordance with the identified species from the studies in Benin (Hausberger et al. 2011; Hausberger & Korb 2015, 2016).

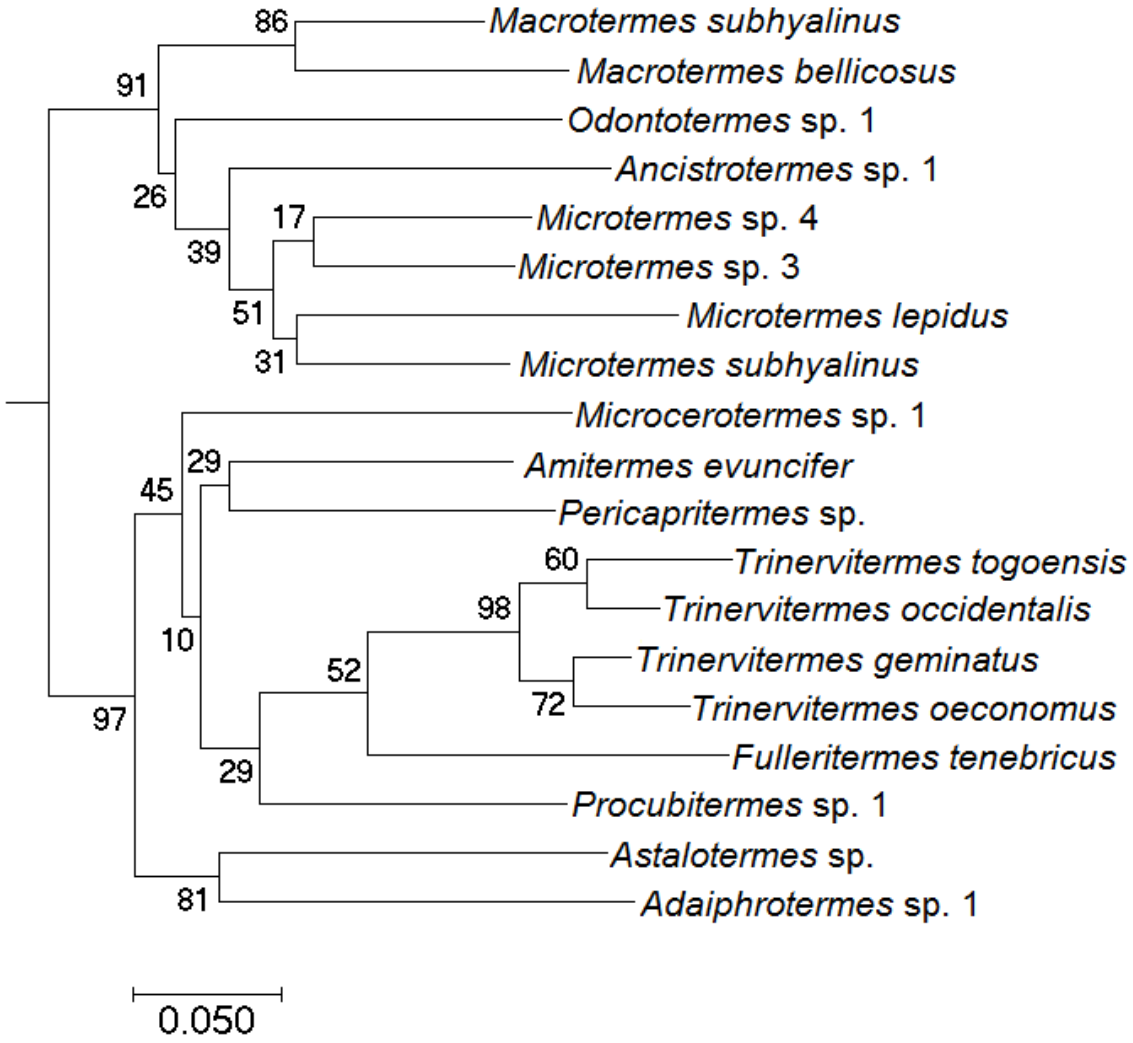

Figure 2. Input Bayesian phylogeny for Phylocom based on the gene cytochrome oxidase II using MrBayes v3.1.2. Analysis was done with 10^7 generations, number of chains=4, sample frequency=1000 and a finalizing burn-in of 2500. Node numbers are the posterior probabilities calculated to assess branch support.

Phylogenetic community structure

The NRI values, measuring the phylogenetic community composition, ranged from -0.72 to 4.21. Three plots showed significant signals of environmental clustering (Plot S: NRI: 2.83; Plot W: NRI: 2.80; Plot 5: NRI: 4.41; all $P < 0.05$). NRI values did not correlate with fallow age (Spearman-rank correlation: N = 13, P= 0.131) nor with species richness (Spearman-rank correlation: N = 13, P = 0.890). However, there was an indication that vegetation type affects phylogenetic community structure (ANOVA: F = 3.21, P = 0.084, Fig. 3).

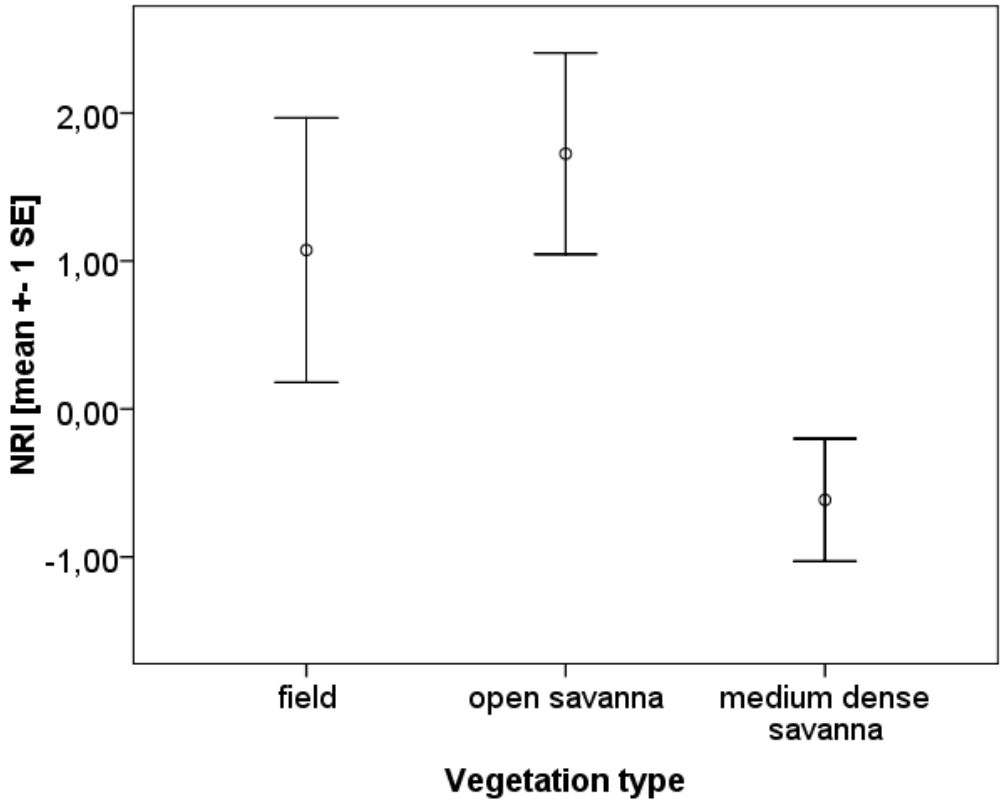

Figure 3. NRI (Net Relatedness Index) and vegetation type. There was an indication that vegetation patterns affect termite community composition, as communities were more clustered (more closely related) in open savannahs.

Communities may be more phylogenetically clustered in fields (Tukey-HSD *post-hoc* test: P = 0.072) and open savannahs (Tamhane *post-hoc* test: P = 0.058). Similarly, *M. bellicosus* may have an effect on phylogenetic structuring: when *M. bellicosus* was present NRIs were higher (i.e. more phylogenetically clustered communities) than when it was absent, although not significantly (Mann-Whitney-U test, Z = -1.76, N = 13, P = 0.079; Fig. 4).

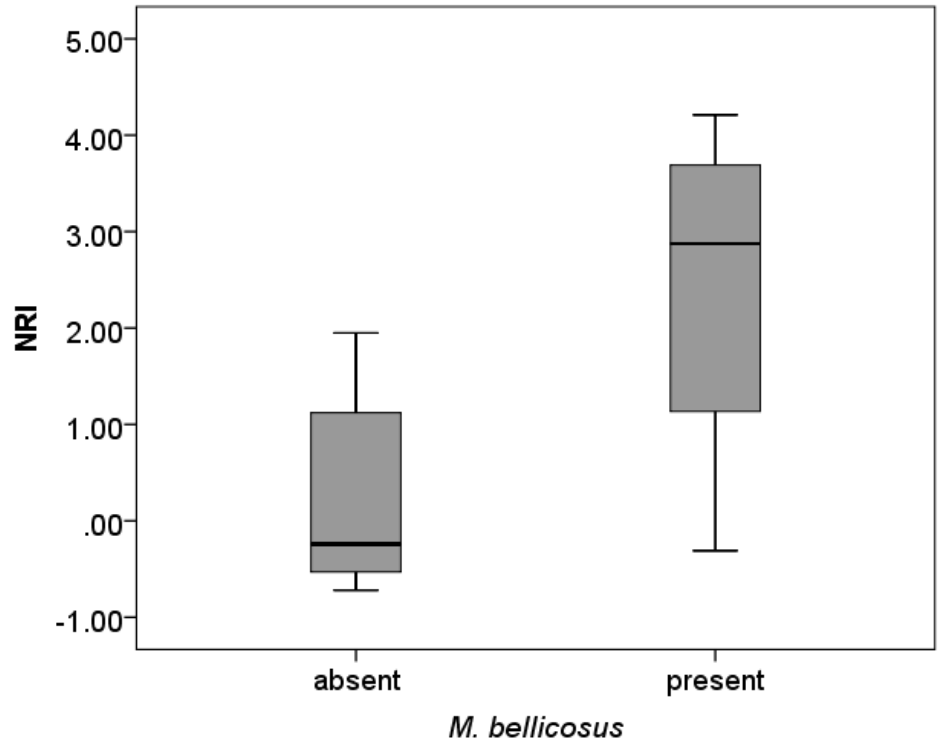

Figure 4. NRI and presence of *M. bellicosus*. There may be an effect of *M. bellicosus* on phylogenetic community structure. NRIs were higher (i.e. more phylogenetically clustered communities) when *M. bellicosus* was present than when it was absent (P=0.079).

Similarity between fallows

The compositional similarity between sites varied, with the Bray-Curtis index ranging from 0.075 to 0.785. Mean species richness per site was 10.1 (± SD 1.75) species and mean number of shared species between sites was 6.1 (± SD 1.64) species. When comparing sites of different vegetation types to each other, the Bray-Curtis index revealed that there is a significant difference in species composition between vegetation types (ANOVA: F = 4.329, P = 0.002, Fig. 5). Fields (f/f) are significantly less similar to each other in species composition than open/medium dense savannahs (o/m) and medium-dense savannah sites (m/m) are to each other (Tukey-HSD *post-hoc* test: o/m: P = 0.022; m/m: P = 0.016), both showing higher species similarity. The other compared vegetation types between these extremes (f/o, f/m, o/o) are variable, but there is a clear pattern that compositional species similarity rises, the less disturbed the sites are.

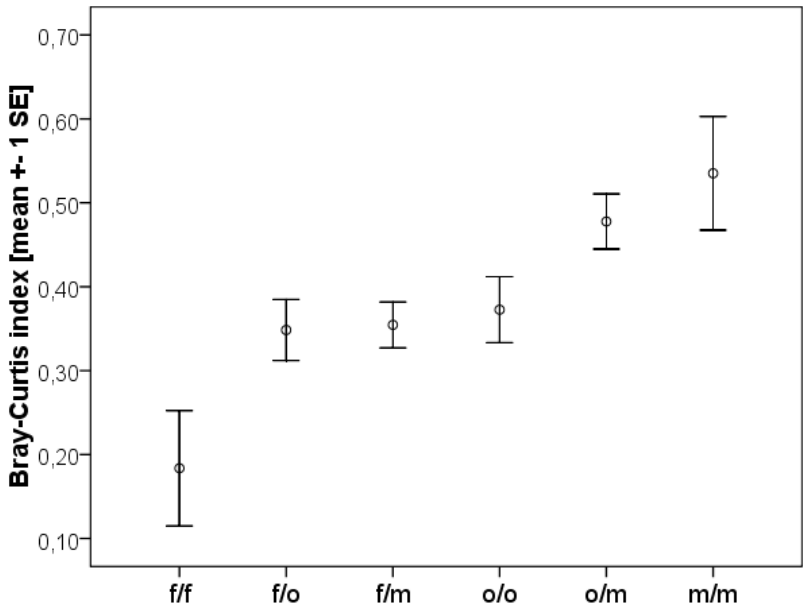

Figure 5. Compositional species similarity between plots of different vegetation type measured with the Bray-Curtis sample similarity index. It revealed a significant difference in species similarity between sites of different vegetation type.

Pest species

We could identify several termite species in our study sites that are known pest species (Wood et al. 1980; Rouland-Lefèvre 2011; Cowie et al. 1989; Collins 1984). These are *M. subhyalinus, Odontotermes* sp., *Microtermes* sp., *Pericapritermes sp., Amitermes evuncifer* and *Ancistrotermes* sp. and they occurred throughout all fallows, but were also present in young fallows where other sampled species did not occur frequently (0-2 years; vegetation type 'field', Table 1). Especially *Microtermes* species, *Amitermes evuncifer* and *Ancistrotermes* sp. were more common in the young fallows compared to the older sites and *Pericapritermes* sp. was only sampled in young fallows. With *Odontotermes* sp. and *Macrotermes subhyalinus* we could not show a specific pattern. These species occurred in young and older fallows alike, but this could be due to the fact that these species were not very common in general and therefore not sampled in high numbers to show a certain pattern.

Table 1 Abundances and encounters of the 19 species of the regional species pool in all study plots including data on fallow age and vegetation type.

	f	sf	fg	L	M	N	O	P	R	S	T	U	W	2	3	5
Trinervitermes occidentalis	Te	N	II_g	15	2	2	1	5	5	3	8	9	0	1	0	0
Trinervitermes geminatus	Te	N	II_g	3	2	4	0	7	6	6	2	13	0	1	0	0
Trinervitermes oeconomus	Te	N	II_g	5	6	2	0	2	0	3	1	3	0	4	1	0
Trinervitermes togoensis	Te	N	II_g	8	2	6	0	6	12	13	0	2	0	1	2	0
Fulleritermes tenebricus	Te	N	II	0	0	0	0	0	0	0	0	1	0	1	0	0
Microtermes subhyalinus	Te	M	II_f	0	2	1	4	2	3	0	0	0	3	5	0	2
Microtermes lepidus	Te	M	II_f	1	0	4	5	1	0	0	6	6	13	2	1	6
***Microtermes* sp.3**	Te	M	II_f	4	10	3	3	4	0	2	1	0	2	5	5	2
***Microtermes* sp.4**	Te	M	II_f	1	0	3	8	0	1	0	1	1	4	2	0	2
Macrotermes bellicosus	Te	M	II_f	0	2	0	2	0	0	0	0	2	0	5	0	18
Macrotermes subhyalinus	Te	M	II_f	0	1	0	0	0	2	0	0	0	0	0	0	3
***Ancistrotermes* sp.1**	Te	M	II_f	0	0	0	25	0	0	0	0	7	19	28	10	16
***Odontotermes* sp.1**	Te	M	II_f	0	0	1	0	0	0	0	9	9	3	0	0	1
***Astalotermes* sp.**	Te	Ap	III	4	2	1	0	0	3	3	0	1	1	0	0	0
***Adaiphrotermes* sp.1**	Te	Ap	III	0	0	2	1	1	0	0	1	4	0	0	1	2
***Microcerotermes* sp.1**	Te	T	II	6	0	11	13	11	17	23	33	15	5	14	15	2
Amitermes evuncifer	Te	T	II	0	0	0	1	0	3	0	5	0	13	0	5	0
***Procubitermes* sp.1**	Te	T	IV	0	0	0	0	0	0	0	1	0	0	1	0	0
***Pericapritermes* sp.**	Te	T	III	0	1	0	0	0	0	0	0	0	0	0	1	0
Number of species				9	10	12	10	9	9	7	11	13	9	13	9	10
Number of encounters				47	30	40	63	39	52	53	68	73	63	70	41	54
Fallow age (years)				8	0	6	2	4	10	12	0	10	2	1	1	10
Vegetation type				1	0	2	1	2	2	1	0	1	0	2	1	1

Shown are encounters and number of species per study plot together with feeding groups (fg). Plots L, M, N, O, P, R, S were sampled in 2012, T, U, W, 2, 3 and 5 were sampled in 2014. f: family; Termitidae (Te), sf: subfamily: Macrotermitinae (M), Nasutitermitinae (N), Termitinae (T), Apicotermitinae (Ap). The classification of feeding groups follows Donovan *et al.* (2001): I: dead wood-feeders; II: wood-litter-feeders (II_g: grass-feeders; II_f: fungus-growers); III: humus-feeders; IV: *true* soil-feeders. The classification of vegetation types are: 0= field, 1= open, 2= medium dense

Discussion

Our results support the hypothesis that strong anthropogenic disturbance selects for a subset of termite species and that these species are common crop pests. In our study region, disturbance is associated with environmental filtering which is obvious even after 10 years of re-generation.

Disturbance and community composition in termites

Our study is mainly in line with the results of the study in Benin (Hausberger and Korb 2016). It confirms that disturbance is associated with environmental filtering in West African savannah regions, as young fallows with a higher degree of disturbance have a different species composition than older fallows. Additionally, we could show that vegetation type had an influence on phylogenetic and compositional species similarity. Fields were characterized by species/genera which are known as crop pests in West-Africa, especially *Amitermes evuncifer, Ancistrotermes* sp., *Microtermes* spp. (Table 1) (Wood et al. 1980; Rouland-Lefèvre 2011; Cowie et al. 1989; Collins 1984). Whether the occurring termite species are pests because they are more resilient against disturbance or whether selection as pests made them more resilient is difficult to test. As some of the sampled pest species also occurred in some older fallows, in particular *Odontotermes* sp. and *Macrotermes subhyalinus*, this suggests that they are generalists that can cope better with human disturbance. By contrast, grass-feeding *Trinervitermes* species (*T. togoensis, T. geminatus, T. oeconomus* and *T. occidentalis*) were mainly found in older fallows (Table 1), implying that they are less resilient against disturbance. As grass is also commonly available in young fallows, it is unlikely that limited food availability can account for their absence. Nevertheless, fields seem to be very heterogeneous among each other concerning species composition, which could be

due to additional factors like the kind of crop that was cultivated or other biotic and abiotic factors, influencing which termite species occur in the respective fields.

Against expectation, species richness did not increase with fallow age. It seems that a higher degree of disturbance in younger fallows creates a certain set of species and that this set of species then changes with decreasing disturbance in older fallows, but species richness itself is not affected by this. This is in contrast to the results from Benin by Hausberger and Korb (2016), where a decline in species richness was detected in village sites of intensive land-use and young fallows with diminished vegetation cover. An explanation for these different results could be that the study region in Benin is geographically more to the north-east in the West Sudanian biome and has a drier climate than the Oti-Kéran National Park in Togo. Furthermore, we did not sample directly within villages with ongoing land-use.

As in Benin (Hausberger and Korb 2015), several closely related fungus-growers were associated with the occurrence of *M. bellicosus* (including *Microtermes* spp., *Ancistrotermes* sp.1 and *Macrotermes subhyalinus*), reflected in phylogenetic clustering (Fig. 4). *Macrotermes* mounds can provide micro-habitats for other fungus-growers as well as facilitating their occurrence by concentrating nutrients and clay through their nest building and foraging activities (Joseph et al. 2013), thereby explaining the increased phylogenetic clustering in sites with *M. bellicosus* mounds.

Comparison with other community studies in West Africa

There are few studies on West African termite communities and besides the above mentioned recent studies in Benin, none used a molecular approach necessary for unambiguous species identification of West African termites. Dosso et al. (2013) studied termite communities near Lamto in the Ivory Coast (West Africa) in land-use systems, ranging from a semi-deciduous forest, over plantations, to a crop field and a 4-year old fallow. As is typical for forests (Eggleton et al. 2002), species richness declined, and especially soil-feeders disappeared, with

disturbance and a transition from forest to a more open habitat. The crop field and the 4-year old fallow, which are most comparable to our study sites, harboured 11 and 7 morpho-species, respectively. Several of these species are typical forest species and hence absent in our study (e.g. *Nasutitermes, Basidentitermes*). Only a single *Microtermes* species was found in Lamto, compared to four in this study and in Benin (Hausberger et al. 2011). One species might be an underestimation as *Microtermes* species are difficult to identify without genetic means. Strikingly, only one *Trinervitermes* species was found in Lamto and this in the 4-year old fallow. This supports our conclusion that the former are susceptible to disturbance. Another study near Lamto tested the influence of annual fires on termite diversity (Dosso et al. 2010). Here, the occurrence of *Trinervitermes* spp. in burnt areas decreased, further supporting the hypothesis that they are less resilient species.

In contrast to our study, some studies implicated evidence for interspecific competition in structuring termite communities (Su and Scheffrahn 1988; Leponce et al. 1996; Korb and Linsenmair 2001a; Bourguignon et al. 2009, 2011; Li et al. 2015; Basu 2011). Reasons for these diverse conclusions include differences between study sites, disturbance regimes, and lack of testing against null hypothesis of random assembly. Additionally, most studies focused on a few species only and did not study whole termite communities, therefore addressing a different scale of analysis. More studies, spanning more regions, are necessary to derive general conclusions. Such studies should cover complete communities of genetically identified species where species co-occurrences are tested against random assemblages. Genetic identification is helpful as otherwise especially the most closely related species may be misidentified, which can lead to blurring signals of environmental filtering or interspecific competition.

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Chapter 2

Differences between termite communities in a West African savannah and forest ecosystem

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submitted to: *PLOS ONE*

Abstract

Termites (Isoptera) are important ecosystem engineers of tropical ecosystems. However, they are notoriously difficult to identify, which hinders ecological research. To overcome these problems, we comparatively studied termite communities in the two major West African ecosystems, savannah and forest, both under natural settings and along disturbance gradients. We identified all species using both morphological as well as genetic markers thus establishing the most comprehensive and reliable species repertoire for this region. Overall we found more species in the forest than in the savannah. However, alpha diversity per site did not differ between both ecosystems with on average around ten species. For both ecosystems, species diversity did not decrease along the studied disturbance gradient but encounter rates did. For the forest, we did not detect a decline in soil feeding termites and an increase of the fungus growers Macrotermitinae with disturbance as some other studies did. Yet, soil-feeders were generally rare. Strikingly, the set of morphologically difficult-to-identify Macrotermitinae (*Microtermes* and *Ancistrotermes*) was as high in the forest as in the savannah with little species overlap between both ecosystems. Using phylogenetic community analyses, we found little evidence for strong community structuring mechanisms such as environmental filtering or interspecific competition. Most local communities did not differ

significantly from random assemblages of the regional species pool. Our study is the most comprehensive of its kind. It provides the most reliable termite species list for West Africa that builds the basis for further ecological studies.

Introduction

Termites are important ecosystem engineers that provide essential ecosystem services in tropical ecosystems. As the main macro-detritivores they influence nutrient flux and food webs and enhance soil fertility, bioturbation and water infiltration rates (reviewed in Bignell & Eggleton, 2000; Evans *et al.*, 2011; Dahlsjö *et al*., 2015). They are prey for animals from insects to mammals. For instance, application of the insecticide fibrinol in Madagascar showed how especially termite feeding mammals, such as the lesser hedgehog tenrec *Echinops telfari*, disappeared after the death of termite colonies (Peveling *et al.*, 2003). Additionally, large termite mounds (termitaria), such as those of fungus growing Macrotermitinae, provide special micro-habitats for animals and plants alike. They are islands of faunal and floral diversity that increase biodiversity in tropical savannah regions and structure whole ecosystems (Pringle *et al.*, 2010; Davies *et al.*, 2014; Joseph *et al.*, 2013).

Termite diversity is strongly affected by anthropogenic disturbance. Species richness drastically declines when forests are cleared (Davies *et al.*, 2003; Dosso *et al.*, 2013) or savannahs are turned into fallows (Hausberger & Korb, 2016). Along comes also a change in species composition and 'function'. In forests, several seminal studies have shown that especially soil feeding termites disappear which thrive on soil, rich in organic material (Davies *et al.*, 2003; Palin *et al.*, 2011). Yet our knowledge is still very fragmentary. Studying termite diversity is becoming ever more important in face of intensification of land-use, especially in West Africa where population pressure is increasing (UNDP, 2010). Knowing how termite communities are structured and which processes influence community structure

in natural, undisturbed habitats builds the basis to understand how termite species communities and the associated ecological processes change with anthropogenic disturbance. Using a standardized approach, we comparatively studied termite communities in savannah and forest ecosystems in West-Africa. For each habitat, we compared protected 'pristine' sites with disturbed sites that had been un-affected by strong anthropogenic disturbance since varying time periods ('recovery gradient'). Using this approach, we aimed at (i) comparing savannah with forest ecosystems, and (ii) studying how termite communities are affected by anthropogenic disturbance in form of intensive land-use to reveal common principles and differences across ecosystems. To do this, we first identified all species occurring in the different communities using morphological and genetic markers. A genetic approach is necessary to unambiguously identify all termite samples. To obtain first insights into the mechanisms that structure these communities, we applied phylogenetic community analyses. They test the composition of our studied communities against communities that are drawn at random from the regional species pool. This approach can provide first hinds on the importance of interspecific competition or habitat / environmental filtering in structuring communities (Emerson & Gillespie, 2008; Bryant *et al.*, 2008).

Materials and Methods

Study sites

As a savannah ecosystem, we investigated termite communities in the relatively natural Oti-Kéran National Park (West Africa; 10°17' to 10°08' N; 0°28' to 0°51' E; Fig. 1) in Togo, and compared these communities with those from a previous study of anthropogenically disturbed habitats (fallows) in the same region (Schyra & Korb, 2017). The Oti-Kéran National Park is situated in northern Togo, representing a typical West African savannah, lying in the center of the West Sudanian biome (mean annual precipitation: 1100 mm and mean annual

temperature: 28°C, range: 17°C to 39°C; Worldclim database). The park was established in 1950 with an original surface area of 163,640 ha. Since then it has undergone several changes due to socio-political conflicts that reached a climax in the 1990s when the local population invaded the protected area and there was widespread destruction of floral and faunal diversity (UNDP, 2010). In 1999, the government reformed the park boundaries, resulting in a drastic reduction of the park's surface to 69,000 ha (UNDP, 2010). Today, fields and villages are distributed along the boundaries of the park, but an encroachment of fields and villages inside the protected area can be noticed (Bouché *et al.*, 2004). Our 'protected' study sites were located in areas which were not obviously affected by such human influences.

Our protected forest sites were located in the south east of Togo, in the Reserve de Faune de Togodo (6°40' to 6°50' N and 1°20'to 1°40' E, Fig. 1). This reserve covers an area of about 25,500 ha and has an equatorial climate, with 1000 to 1300 mm of rainfall per year and mean annual temperatures of 27°C (range: 25°C to 29°C) (Adjonou *et al.*, 2010). Sampling of disturbed sites was carried out around the reserves boundaries in anthropogenically established forests, teak plantations.

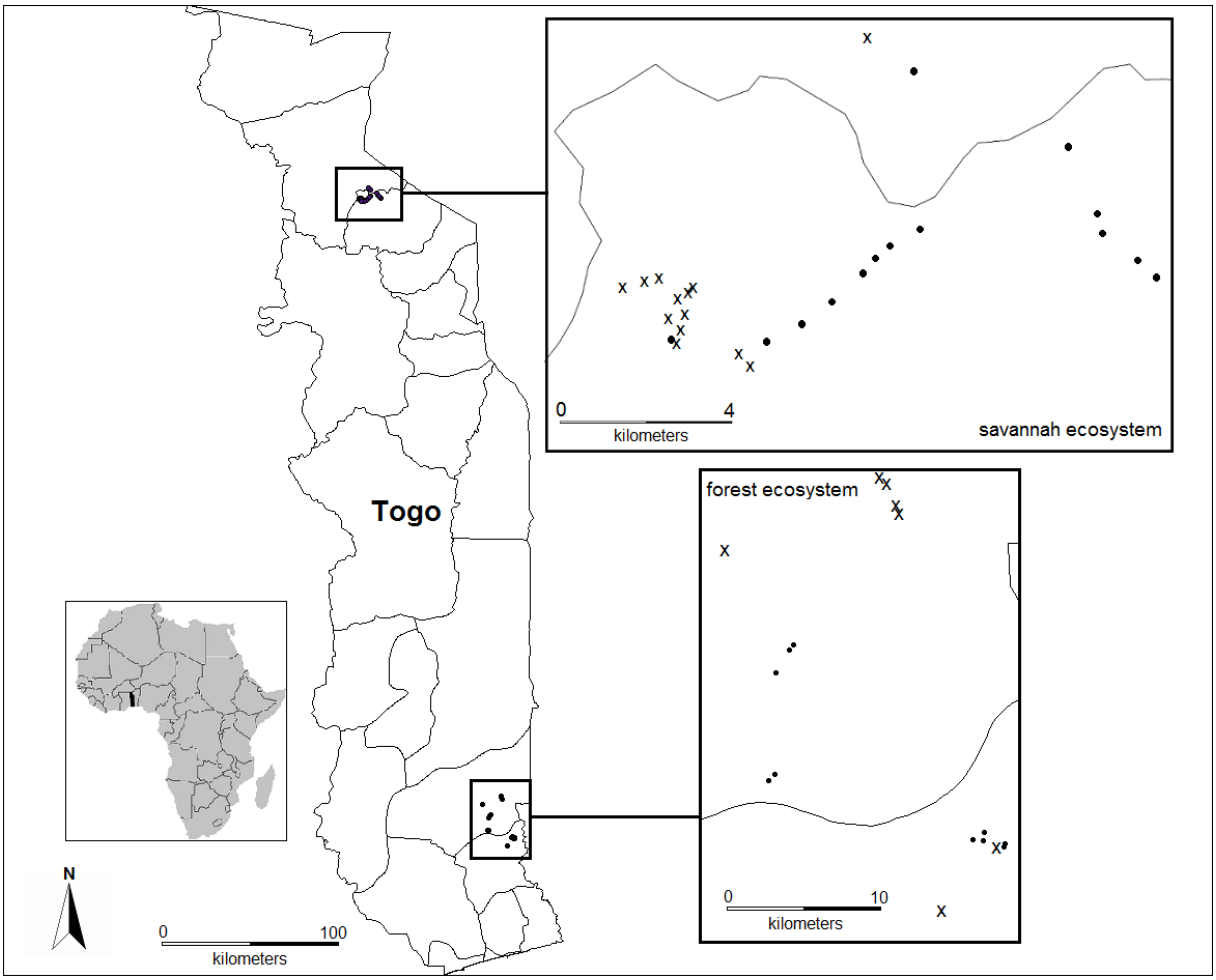

Figure 1. Map of Africa with the location of the two sampling regions savannah and forest in Togo. The savannah in northern Togo with the distribution of the 14 protected sampling sites (Park) and 13 fallows and the forest in the south east of Togo with 10 protected forest sites and seven teak plantation sites. ● = protected sites; **x**= disturbed sites.

Similar to fallows in the savannah, teak plantations can be regarded to reflect anthropogenic disturbance gradients for forests in this region. Disturbance is maximal, when teak plantations are established as the original vegetation is completely removed (corresponding to fields in the savannah region). Disturbance declines with increasing time since start of the plantation (corresponding to fallow age in the savannah). The comparison suffers from the fact that teak plantations are still largely mono-cultures. Yet, teak plantations are the best equivalent present in Togo, as secondary forests of known age are lacking. Additionally, they present a large part of converted land in equatorial West Africa (Kokutse *et*

al., 2004; Adjonou *et al.*, 2010), hence, being of fundamental economic and ecological importance.

Termite sampling

Termites were systematically collected when they were most active. For the savannah, termites were collected during the beginning of the rainy season in 2012 from nine plots in the Oti-Kéran National Park and from seven fallows of age 0, 2, 4, 6, 8, 10 and 12 years in its surroundings. In 2014, we added five new plots for the natural habitat and six plots for the fallows of age 0, 0, 1, 2, 10 and 10 years. The sampling regime was constrained by the availability of fallows with known age.

For the forest, we sampled ten sites in September and in December 2012 in the Reserve de Faune de Togodo. Sampling of disturbed sites was carried out in September/October and December 2012. Similar to the study in the savannah, seven teak plantations of ages 0, 2, 4, 6, 8, 10 and 12 years were sampled.

Sampling was done using a standardized belt transect protocol first developed for sampling termites in forests (Jones & Eggleton, 2000) and then adapted to savannahs (Hausberger *et al.*, 2011). In short, the protocol consists of a thorough search of dead plant material on the ground, on and in trees and mounds as well as soil sampling to assess termite diversity (Jones & Eggleton, 2000). For both regions, plot size was one hectare with three transects arbitrarily located within each plot. Corresponding to the established protocols, in the savannah each transect measured 50 m x 2 m, divided into ten 5 m x 2 m sections, while those for the forest were 100 m x 2 m with twenty 5 m x 2 m sections. Each transect section was searched by a trained person systematically for termites for 15 minutes in the savannah, and 30 minutes in the forest. Additionally, we sampled eight soil scrapes per transect section measuring 15 cm x 15 cm x 10 cm.

All encountered termites were stored in 99% ethanol for subsequent molecular analyses. As in the former studies (Hausberger *et al.*, 2011; Jones & Eggleton, 2000; Korb & Linsenmair, 2001), we chose a plot size of one hectare because the foraging ranges of termite colonies is within 100 m (Korb & Linsenmair, 2001) and hence one hectare represents the local scale where interactions between colonies occur, i.e. it reflects the Darwin-Hutchinson-Zone, which is most relevant to study assembly of local communities (Vamosi *et al.*, 2009).

Identification and phylogenetic analyses

All samples were identified to the species level: First, samples containing soldiers were identified to the genus and species level using the keys by Webb (1961), Sands (1965), Bouillon & Mathot (1965), Harris (1968), Grassé (1937), Pearce *et al.* (1993) and Sands (1992, 1998) and then confirmed by molecular genetic analyses (see below). For samples with workers only, morphological identification was impossible, they were genetically analysed (see below). We followed the anatomical criteria by Donovan *et al.* (2001) to assign the feeding group to each sample. The presence / absence of each species within each plot was recorded as well as the encounter rate (i.e., the number of samples per species and plot), which is used as a surrogate of species abundance (Davies, 2002).

To allow unambiguous species identification, we isolated DNA and sequenced fragments of three genes as described elsewhere (Hausberger *et al.*, 2011) (see also Appendix 2, Table S1): *cytochrome oxidase subunit I* (*COI*; total length 680bp), *cytochrome oxidase subunit II* (*COII*; total length 740 bp), and *12S* (total length 350 bp). These sequences were used to re-construct phylogenetic trees using three approaches (Bayesian method, maximum-parsimony analysis, and maximum-likelihood analysis) to delimitate and identify species (for more details see Appendix 2). As in former termite studies (Legendre *et al.*, 2008; Hausberger *et al.*, 2011), *COII* was most useful for 'barcoding' (i.e., assigning species to samples) because it amplified well and gave appropriate resolution for species identification. All

samples were identified and we used available species names. Species names correspond to those given in Hausberger *et al.* (2011) and Hausberger & Korb (2015, 2016) for Benin. *Amitermes* sp1 from the Benin studies is *Amitermes evuncifer*. To obtain corresponding species identities, we constructed a phylogeny comprising all species occurring in Togo and Benin. Samples forming a species cluster were named identically.

Phylogenetic community structure analyses

We analysed the local community structure with PHYLOCOM 4.2 (Webb *et al.,* 2008). As input tree for the phylogenetic community structure analyses we used the *COII* gene tree, which was pruned prior to analysis so as to have only species of the regional species pool included and only one representative per species in the tree. This representative was the sequence with the highest quality values for each base (maximum value of 61, multiplied by ten) as defined in Chromas 2.4.4 (1998-2016, Technilysium Pty Ltd).

We calculated the net relatedness index (NRI) that measures whether locally co-occurring species are phylogenetically more / less closely related than expected by chance. It uses phylogenetic branch length to measure the distance between each sample to every other terminal sample in the phylogenetic tree, and hence the degree of overall clustering (Webb *et al.,* 2008). The NRI is the difference between the mean phylogenetic distance (MPD) of the tested local community and the MPD of the total community (regional) divided by the standard deviation of the latter. High positive values indicate clustering (high similarity); low negative values overdispersion (low similarity) (Webb *et al.,* 2002). We tested whether our data significantly deviated from 999 random communities derived from null models using the independent swap algorithm on presence / absence data (Gotelli & Entsminger, 2003; Hardy, 2008). The swap algorithm creates swapped versions of the sample / species matrix and constrains row (species) and column (species' presence or absence) totals to match the original matrix. The regional species pool consisted of all species from all studied localities.

As suggested by Webb *et al.* (2008), we used two-tailed significance tests based on the ranks that describe how often the values for the observed community were lower or higher than the random communities. With 999 randomizations, ranks equal or higher than 975 or equal and lower than 25 are significant at $P \leq 0.05$ (Bryant *et al*., 2008).

Similarity between fallows

We quantified the compositional similarity (ß-diversity) between all localities using the Bray-Curtis sample similarity index (Magurran, 1988), which was calculated in EstimateS version 8.2.0 (Colwell, 2013). It ranges from 0 to 1, with low values indicating low similarity and high values the reverse. In analogy to this, we assessed the pairwise phylogenetic similarities between sites using phylo-ß-diversity, which measures how phylogenetic relatedness changes between sites (Graham & Fine, 2008). Here high values indicate high phylogenetic similarity and low values low phylogenetic similarity between communities (Bryant *et al.*, 2008). This PhyloSor index was calculated with the package 'picante' in R (Kembel *et al.*, 2010).

Other statistical analyses

All inferential statistics were done with the statistical package IBM SPSS 16. All tests were two-tailed. Data were tested for assumptions of parametric testing and analyses were done accordingly. For all data, qualitatively the same results (i.e., effects were significant or non-significant) were obtained when testing parametrically or non-parametrically.

Results

Diversity

Savannah. We identified a total of 22 termite species in the savannah, representing the regional species pool, with 20 species in the protected national park (three species unique to

this habitat) and 19 species in the sampled fallows (two species unique for this habitat) (Table 1, Fig. 2a). The park sites and fallows shared 17 species of the regional species pool. All species belonged to the higher termites (Termitidae). As is typical for African savannahs, the fungus-growing Macrotermitinae dominated under both habitat regimes with nine species in the Park and eight species in the fallows. We found two Apicotermitinae each in the Park and fallows, five Termitinae in the Park and four in the fallows, and four Nasutitermitinae in the Park and five in the fallows (Table 1). Species richness did not increase with fallow age (Spearman-rank correlation: N = 13, P = 0.324).

Forest. In the forest, we identified a total of 33 termite species (Fig. 2b). Thus, the regional species pool was more diverse in the sampled forest sites and teak plantations than in the savannah, although overall species richness per site was not significantly different (Mann-Whitney-U test, Z = -0.012, N = 44, P = 0.990). 29 species were sampled in the natural forests, with 10 species being unique for this protected area, and 23 species in the teak plantations, of which 4 species were unique for this habitat (Table 1). The protected sites and the teak plantations shared 19 termite species and most species belonged to the higher termites, with 10 Macrotermitinae in the forest and eight in the teak plantations, eight Termitinae in the forest and teak plantations each, three Apicotermitinae each in both habitats, and six Nasutitermitinae in the forest and only two in the teak plantations. Additionally, two representatives of the lower termites were sampled in the forest habitat which did not occur in the savannah: one species of the Rhinotermitinae and one species of the Coptotermitinae. Similar to the results in the savannah, species richness did not increase with increasing plantation age (Spearman-rank correlation: N = 7, P = 0.534). As is typical for forests, more soil feeders (feeding group IV) were sampled here compared to the savannah (Table 1).

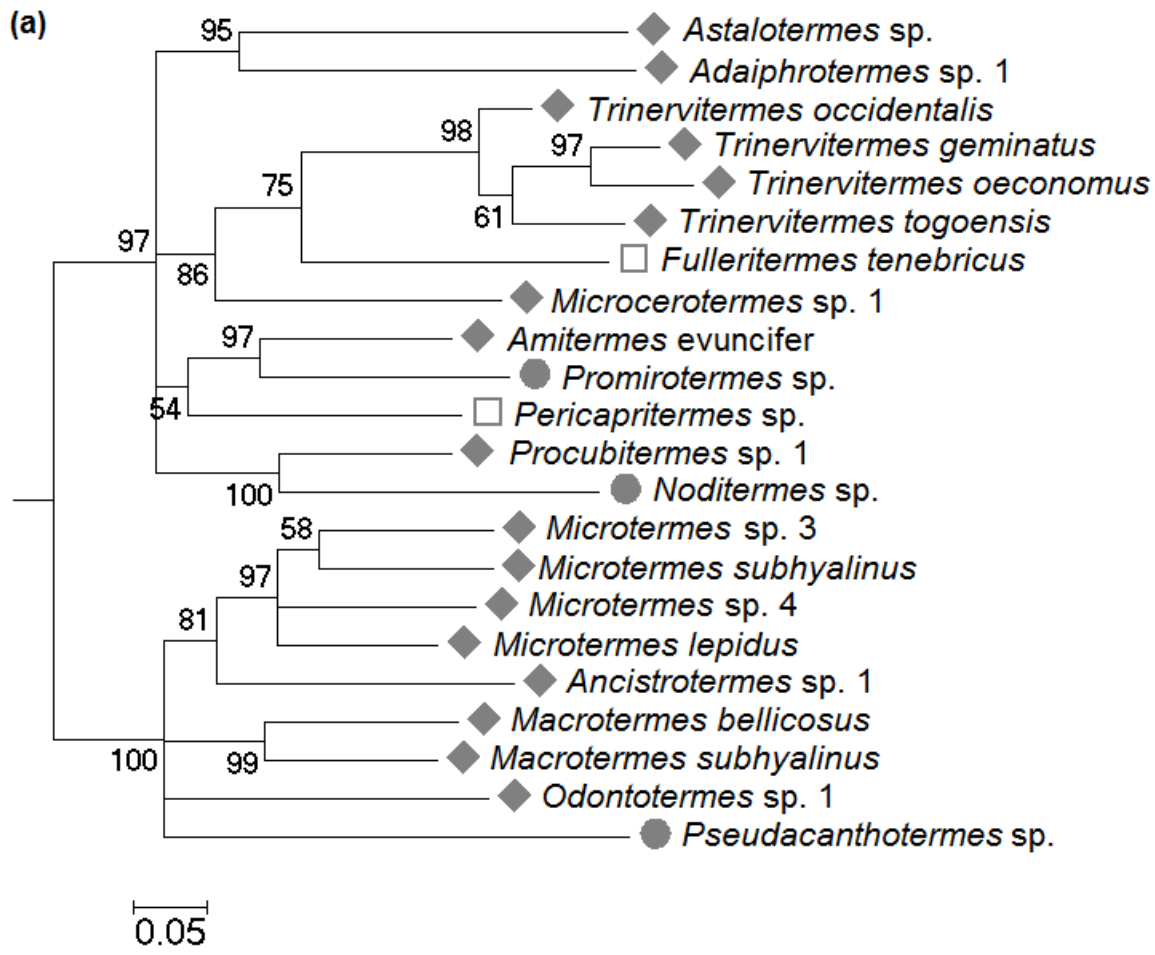

Figure 2a. Input Bayesian phylogenies of the savannah ecosystems for the program Phylocom based on the gene *cytochrome oxidase II*. Analysis was done with 10^7 generations, number of chains=4, sample frequency=1000 and a finalizing burn-in of 2500. Occurrence of species: ♦ = in both regimes; ● = protected only; □ = disturbed only.

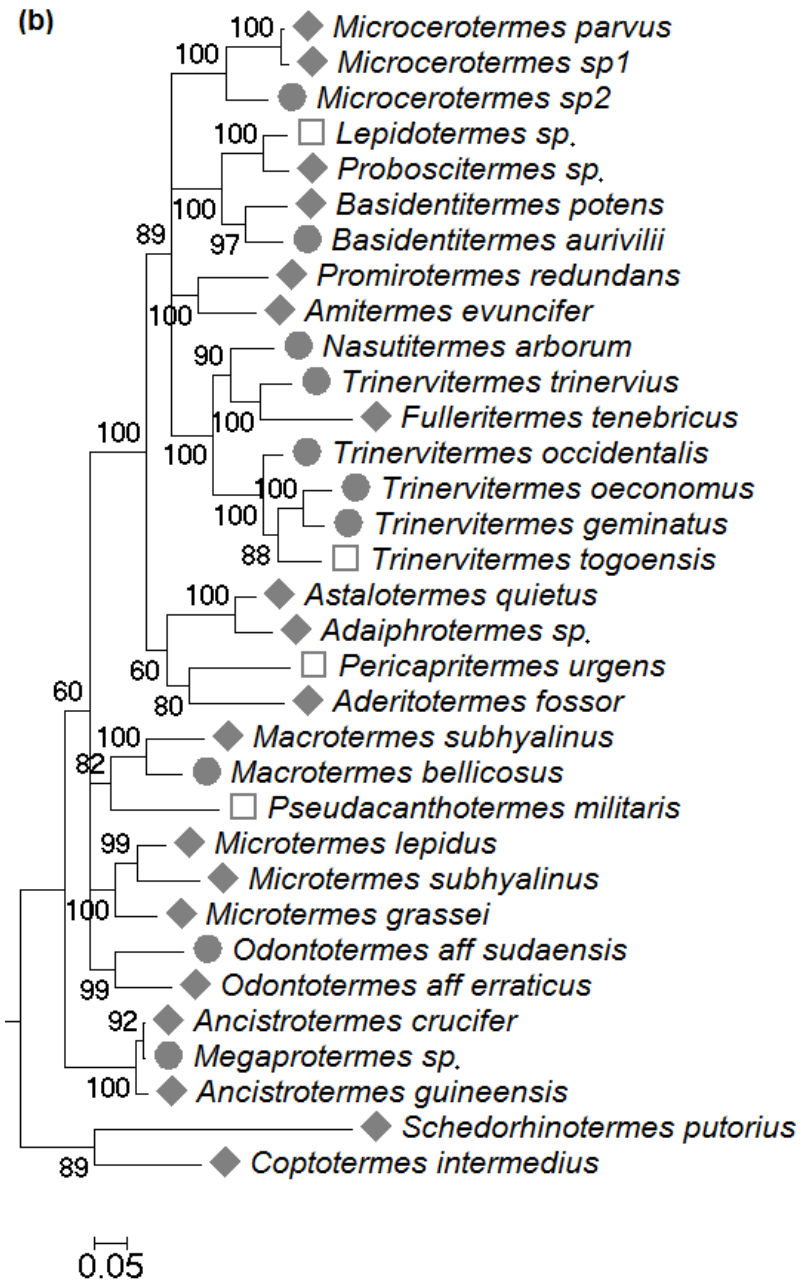

Figure 2b. Input Bayesian phylogenies of the (b) tropical forest ecosystems for the program Phylocom based on the gene *cytochrome oxidase II*. Analysis was done with 10^7 generations, number of chains=4, sample frequency=1000 and a finalizing burn-in of 2500. Occurrence of species: ♦ = in both regimes; ● = protected only; □ = disturbed only.

Table 1 Comparison of the regional species pools for the savannah and tropical forest with presence/absence and total species richness.

		savannah		tropical forest	
	fg	**Park**	**fallows**	**Forest**	**Teak pl.**
RHINOTERMITIDAE					
Rhinotermitinae					
Schedorhinotermes putorius	I	-	-	X	X
Coptotermitinae					
Coptotermes intermedius	I	-	-	X	X
TERMITIDAE					
Nasutitermitinae					
Trinervitermes trinervius	II_g	-	-	X	-
Trinervitermes occidentalis	II_g	X	X	X	-
Trinervitermes geminatus	II_g	X	X	X	-
Trinervitermes oeconomus	II_g	X	X	X	-
Trinervitermes togoensis	II_g	X	X	-	X
Fulleritermes tenebricus	II	-	X	X	X
Nasutitermes arborum	II	-	-	X	-
Macrotermitinae					
Microtermes subhyalinus	II_f	X	X	X	X
Microtermes lepidus	II_f	X	X	X	X
Microtermes grassei	II_f	-	-	X	X
Microtermes sp.3	II_f	X	X	-	-
Microtermes sp.4	II_f	X	X	-	-
Ancistrotermes crucifer	II_f	-	-	X	X
Ancistrotermes guineensis	II_f	-	-	X	X
Ancistrotermes sp.1	II_f	X	X	-	-
Macrotermes bellicosus	II_f	X	X	X	-
Macrotermes subhyalinus	II_f	X	X	X	X
Odontotermes aff. erraticus	II_f	-	-	X	X
Odontotermes aff. sudaensis	II_f	-	-	X	-
Odontotermes sp.1	II_f	X	X	-	-
Pseudacanthotermes militaris	II_f	-	-	-	X
Pseudacanthotermes sp.	II_f	X	-	-	-
Magaprotermes sp.	II_f	-	-	X	-
Apicotermitinae					
Astalotermes quietus	III	-	-	X	X
Astalotermes sp.	III	X	X	-	-
Adaiphrotermes sp.	III	X	X	X	X

Aderitotermes fossor	III	-	-	X	X
Termitinae					
Microcerotermes sp.1	II	X	X	X	X
Microcerotermes sp.2	II	-	-	X	-
Microcerotermes parvus	II	-	-	X	X
Basidentitermes potens	IV	-	-	X	X
Basidentitermes aurivilli	IV	-	-	X	-
Promirotermes redundans	III	-	-	X	X
Promirotermes sp.	II	X	-	-	-
Proboscitermes sp.	IV	-	-	X	X
Amitermes evuncifer	II	X	X	X	X
Pericapritermes urgens	III	-	-	-	X
Pericapritermes sp.	III	-	X	-	-
Lepidotermes sp.	IV	-	-	-	X
Noditermes sp.	IV	X	-	-	-
Procubitermes sp.1	III	X	X	-	-
total species		**20**	**19**	**29**	**23**

Shown are presence/absence and total numbers of species including feeding groups (fg) for the two ecosystems savannah and tropical forest with its classification into protected and disturbed habitats. The classification of feeding groups follows Donovan *et al.* (2001): I: dead wood-feeders; II: wood-litter feeders (II_g: grass feeders; II_f: fungus growers); III: humus feeders; IV: *true* soil feeders.

Local phylogenetic community structure

Savannah. The NRI values, measuring if locally co-occurring termite species are phylogenetically more or less closely related than expected by chance, ranged from -1.05 to 3.28 in the Park and from -0.72 to 4.21 in the fallows. Only a few plots in the Park and fallows showed significant phylogenetic clustering or overdispersion. In the Park, two plots were significantly clustered (Plot I: NRI = 4.46; Plot 1: NRI = 1.99, $P < 0.05$) and one plot had a significant signal of overdispersion (Plot D: -1.38, $P < 0.05$). In the fallows three plots showed significant signals of clustering (Plot S: NRI = 2.83; Plot W: NRI = 2.80; Plot 5: NRI = 4.41, $P < 0.05$).

NRI values and species richness did not significantly differ between habitat regimes (Mann-Whitney-U test, NRI: Z = -0.09, N = 27, P = 0.923; species richness: Z = -0.71, N =

27, P = 0.473) (Fig. 3a, b). The number of total encounters of termites seemed slightly (though not significantly) lower in the fallows than in the Park (Mann-Whitney-U test, Z = -1.52, N= 27, P = 0.126, Fig. 3c).

Forest. NRI values ranged from -1.52 to 1.3 in the forest and from -2.01 to 0.62 in the teak plantations. NRI values were higher in the savannah than in the forest, but not significantly (Mann-Whitney-U test: Z = -1.53, N = 44, P = 0.126). Similar to the savannah, forest and teak plantations showed little or no phylogenetic structuring. In the natural forests three out of ten communities were significantly structured, with one plot significantly clustered (Plot B: NRI = 1.31, P < 0.05) and two communities significantly overdispersed (Plot E: NRI = -1.50; Plot L: NRI = -1.52, P < 0.05), whereas the teak plantations showed no phylogenetic structuring. Here NRI values did not deviate from random assemblages.

NRI values did not significantly differ between forest and teak plantation sites (Mann-Whitney-U test, Z = -0.87, N = 17, P = 0.417; Fig. 3d), but species richness was significantly different between both habitat regimes with more species in the forest than teak plantations (Mann-Whitney-U test, Z = -2.31, N = 17, P = 0.019; Fig. 3e). Also the number of total encounters was significantly higher in the forest sites than in the teak plantations (Mann-Whitney-U test, Z = -3.12, N = 17, P = 0.001; Fig. 3f). Furthermore, there was a highly significant difference between the encounter rates of termites in the tropical forest and savannah sites, with many more termites encountered in the forest compared to the savannah (Mann-Whitney-U test, Z = -5.53, N = 44, P < 0.001).

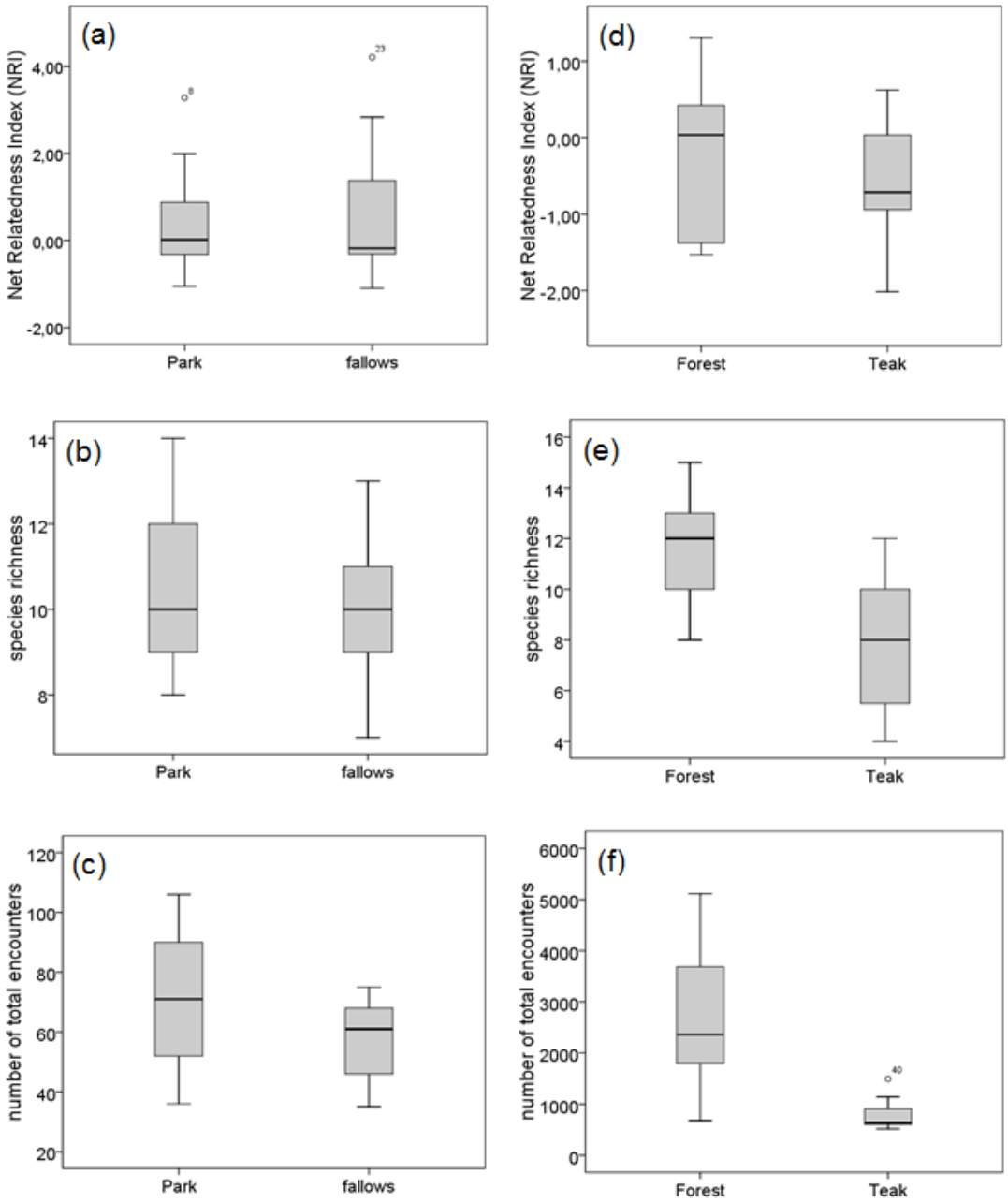

Figure 3. Comparison of (a) Net Relatedness Index (NRI), (b) species richness and (c) number of total encounters between Park and fallows in comparison with (d) Net Relatedness Index (NRI), (e) species richness and (f) number of total encounters between Forest and teak plantations.

Similarity within and between habitat regimes

Savannah. The compositional similarity varied between sites. The Bray-Curtis similarity index ranged from 0.029 to 0.772 for the protected Park and 0.108 to 0.785 for the fallows. The phylogenetic similarity between sites, measured with PhyloSor, varied from 0.145 to

0.981 in the Park and 0.145 to 0.951 in the fallows (Appendix 2, Table S2). Mean species richness per site was 10.6 (+- SD 1.93) in the Park and 10.1 (+- SD 1.75) in the fallows and mean number of shared species between sites was 6.8 (+- SD 1.62) in the Park and 5.2 (± SD 1.56) in the fallows. The number of shared species differed significantly when comparing sites within and between habitat regimes (ANOVA: $F = 21.03$, $P < 0.001$, Fig. 4a). The number of shared species was higher among Park sites than in the fallows, with intermediate values when comparing Park with fallow sites. Similarly, the Bray-Curtis index and the PhyloSor index showed significant differences in compositional and phylogenetic similarity within and between habitat regimes (Bray-Curtis: ANOVA: $F = 3.12$, $P = 0.045$; PhyloSor: ANOVA: $F = 7.31$, $P = 0.001$; Fig. 4b, c). Park sites seemed to consist of more similar species, compositionally and phylogenetically, compared to the fallows, where species - and phylogenetic composition was less similar between sites.

Forest. The compositional similarity between sites varied in the forest as well. In the protected forest the Bray-Curtis similarity index ranged from 0.086 to 0.781 and in the teak plantations from 0.111 to 0.687 (Appendix 2, Table S3). The PhyloSor index ranged from 0.303 to 0.899 in the forest and from 0.468 to 0.857 in the teak plantations. Mean species richness per site was 11.6 (+- SD 2.27) in the forest and 7.8 (+- SD 2.96) in the teak plantations. Mean number of shared species between sites was 6.8 (+- SD 1.38) in the forest and 3.4 (± SD 1.02) in the teak plantations. Therefore, the number of shared species differed significantly between protected forest sites and teak plantations (ANOVA: $F = 65.84$, $P < 0.001$; Fig. 4d). Teak plantation sites shared significantly fewer species than the forest sites and also the number of shared species across plantation and forest sites was low. Compositional similarity, measured with the Bray-Curtis index, also significantly differed between the two habitat regimes, with the forest sites having a significantly higher compositional similarity than the teak plantations (ANOVA: $F = 36.06$, $P < 0.001$; Fig. 4e). These results are in accordance with the results for the savannah, where disturbed sites shared

fewer species and had a significantly lower compositional termite species similarity as well. Only the phylogenetic similarity of forest and teak plantations, measured with the PhyloSor index, did not differ significantly (ANOVA: F = 1.76, P = 0.176; Fig.4f), which was different in the savannah.

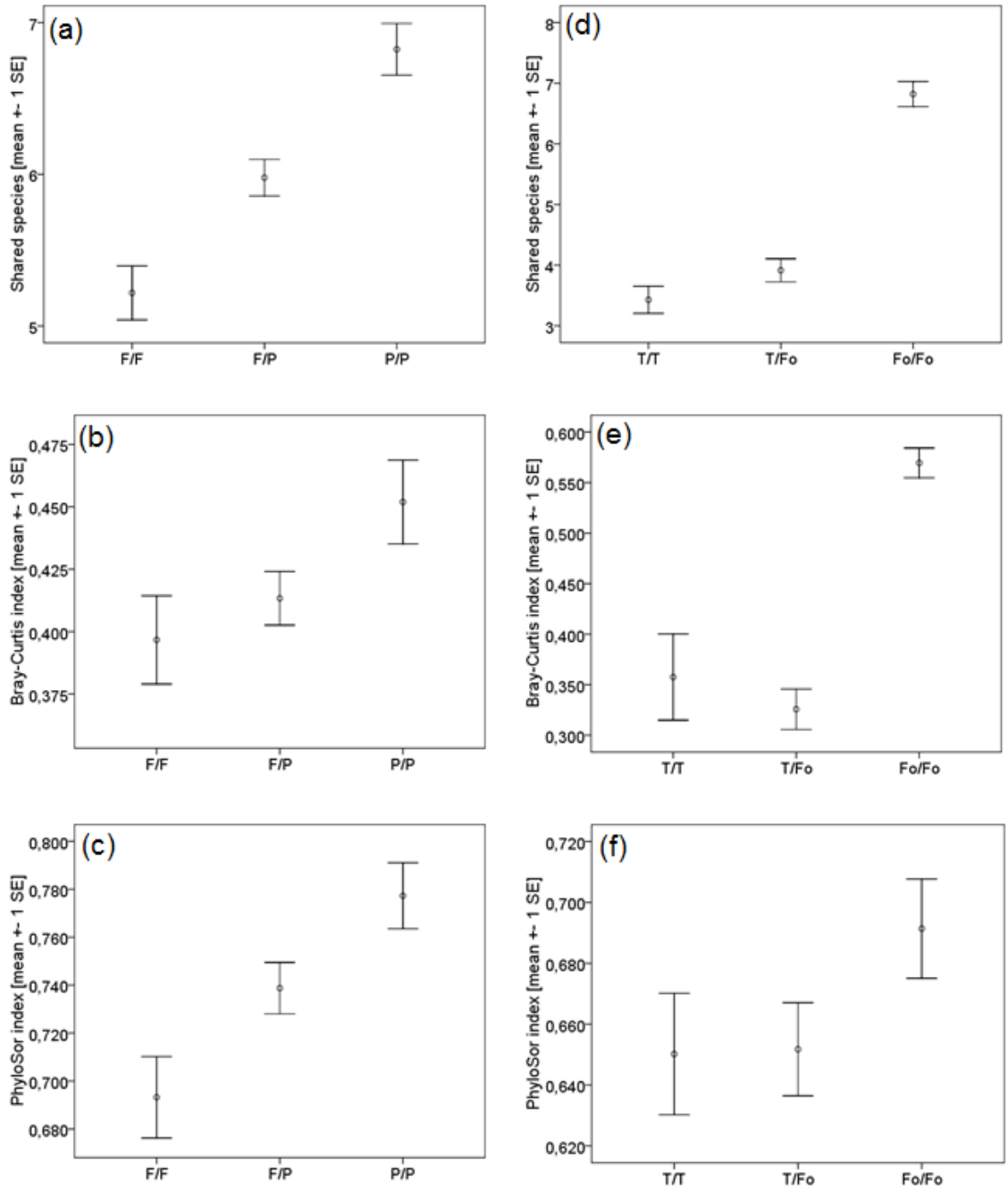

Figure 4. Similarity among sites within and between habitat regimes in the savannah (a-c) and forest (d-f) ecosystem. (a) and (d) show the number of shared species, (b,e) compositional similarity measured with the Bray-Curtis index and (c,f) phylogenetic similarity measured with the PhyloSor index. F = fallows, P = Park; T = Teak plantation, Fo = Forest.

Discussion

This is the first study that comparatively investigated forest and savannah ecosystems using the same means. We found striking similarities and differences between the forest and savannah ecosystems when analyzing protected and disturbed sites. First, in neither ecosystem did species richness or NRI change with time since disturbance. Second, in both ecosystems, NRI did not differ between disturbed and protected sites and there were few signs of phylogenetic structuring. However, species richness did decline in the forests while this was not the case for the savannah. Third, as expected, we found in total more species in the forest than the savannah and also the termite encounter rates were higher in the former. Finally, while the similarity in termite composition between protected and disturbed sites was intermediate between fallow and protected savannahs sites, it was low between protected forests and teak plantations (Fig. 4). In both ecosystems, species similarity between disturbed sites was low, while it was high between protected sites.

Savannah: Phylogenetic and compositional community structure

Our study revealed that the communities of the two studied savannah regimes differed significantly in their compositional (measured by shared species and with the Bray-Curtis index) and phylogenetic similarity (measured with the Phylosor index) (Fig. 4a-c). Communities in the Park are more similar to each other compositionally and phylogenetically than the ones in the fallows with intermediate similarities between both regimes (Fig. 4a-c). Park communities seem to have very similar species compositions in each sampled site, specific for this ecosystem. As one can assume communities in a National Park to be less disturbed, they have a long ‘assembly history’, with more or less stable abiotic and biotic factors. Disturbed communities seem to experience a higher turnover of species, resulting in an apparently less similar species composition. Despite the fact that NRI values did not

change with fallow age, our previous study showed that species composition actually differed depending on the respective age of the fallow (Schyra & Korb, 2017). Younger fallows had other species (*Amitermes evuncifer*, *Pericapritermes* sp., *Ancistrotermes* sp., *Microtermes* sp.) than older fallows, and these older fallows species were still different (*Pseudacanthotermes* sp., *Fulleritermes tenebricus*) to those occurring in the Park, although the oldest fallows had an age of 12 years. Therefore, comparing species composition of the different aged fallows can explain these intermediate similarities between Park and fallow sites.

Comparison to similar studies

Our results partially correspond with a similar study in West Africa, looking at termite community assembly in Benin (Hausberger & Korb, 2016). Here the impact of anthropogenic disturbance on termite communities in areas of intensive land-use was studied in comparison to communities in a National Park. As in our study, protected sites were similar to each other but differed in similarity to those from disturbed village sites. In contrast to our study in Togo, however, the disturbed sites in Benin were similar to each other and had very few termite species. This difference is in line with the much stronger degree of disturbance in Benin where disturbed study sites were next to villages and included active agricultural fields, compared to the fallows in our current study that lack on-going disturbance. In both studies, termite encounter rates were lower under disturbed than protected regimes. This also applied to our forest results and suggests that there is a general pattern: first species abundance declines with disturbance, and later with more intensive disturbance, species numbers dwindle.

The decline of termite species richness with disturbance has been found in several studies across all continents (e.g. Ivory Coast: Coulibaly *et al.*, 2016; Borneo: Luke *et al.*, 2014; Vietnam: Neoh *et al.*, 2015; Panama: Basset *et al.*, 2017) supporting the hypothesis that

it is a global pattern. Generally, the effect is more prominent in tropical forest regions than in savannahs.

Forests: Phylogenetic and compositional community structure

Similar to the savannah, compositional and phylogenetic similarity in the forests were high among protected forest sites, but low between disturbed teak sites (Fig. 4d-f), probably for the same reasons as in the savannah that no or low disturbance in the protected sites lead to similar stable conditions and similar communities. In contrast to the savannah, however, the similarity between protected forest and teak plantations is low, while it was intermediate in the savannah. This is due to some changes in species composition. In the teak plantations mainly Nasutitermitinae disappeared; three out of four *Trinervitermes* species were missing which are mainly grass-feeders (Dosso *et al.*, 2012). Grass is completely absent in the teak mono-cultures, which are characterized by an open and plant-poor understory with the ground mainly covered by dead teak leaves.

Comparison to similar studies

In other forest studies there was a notable decline of soil-feeders with the transformation of forests into plantations and an increase in fungus-growing Macrotermitinae (Eggleton *et al.*, 2002; Jones *et al.*, 2003). This was not the case in our study (Table 1). Two Macrotermitinae (*M. bellicosus* and one *Odontotermes* species) disappeared in the plantations but one fungus-grower, *Pseudacanthotermes militaris*, was only found in the plantations. In general, there were few true soil- (feeding group IV; four species) and humus-feeders (feeding group III; five species) in our study. Three true soil-feeders occurred in both forest types, while the plantations had all five humus-feeders but one was missing from the protected forest.

These differences in the effect of disturbance on termite community composition compared to other forest studies might be due to regional differences. Our species richness was rather low

compared to tropical forests in central Africa or America, which have many more soil- and humus-feeders, especially Apicotermitinae. The fact that teak plantations are still forests, and not open areas like fallows or cultivated fields, may explain why we did not see an increase in Macrotermitinae with disturbance.

Comparing forests and savannahs

Comparing forests and savannahs, both ecosystems differed in the number of soil-feeders with *Basidentitermes*, *Proboscitermes* and *Lepidotermes* only occurring in the former. The single soil-feeder found in the savannah was a *Noditermes* sp.. Correspondingly, the higher species richness in the forest was mainly due to more Termitinae. In addition, two lower termites occurred in the forest while the savannah had only higher termites (Table 1). The number of humus-feeding termites, fungus-growing termites and grass-feeders were similar in both ecosystems, yet species overlap was small for the first two. *Procubitermes* sp. and *Astalotermes* sp. were savannah-specific while we found *Aderitotermes fossor*, *Promirotermes redundans* and *Astalotermes quietus* only in the forest. For fungus-growers, except for *Macrotermes*, the complete species repertoire differed between both ecosystems. Strikingly, a completely different set of *Ancistrotermes* and partly also *Microtermes* species were identified for the savannah and the forest, with only a few of the described species occurring in the savannah (Table 1). As species from these genera are extremely difficult to distinguish morphologically, savannah species might have been misclassified in other studies.

Overall, we found three species that occurred in all four studied habitats: *Adaiphrotermes* sp., *Microcerotermes* sp.1 and *Amitermes evuncifer*. All three species have been associated with disturbance (Schyra & Korb, 2017) and are important pests. *A. evuncifer* causes considerable damage in teak plantations (Gbenyedji *et al*., 2016). This widespread occurrence implies that they are generalists with low habitat requirements.

Comparing NRI values, we found less evidence for phylogenetic structuring of termite communities. Niche traits like feeding type are phylogenetically conserved in termites (Schyra & Korb, 2017), so that phylogenetic overdispersion would indicate to interspecific competition and phylogenetic clustering to environmental filtering. The community of some plots differed from random assemblages but not consistently across ecosystems or disturbance regimes. Also, we did not find evidence that the structuring mechanisms change with the time since last disturbance.

To summarize, our study reliably identified a total of 45 termite species, covering the two major West African ecosystems, savannah and forest, including natural as well as disturbed sites. Thus, this study can serve as the basis for upcoming ecological research, which relies on proper and exact species identification. Although we found in total more species in the forests than in the savannah, the local species richness was with a mean of around 10 species not different. The species repertoire, especially of fungus-growers, differed greatly between both ecosystems but we also identified three generalist species. We have no evidence that community structuring mechanisms differ systematically from random assemblages but disturbance rather generally seems to lead first to a decline in termite abundance and then in species richness**.** Given the importance that termites play as ecosystem engineers, this implies declining ecosystem services with increasing disturbance.

Acknowledgements

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Chapter 3

Cryptic niche differentiation in West African savannah termites as indicated by stable isotopes

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submitted to: *Ecological Entomology*

Abstract

According to the classical niche concept, several species cannot co-exist if they occupy the same niche. Termites (Isoptera) of African savannahs have been described to have very similar niche requirements. However, still up to 15 species can locally co-exist that are classified into the same feeding group as wood-litter-feeders. Especially striking is the co-occurrence of up to eight Macrotermitinae and five *Trinervitermes* species, which each have apparently identical food niches being fungus-growers and grass-feeders, respectively. We tested whether there is fine-scaled niche differentiation along the food axis, using $\delta^{15}N$ and $\delta^{13}C$ isotope analyses. Despite a phylogenetic signal that species from the same subfamily and congenerics have correlated isotope signatures, we found evidence for niche differentiation. Strikingly, species which were very similar with regard to $\delta^{15}N$ values generally differed for $\delta^{13}C$ values, and vice versa. The dominant mound building fungus-grower *Macrotermes bellicosus* had the lowest $\delta^{15}N$ values among all fungus-growers indicating that it occupies a different food niche. This fine-scaled differentiation along the food niche axis can contribute to explain why so many apparently identical termite species co-exist.

Introduction

Termites are ecologically significant insects in the tropics with up to 150 species at some sites and biomasses exceeding those of mammals in African savannahs (Davies et al. 2003a). They are important decomposers of organic matter and mediators of soil properties and humification processes (Abe 1979; Eggleton et al. 1994, 1996; Holt & Lepage 2000). Studies have confirmed the importance of termites as decomposers of dead-plant material in savannah systems (Wood & Sands, 1978; Eggleton et al. 1996).

Termites consume a wide range of plant material at different stages of decomposition, from living plants to highly degraded material in the soil, which has been titled a 'humification gradient' (Donovan et al. 2001; Bignell & Eggleton 1995). Accordingly, termite species have been classified into 'feeding groups' or 'functional taxonomic groups' based on their foraging habitat, feeding habits and gut content analysis (Eggleton & Tayasu, 2001; Donovan et al. 2001; Davies et al. 2003a; Bignell & Eggleton 2000). For instance, Donovan et al. (2001) proposed four feeding groups according to their preferred food source along the humification gradient as determined by gut content analysis: dead wood-feeders (group I), dead wood, micro-epiphytes, leaf litter and grass-feeders (group II), humus-feeders (group III) and true soil-feeders ingesting apparently mineral soil (group IV).

African savannah ecosystems harbour many termite species from several termite families, yet most belong to the Termitidae (higher termites) (Hausberger et al. 2011). Certain genera are more diverse here than on other continents while others are rare or lacking entirely. Almost all species are wood-litter feeders (group II), including fungus-growing Macrotermitinae and the specialist grass-feeders *Trinervitermes*. Macrotermitinae often make up more than 50 % of the species richness (Hausberger & Korb 2015, 2016). They are responsible for 95% of the litter removed by termites, which on average is 23% of the annual litter production in savannahs (Collins 1981). This shows the dominance and importance of

fungus-growing termites for African savannah ecosystems. Such ecological studies implicated that all Macrotermitinae consume the same food (Korb & Linsenmair, 2001) and occupy very similar niches (Hausberger & Korb 2015, 2016). Nevertheless, up to eight species can co-exist locally and there is no evidence of interspecific competition shaping these communities (Hausberger & Korb 2015, 2016). This opens the question whether finer scaled food niche differentiation exists.

Stable isotope analysis is a powerful tool to investigate arthropod food webs and ecosystem processes (Hood-Nowotny & Knols 2007). In natural abundance studies the innate differences in stable isotope signatures can be used among others to trace food-web structure, migration patterns and feeding preferences (reviewed in Hood-Nowotny & Knols 2007; Hobson & Clark 1992; Wassenaar & Hobson 1998; Wolf et al., 2009; Martinez del Rio et al. 2009). Stable carbon isotope ratios and stable nitrogen isotope ratios (hereafter expressed as $\delta^{13}C$ and $\delta^{15}N$) are widely used in ecological studies. Stable isotope analyses have advantages over traditional techniques such as gut content analysis and observation, as these allow for long-term studies which are less time consuming (Hood-Nowotny & Knols 2007). Further, stable isotope analysis of organisms provides information on trophic relationships and reflects what an individual organism has assimilated. Observations have shown that during food assimilation and excretion, there are trophic shifts in enrichment (Hood-Nowotny & Knols 2007). McCutchan et al. (2003) estimated the trophic shift for N and C as follows: consumers are enriched by 2.3 ± 0.18 ‰ $\Delta\delta^{15}N$ (mean ±SE) and 0.5 ± 0.13 ‰ $\Delta\delta^{13}C$ (mean ± SE), where Δ denotes the change in isotope ratio between diet and consumer (Vanderklift & Ponsard, 2003).

Stable isotope studies in termites have shown that analysis of $\delta^{15}N$ is suitable to reveal the trophic position of termites, as $\delta^{15}N$ increases along a trophic gradient from wood over soil-wood-interface to soil-feeders (Tayasu et al. 1997; Bourguignon et al. 2009, 2011b). $\delta^{13}C$ has less discriminatory value than nitrogen, but can distinguish between C3 (largely woody

forms) and C4 (mostly tropical grasses) plants (Boutton et al. 1983; Lepage et al. 1993), characterizing dietary preferences of termites and separating grass- from wood- and also soil-feeders (Tayasu et al. 1997, 1998, 2002; Bourguignon et al. 2009). Therefore, $\delta^{15}N$ and $\delta^{13}C$ ratios are powerful indicators of the functional position of termites in the humification process and reflect food preferences and differences among feeding groups and species (Tayasu et al. 1997, 1998; Bourguignon et al. 2009).

We examined stable isotope signatures of West African savannah termites to test the feeding group concept of Donovan et al (2001) and others (Eggleton & Tayasu, 2001; Davies et al. 2003a) for savannah termite species. In the past, this has mainly been examined for forest termites; there are only few studies investigating trophic niches of savannah termites using natural variations in stable isotope ratios (Boutton et al. 1983; Lepage et al. 1993). Additionally, we tested the hypothesis that there is fine-scaled food niche differentiation among savannah termites, especially within fungus-growing Macrotermitinae as well as among grass-feeding *Trinervitermes* species.

Materials and Methods

Study site

Termites were systematically collected when they were most active during the beginning of the rainy season in June 2012 and again in June 2014 in the Oti-Kéran National Park in northern Togo (West Africa; 10°17’ to 10°08’ N; 0°28’ to 0°51’ E). This region is a typical West African savannah lying in the centre of the West Sudanian biome (mean annual precipitation: 1100 mm, mean annual temperature: 28°C, range: 17°C to 39°C; Worldclim database).

Termite sampling

Sampling was done using a standardized belt transect protocol first developed for sampling termites in forests (Jones and Eggleton 2000) and then adapted to savannahs (Hausberger *et al.* 2011). In short, the sampling consists of a thorough search of dead plant material on the ground, on and in trees and mounds as well as soil sampling to assess termite diversity (Jones and Eggleton 2000). Plot size was one hectare with three transects each measuring 50 x 2 m, divided into ten 5 x 2 m sections, arbitrarily located within each plot. Each transect section was searched systematically for termites for 15 min by a trained person. Additionally, we sampled eight soil scrapes per transect section measuring 15 x 15 x 10 cm. Samples were stored in 99% alcohol for species identification and subsequent analysis. All samples were identified to the species level: First, samples containing soldiers were identified to the genus and species level using the keys by Webb (1961) and Sands (1965) and then confirmed by molecular genetic analyses (for further details see Appendix 2). For samples with workers only, morphological identification was impossible, they were genetically analysed. We followed the anatomical criteria by Donovan et al. (2001) to assign the feeding group to each sample.

Stable isotope analysis

We used 10 workers per species, with three workers each coming from three different plots and one worker coming from a forth plot to obtain more information about the feeding niches of the studied termites. Only workers were taken into account to eliminate the effect of inter-caste differences in isotopic values, which could bias cross-species comparisons (Bourguignon et al. 2009). Samples were dried at 40°C for 24 h and then weighed into tin capsules. Carbon and nitrogen stable isotope ratios were measured on an elemental analyzer (NA 1500, Fisons-Instruments, Rodano, Milan, Italy) and an isotope ratio mass spectrometer

(Delta V Plus, Thermo Fisher Scientific, Bremen, Germany; Reineking et al., 1993). Stable isotope ratios were expressed using the delta (δ) notation in ‰ according to

$$\delta X = \left(\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}}\right) \text{x } 1000$$

with R_{sample} the isotopic ratio of the sample ($^{13}C/^{12}C$ or $^{15}N/^{14}N$), R_{standard} the isotopic ratio of the international standard and X the respective element (^{13}C or ^{15}N). For ^{13}C V-PDB and for ^{15}N atmospheric nitrogen was used as standard. Acetanilide (C_8H_9NO, Merck, Darmstadt, Germany) was used for internal calibration. At the amount of animal tissue analysed per sample, precision of the measurement is about 0.1 ‰ for ^{13}C and 0.2 ‰ for ^{15}N.

Data analysis

In order to test if trophic niches differ between species, we compared $\delta^{13}C$ and $\delta^{15}N$ values using a two-way ANOVA. We analysed (i) 'feeding groups', then (ii) tested among fungus-growers and (iii) among grass-feeding *Trinervitermes*. We chose to analyse these two additional groups separately because the fungus grower group and the *Trinervitermes*-group are special in their feeding habits and representatives of each group are supposed to have identical feeding niches. Tukey's honestly significant difference post hoc test was performed to compare pairs of species/groups if ANOVA results were significant. Pearson correlations were calculated to test if $\delta^{15}N$ and $\delta^{13}C$ values were correlated. All inferential statistics were done with the statistical package IBM SPSS 16.

To test for phylogenetic patterns of termite diet and to inspect if these niche traits are phylogenetically conserved, we constructed phylogenetic correlograms of species mean $\delta^{13}C$ and $\delta^{15}N$ values using Moran's I index as autocorrelation coefficient (Gittleman & Kot 1990). Using the true phylogeny, we analysed three phylogenetic distances: intra-generic, intra-subfamily and inter-subfamily. If the observed value of Moran's I (I_{obs}) is significantly greater

than the expected value of I under the null hypothesis (I_0 = random distribution of species ecological traits), then the values are positively autocorrelated, whereas if I_{obs} is smaller than I_0, this indicates negative autocorrelation (Gittleman & Kot, 1990). Statistical significance of the deviation of I_{obs} from I_0 was tested for each class with 999 permutations of species mean $\delta^{13}C$ and $\delta^{15}N$ values. Moran's I > 0 indicates phylogenetic clustering (species compared in the respective class are more similar than expected), whereas Moran's I < 0 indicates overdispersion (species compared are less similar) (Bourguignon et al., 2011). The analysis was performed using the ape package in the R software with the *Moran.I* and *correlogram.formula* functions (Paradis 2006, 2017).

Results

In total, we analysed 165 samples representing 22 termite species. $\delta^{15}N$ values ranged between -5.27 and 13.65 ‰ (Fig. 1), and $\delta^{13}C$ values from -29.8 to -14.8 ‰ (Fig. 2) for all species. $\delta^{15}N$ and $\delta^{13}C$ values were positively correlated (Pearson's r = 0.383, P < 0.001).

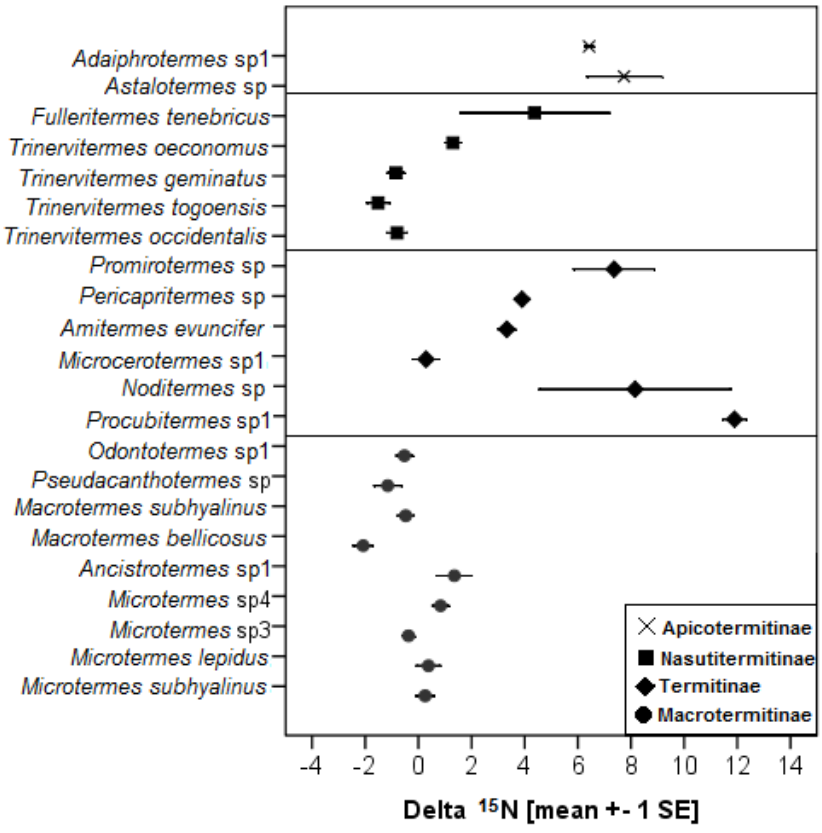

Figure 1. Stable nitrogen isotopic values of the regional species pool sorted into subfamilies. Range of $\delta^{15}N$ values are shown for each species.

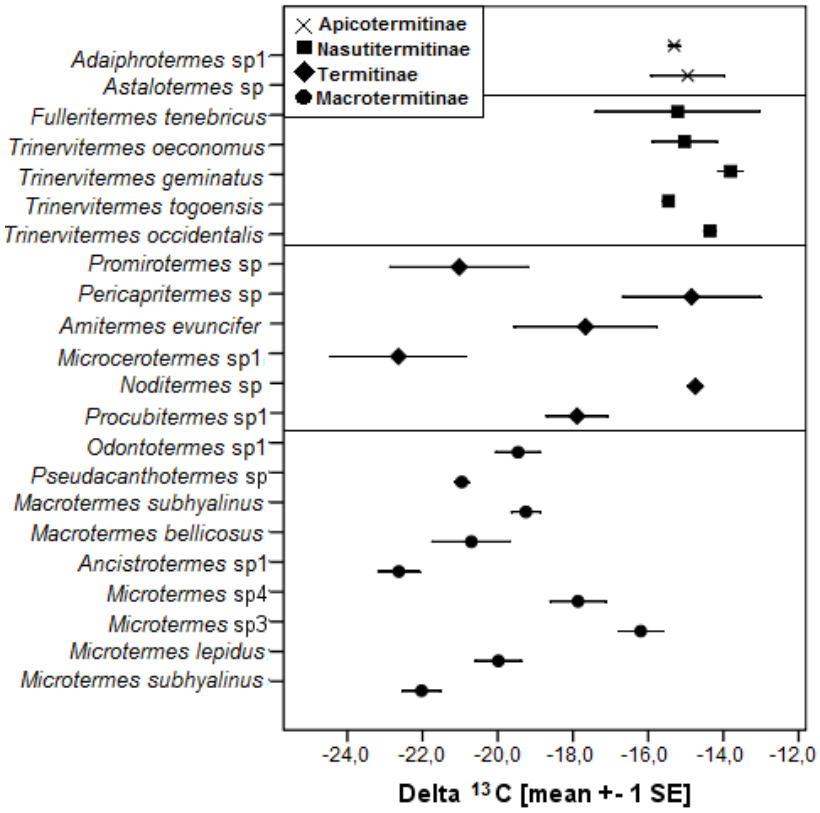

Figure 2. Stable carbon isotopic values of the regional species pool sorted into subfamilies. Range of $\delta^{13}C$ values are shown for each species.

Feeding groups

Overall, the $\delta^{15}N$ and $\delta^{13}C$ values significantly differed between feeding groups and each feeding group had a specific $\delta^{15}N$ and $\delta^{13}C$ signature (ANOVA: $\delta^{15}N$: $F = 57.53$, $P < 0.001$; $\delta^{13}C$: $F = 21.08$, $P < 0.001$; Fig. 3a, b). The soil-feeding groups III and IV had significantly higher $\delta^{15}N$ values than all feeding group II representatives. Yet, group III and IV termites did not differ significantly in $\delta^{15}N$ nor did the fungus-growers differ from the grass-feeding *Trinervitermes* (Fig. 3a). However, with regard to $\delta^{13}C$ these groups did differ (Fig. 3b). Soil-feeders from group IV had significantly higher $\delta^{13}C$ values than group III soil-feeders, and *Trinervitermes* species higher values than fungus-growers (Fig. 3b).

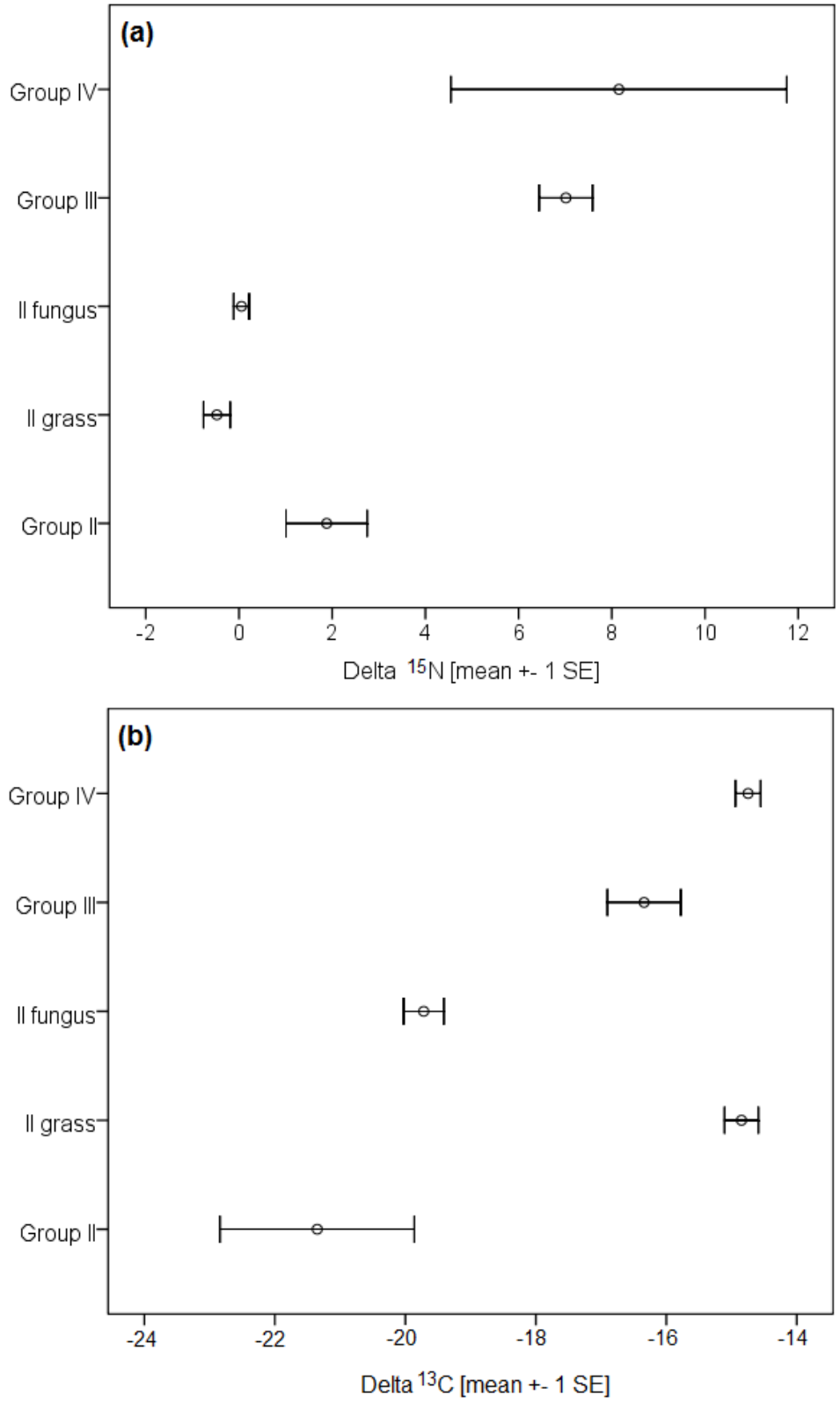

Figure 3. Stable isotope analysis of feeding groups. (a) $\delta^{15}N$ values for feeding groups II - IV. (b) $\delta^{13}C$ values for feeding groups II - IV. Feeding group II is further separated into fungus growers (II_{fungus}) and grass feeders (II_{grass}).

Fungus-growers

Fungus-growers (Macrotermitinae) had significantly different $\delta^{15}N$ and $\delta^{13}C$ signatures (ANOVA: $\delta^{15}N$: $F = 4.93$, $P < 0.001$; $\delta^{13}C$: $F = 11.56$, $P < 0.001$; Fig. 1, 2). Interestingly, *Macrotermes bellicosus* had significantly lower $\delta^{15}N$ values than all other fungus-growers. Overall, some 'pairs' of species can be distinguished that had very similar $\delta^{15}N$ values, such as *Microtermes subhyalinus* / *Microtermes lepidus* or *Microtermes sp. 4* / *Ancistrotermes sp. 1* (Fig. 1). Strikingly, these species pairs which were most similar in $\delta^{15}N$ values differed in their $\delta^{13}C$ signatures (Fig. 2): *Microtermes lepidus* had higher values than *Microtermes subhyalinus* and *Microtermes sp. 4* higher values than *Ancistrotermes sp. 1*. The $\delta^{13}C$ signature of the three mound building species *Macrotermes bellicosus, Macrotermes subhyalinus* and *Odontotermes sp. 1* did not differ significantly. Overall, the results show a complementary pattern in that species, which did not differ in $\delta^{15}N$ values, differed in their $\delta^{13}C$ signature, and vice versa. This implies differentiation in the food niche either along the nitrogen or carbon gradient.

Grass-feeders

There were also significant differences in $\delta^{15}N$ values between the grass-feeding *Trinervitermes* species (ANOVA: $F = 10.86$, $P < 0.001$; Fig. 3a). This was not the case for the $\delta^{13}C$ values (ANOVA: $F = 1.85$, $P = 0.162$; Fig. 3b), which was probably due to the high variability in *Trinervitermes oeconomus*. Most strikingly, *T. oeconomus* had significantly higher $\delta^{15}N$ values than all other *Trinervitermes* species. The most similar $\delta^{15}N$ as well as $\delta^{13}C$ signatures had *Trinervitermes geminatus* and *Trinervitermes occidentalis*, for which neither signature differed significantly implying that they occupy a very similar trophic niche.

Phylogenetic patterns of feeding habits

Phylogenetic correlograms showed significant positive autocorrelation for species within the same genus (intra-generic) for $\delta^{13}C$ values (Moran's I = 0.52, P = 0.049). This was less pronounced for $\delta^{15}N$ values were we had a trend (Moran's I = 0.47, P = 0.064). At the subfamily level (between genera), the analysis showed significant positive autocorrelation for both $\delta^{13}C$ and $\delta^{15}N$ values ($\delta^{13}C$: Moran's I = 0.54, P < 0.001; $\delta^{15}N$: Moran's I = 0.44, P = 0.002). The inter-subfamily level revealed that species from different subfamilies are significantly negative autocorrelated for both $\delta^{13}C$ and $\delta^{15}N$ values ($\delta^{13}C$: Moran's I = -0.27, P < 0.001; $\delta^{15}N$: Moran's I = -0.24, P < 0.001) (Fig. 4).

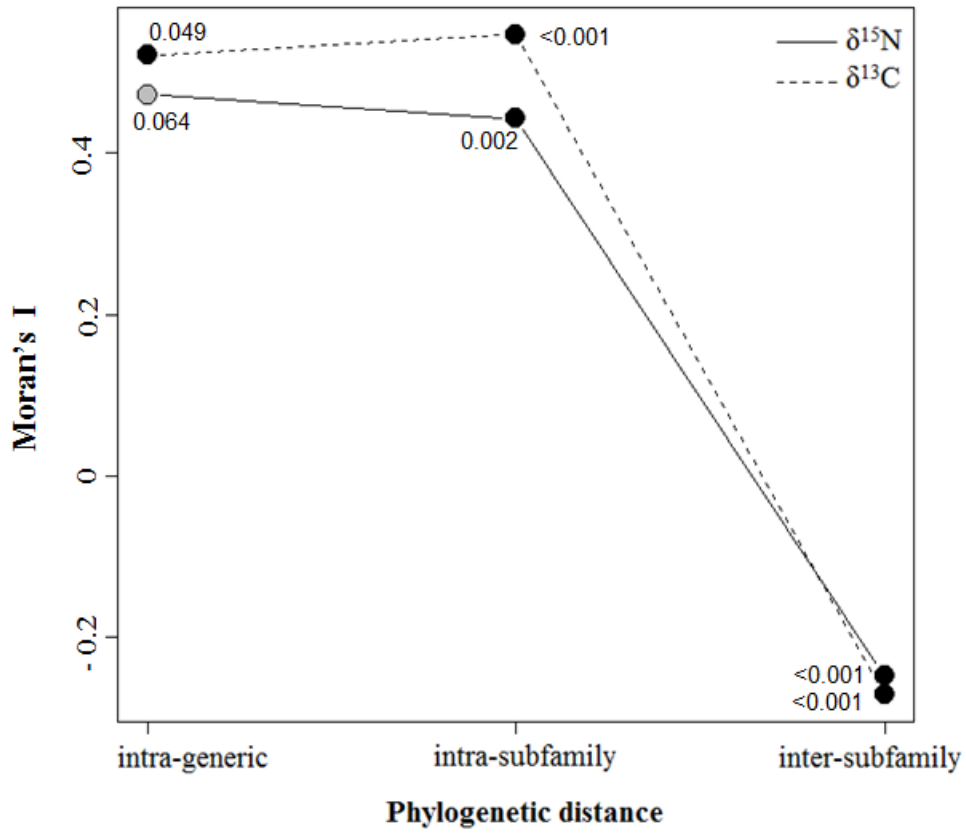

Figure 4. Phylogenetic correlogram of $\delta^{15}N$ and $\delta^{13}C$ values using Moran's I coefficients for three phylogenetic distances between species. All species of the regional species pool were analysed. Moran's I > 0 indicates phylogenetic clustering and Moran's I < 0 indicates overdispersion. The significance of the deviation from Moran's I = 0 is given as P-values next to the symbols.

Discussion

The aim of our study was to test the hypothesis that fine-scaled differentiation of the feeding niche exists between termites from an African savannah ecosystem that supposedly consume the same dead plant material. Our results provide support for this hypothesis as closely related species either differed in their $\delta^{15}N$ and /or $\delta^{13}C$ signatures, despite a phylogenetic signal that relatedness positively correlates with isotope signature within subfamilies as indicated by Moran's I. Our results also confirm former studies from forests and extend them to savannahs that the four commonly recognized feeding groups can generally be distinguished by isotope signatures (Bourguignon et al., 2011; Tayasu, 1997, 1998), but that there is no discontinuity in $\delta^{15}N$ values between group III and group IV soil-feeders (Bourguignon et al., 2011). Yet, in contrast to the forest, our savannah results show that group III and group IV soil-feeders differed in their $\delta^{13}C$ signature.

Comparison with forest studies

Other recent studies concentrated on natural variation of stable isotopes of forest termite assemblages (Bourguignon et al., 2009, 2011). Compared to these studies, we measured lower $\delta^{15}N$ values, especially at the lower end but also the maxima were lower ($\delta^{15}N$: our study: -5.27 to 13.65 ‰; Bourguignon et al. 2011: 0.4 to 16.5 ‰, Bourguignon et al. 2009: 6.4 to 16.5 ‰). An explanation for our maxima being lower may be that we studied savannah assemblages, which lack many soil-feeders of the forest and also that there probably are differences in $\delta^{15}N$ values of the basal recourses consumed. The high negative values are mainly due to the fungus-growers, especially *M. bellicosus* and *Pseudacanthotermes* sp., and partly due to *Trinervitermes*. These groups are largely lacking in forests. With regard to $\delta^{13}C$ isotopes, our values are similar to those measured in the forests (our study: -29.8 to -14.8 ‰; Bourguignon et al. 2009: -29.1‰ to -23.8), but the range of $\delta^{13}C$ values is wider in the

savannah. This could be due to a higher proportion of grasses (C4 plants) as food that dominate savannahs and are absent in forests.

Similar as for neotropical forest termites (Bourguignon et al. 2011), our results in part support the feeding group classification by Donovan et al. (2001). $\delta^{15}N$ and $\delta^{13}C$ values increased along the humification gradient with feeding group II at the relatively non-humified end and lower $\delta^{15}N$ and $\delta^{13}C$ values than group III and IV, which were at the humified end with higher $\delta^{15}N$ and $\delta^{13}C$ values. The results by Bourguignon et al. (2011) revealed that although the species from the four feeding groups differed significantly in their $\delta^{15}N$ values, not all feeding groups differed significantly from one another. This was different in our study as each feeding groups had a specific $\delta^{15}N$ and also $\delta^{13}C$ signature. Additionally, we showed for the first time that *Trinervitermes* grass-feeders and fungus-growers, which are both classified as feeding group II species, actually lie outside the range of typical other group II species concerning $\delta^{15}N$ and $\delta^{13}C$ rations.

Food niche differentiation in closely related termites

All fungus-growers are assumed to consume a broad range of dead plant material from wood to grass to leaf litter, and no differentiation in food consumption has been realized (Donovan et al., 2001; Eggleton et al., 2001). Our data indicate that this is not the case, rather, they indicate that trophic niches of even closely related species differ. Strikingly, we found a complementary pattern in that, for instance, fungus-growers that had similar isotope ratios for $\delta^{13}C$ differed in those for $\delta^{15}N$ and vice versa, implying food niche differentiation. These differences in $\delta^{13}C$ may reflect varying proportions of C3 and C4 plants in the food and differences in $\delta^{15}N$ can reflect diverse proportions of variably humified food recources. All four *Microtermes* species differed in their $\delta^{13}C$ signature and the dominant mound builder *M. bellicosus* had a $\delta^{15}N$ ratio lower than all other species (Fig. 1). This can explain why *M. bellicosus*, despite its dominance (Korb & Linsenmair, 2001), does not negatively affect the

composition of termite communities, but rather seems to favour the co-existence of phylogenetically closely related species (Hausberger & Korb, 2015). If food niche differentiation plays a role and termite community assembly is influenced by interspecific competition, we predict that species differing in their isotope niche (either in $\delta^{13}C$ or $\delta^{15}N$) are commonly coexisting, while species with similar niches exclude each other. The latter are *M. subhyalinus*, *Odontotermes* sp.1, and *Microtermes* sp.3.

Similarly, *Trinervitermes* species are generally classified as grass-feeders although their feeding behaviour differs with *T. togoensis* and *T. geminatus* being true 'harvesting' species that transport and store grass fragments in their nests, whereas *T. oeconomus* and *T. occidentalis* feed on grass without storing it (Sands 1961). In choice experiments with a selection of grasses, each *Trinervitermes* species had a preference for different grasses (Sands 1961). This is in line with our findings of the four *Trinervitermes* being separated along the $\delta^{13}C$ but also the $\delta^{13}N$ axis: *T. oeconomus*, which had a very broad range in its $\delta^{13}C$ spectrum, had much higher $\delta^{13}N$ values than its congeners (Fig. 1), whereas the three other species clearly differed in their $\delta^{13}C$ signatures (Fig. 2). The broad range of $\delta^{13}C$ values in *T. oeconomus* is in line with its greater variety of grasses selected in the food choice experiment compared to its congeners (Sands 1961).

Phylogenetic patterns of feeding habits showed that the more related the species are, the more similar their diet seems to be. This was true for both $\delta^{15}N$ and $\delta^{13}C$, although Moran's I for $\delta^{13}C$ was in general slightly higher than for $\delta^{15}N$. We observed phylogenetic clustering at the within genera and within subfamily level. This, at least partly, reflects the coarse ‘traditional’ food niche differentiation into grass-feeders and fungus-growers. Between subfamilies the results showed significant overdispersion, in line with species from different subfamilies often occupying different niches along the humification gradient. Nevertheless, our results showed that there are fine-tuned food niche differences in closely

related species, despite the phylogenetic clustering at the within genera and within subfamily levels.

It is interesting to speculate on the role of the symbiotic fungus, *Termitomyces*, in mediating such a niche differentiation. *Termitomyces* is essentially involved in the degradation of plant-derived material such as wood, dry grass and leaf-litter (Poulsen et al. 2014; Nobre et al. 2010), and hence C3 and C4 plants. Therefore, it would be interesting to compare the natural variation in stable carbon isotope ratios in relation to the *Termitomyces* symbionts. The single existing study showed that *Termitomyces* is generally richer in ^{13}C than the substrate and that ^{13}C increases along a gradient from old fungus comb to termites to fungal nodules (Hyodo et al., 2003). Studies on the evolution of fungus-growing termites and their mutualistic fungal symbionts have shown that different termite species can have distinct *Termitomyces* symbionts (Aanen et al. 2002). Most of our sampled fungus-growers, especially *Microtermes* spp. and *Macrotermes* spp., have differing mean $\delta^{13}C$ values and, according to Aanen et al (2002), distinct *Termitomyces* symbionts. Thus, the fungal symbionts may contribute to the fine-tuned niche differentiation between coexisting savannah termites. A one to one comparison of our study with Aanen et al. (2002), however, is not possible due to taxonomic difficulties in assigning termite species. Hence, further combined studies are warranted to systematically test for the contribution of the fungal symbionts in fine-scaled niche differentiation of the termites.

Concluding, our findings imply that species similar with regard to $\delta^{15}N$ values generally differed in $\delta^{13}C$ values, and vice versa. $\delta^{15}N$ and / or $\delta^{13}C$ signatures allowed distinguishing fungus-growing and grass-feeding termite species, reflecting distinct feeding habits of coexisting species. The dominant mound building fungus-grower *M. bellicosus* had the lowest $\delta^{15}N$ values among all fungus-growers indicating that it occupies a different food

niche. This fine-scaled differentiation along the food niche axis can contribute to explain why so many apparently identical termite species co-exist in savannah ecosystems.

Acknowledgements

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Chapter 4

Phylogenetic community structure of southern African termites (Isoptera)

Janine Schyra, Barbara Hausberger, Judith Korb

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Research Article

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Abstract

The processes that structure communities are still largely unknown. Therefore, we tested whether southern African termite communities show signs of environmental filtering and / or competition along a rainfall gradient in Namibia using phylogenetic information. Our results revealed a regional species pool of 11 species and we found no evidence for phylogenetic overdispersion or clustering at the local scale. Rather, our results suggest that the assembly of the studied termite communities has as strong random component on the local scale, but that species composition changes along the climatic gradient.

Introduction

The mechanisms that structure communities are still highly debated (Chase & Leibold, 2003; Chave, 2004; Zhou & Zhang, 2008; Holt, 2009). Environmental factors such as temperature and rainfall can act as filters that limit, for instance, the distribution of species and define part of a species niche, especially over larger geographic scales. An understanding of the

importance of local versus regional processes depends on the spatial scale, divided into spatial grain (the size of the sample unit) and the spatial extent (the total area of the study), at which species communities are defined and studied, and the scale at which actual processes operate (Graham & Fine, 2008; Emerson & Gillespie, 2008; Weiher et al., 2011).

Classically, interspecific competition was thought to be a major driving force in structuring communities of ecologically similar species (members of the same guild, functional analoga) (Diamond, 1978; Schoener, 1982). The resulting concept of limiting similarity states that species can only co-exist if they differ in their niche axes (Abrams, 1983). There is supporting evidence, for example, when striking patterns of size or morphological differences were found for co-existing guild members (Bowers & Brown, 1982; Leibold, 1998). Yet, in many cases the concept was taken for granted and local communities were not tested against the null hypothesis of random assemblages from the regional species pools. In more recent years the development of the unified neutral theory of biodiversity and biogeography challenged the classical niche theory and considered niche differences less important (Hubbell, 2001). According to this theory, trophically similar species are demographically equivalent and ecological communities are mainly structured by 'ecological drift' (*i.e.* stochastic factors such as birth, death, random migration and extinction) (Hubbell, 2001; Volkov et al., 2009). A 'niche versus neutrality' debate is largely unproductive and attempts exist to incorporate elements of both theories into more general explanations (Holt, 2009; Weiher et al., 2011).

The high species diversity of tropical ecosystems, where many species of seemingly identical niches coexist, is a challenge for classical niche theory. The fact that tropical insect communities have even less specialists than those of temperate regions (Schleuning et al., 2012; Ollerton et al., 2012) supports the theory that niches may not play such an important role in the tropics. Yet, data that explicitly test structuring processes in tropical animal

communities are scarce (Vamosi et al., 2009). This applies especially for insects whose sheer species richness can hardly be explained by niche differences.

Many termite species occupy apparently very similar niches: they have similar abiotic requirements and are decomposers of organic matter. Currently, four feeding groups are recognized by analysis of gut content (Donovan et al., 2001), representing different stages of decomposition from sound wood to soil organic matter. This classification is also reflected in the four feeding types; wood-, leaf litter-, soil- and true soil- feeders (Eggleton & Tayasu, 2001). Recent stable isotope analyses of a termite assemblage from a forest implied that there is subtle niche differentiation within feeding groups (Bourguignon et al., 2009). Yet, they cannot explain how more than 20 species of leaf litter feeders can co-exist in African savannahs that all forage from the same dead plant material (Hausberger et al., 2011).

We tested whether local termite communities in southern Africa differ from random assemblages of the regional species pool with regard to phylogenetic composition, by looking at communities across a north / south rainfall gradient in Namibia. The northern region is characterized by higher precipitation and therefore more diverse vegetation than the more arid southern region with less vegetation (Jürgens et al., 2010; Grohmann et al., 2010). We investigated whether ß-diversity between sites is related to distance along this gradient.

To do this, we applied phylogenetic community analyses (Webb et al., 2002, 2008; Cavender-Bares et al., 2009; Kembel et al., 2010), which allowed us to explicitly test real communities against null models of random assemblages. By using phylogenetic information, we tested whether local communities are more or less closely related than assemblages drawn randomly from the regional species pool. As ecological traits are phylogenetically conserved for the species studied here (Inward et al., 2007), related species share ecological traits, and therefore assemblages of less closely related species (i.e. phylogenetic overdispersion) indicate interspecific competition because these similar traits prevent species from coexistence. The reverse (i.e. phylogenetic clustering) suggests environmental filtering due to

similar ecological preferences (temperature, rainfall, vegetation density, soil type) (Webb et al., 2002, 2008). Combined with analyses of species turnover between localities (β-diversity; Whittaker, 1972) and its phylogenetic signal (phylogenetic β-diversity; Bryant et al., 2008; Kembel et al., 2010), and an analysis of the impact of environmental variables (Helmus et al., 2007a, 2007b), we tested whether these southern African termite communities differed from random assemblages.

Materials and methods

Termite sampling

Termites were collected in January 2010 from 6 sampling sites (22°50' to 26°11'N; 18°5' to 16°8'E; Namibia; Fig 1) when they were most active, that is, at the beginning of the rainy season, using a standardized transect sampling protocol (Hausberger et al., 2011). This protocol developed for termite diversity assessments consists of soil sampling and a thorough search of dead plant material on the ground, in trees, and in mounds (Jones & Eggleton, 2000). Such transect sampling is recommended to assess termite diversity in regions of intermediate to moderately low rainfall (Davies et al., 2013). A plot size of one ha was chosen because the foraging range of termite colonies is within 100 m (Korb & Linsenmair, 2001) and hence one ha represents the local scale where interactions among colonies occur, i.e. it reflects the Darwin-Hutchinson-Zone, which is most relevant to study the assembly of local communities (Vamosi et al., 2009). Three transects each measuring 2 m x 50 m, divided into ten 2 m x 5 m sections, were arbitrarily located within each plot. Each transect section was searched thoroughly for termites for 15 minutes by a trained person; additionally, we sampled eight soil pits per transect section, each measuring 12 cm x 12 cm x 10 cm. All encountered samples were stored in pure ethanol for subsequent molecular analysis. Due to limitations of the study, additional sampling along the climatic gradient was not possible. However, this

transect method is designed to obtain the best possible 'snapshot' of conditions in a site and has been tested and used frequently in termite diversity studies (Jones & Eggleton, 2000; Donovan et al., 2002; Eggleton et al., 2002; Inoue et al., 2006) and our study design is comparable to other termite studies (Houston et al., 2015; Dahlsjö et al., 2015).

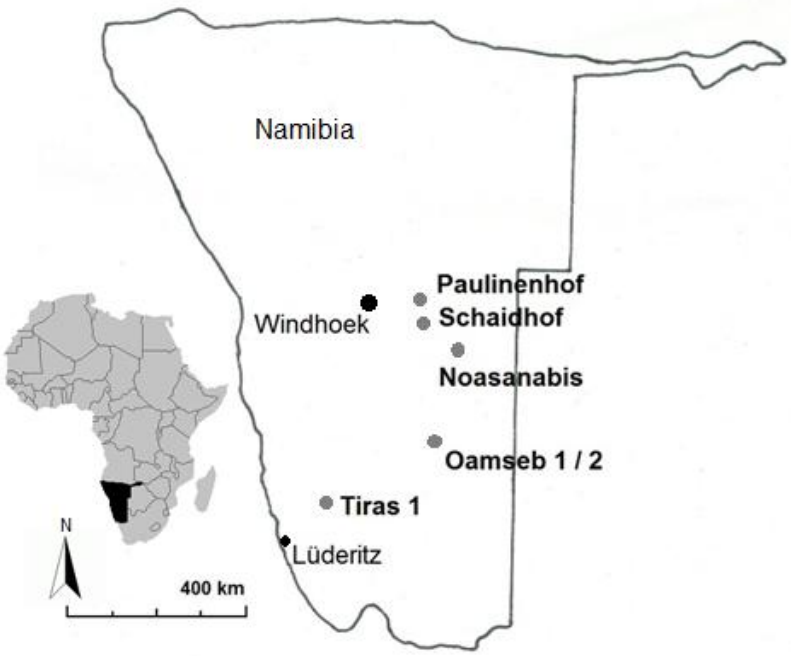

Figure 1. Map of the six sampling sites in Namibia. One sampling site (plot) represents one community with one ha in size.

All samples were identified to species level. First, samples containing soldiers were identified to the genus level using the keys by Webb (1961) and Uys (2002). Then these morphological identifications were confirmed by molecular genetic analyses (see below). For samples with workers only, morphological identification was difficult, they were genetically analysed (see below). The presence / absence of each species within a plot was documented as well as the encounter rate (i.e. the number of samples per species and plot), which is used as a surrogate of species abundance (Davies, 2002).

Genetic analyses

To allow unambiguous species identification, we isolated DNA and sequenced fragments of three genes as described elsewhere (Hausberger et al., 2011) (see also Appendix 3, Table S1): *cytochrome oxidase subunit I* (*COI*; total length 680bp), *cytochrome oxidase subunit II* (*COII*; total length 740 bp), and *12S* (total length 350 bp). These sequences were used to re-construct phylogenetic trees using three approaches (Bayesian method, maximum-parsimony analysis, and maximum-likelihood analysis) to delimitate and identify species (for more details and GenBank accession numbers see Appendix 3, Table S2). As in former termite studies (Legendre et al., 2008; Hausberger et al., 2011), *COII* was most useful for 'barcoding' (i.e., assigning species to samples) because it amplified well and gave appropriate resolution for species identification. All collected samples were sequenced for identification.

Phylogenetic community structure analyses

We analysed the local community structure with PHYLOCOM 4.2 (Webb et al., 2008). As input tree for the phylogenetic community structure analyses we used the *COII* gene tree, which was pruned prior to analysis so as to have only species of the regional species pool included and only one representative per species in the tree. We calculated the net relatedness index (NRI) that measures whether locally co-occurring species are phylogenetically more / less closely related than expected by chance. It uses phylogenetic branch length to measure the distance between each sample to every other terminal sample in the phylogenetic tree, and hence the degree of overall clustering (Webb et al., 2008). The NRI is the difference between the mean phylogenetic distance (MPD) of the tested local community and the MPD of the total community (regional) divided by the standard deviation of the latter. High positive values indicate clustering; low negative values overdispersion (Webb et al., 2002). We chose the NRI and not the nearest taxon index (NTI) because the NRI quantifies overall clustering of taxa on a tree and takes deep-level clustering into account. The NTI quantifies terminal

clustering, independent of deep-level clustering and gave qualitatively the same results as the NRI. We tested whether our data significantly deviated from 999 random communities derived from null models using the independent swap algorithm on presence / absence data (Gotelli & Entsminger, 2003; Hardy, 2008). The swap algorithm creates swapped versions of the sample / species matrix and constrains row (species) and column (species' presence or absence) totals to match the original matrix. The regional species pool consisted of all species from all studied localities. As suggested by Webb et al., (2008), we used two-tailed significance tests based on the ranks that describe how often the values for the observed community were lower or higher than the random communities. With 999 randomizations, ranks equal or higher than 975 or equal and lower than 25 are significant at $P \leq 0.05$ (Bryant et al., 2008).

Comparison between study sites

We quantified the compositional similarity (ß-diversity) between all localities using the Sorensen and Bray Curtis index, which were calculated in EstimateS version 8.2.0 (Colwell, 2013). High values indicate high similarities between plots with regard to species composition and low values the reverse. A Mantel test was used to analyse whether the similarity correlates with distance between plots using XLSTAT, version 2013.2.06. The PhyloSor index quantified the phylogenetic ß-diversity (Bryant et al., 2008). It ranges from 0 (two communities only share a very small root, which means they consist of phylogenetically very different taxa) to 1 (both communities are composed of related taxa). Equivalent to the Phylocom analyses it was tested whether phylogenetic similarities between plots deviated from random by using ‘independent swap’ null models with 999 runs and applying rank tests. Analyses were done with Picante 1.2.0 (Kembel et al., 2010) as implemented in R 3.0.3.

Influence of environmental variables

We also tested if environmental factors influence the assemblage of termite communities using logistic regressions as suggested by Helmus et al. (2007a, b). We retrieved monthly data for the bioclimatic variable mean annual precipitation for our study areas from the WorldClim database (www.worldclim.org; Hijmans et al., 2005), which is a set of global climate layers (climate grids) with a spatial resolution of 1 km^2. We only used one variable because of the small sample size and precipitation seems the most influential variable in arid regions. As termite colonies are perennial and sedentary this data seems more appropriate than recordings for a certain year. We correlated co-occurrence of species pairs with phylogenetic co-occurrence of species pairs, both before and after accounting for environmentally caused variability (mean annual precipitation), and calculated the change in occurrence correlations when including mean annual precipitation as implemented in the R-package "Picante" (Kembel et al., 2010).

Results

Diversity

The phylogeny revealed a regional species pool of 11 species in nine genera (Fig. 2). Nine species belonged to the higher termites (Termitidae), with two Macrotermitinae (*Allodontotermes* sp., *Microtermes* sp.), four Termitinae (*Microcerotermes* sp., *Angulitermes* sp., *Promirotermes* sp., *Amitermes* sp.), and three Nasutitermitinae *(Trinervitermes bettonianus, Trinervitermes trinervoides* and *Trinervitermes* sp.). From the lower termites *Hodotermes mossambicus* (Hodotermitidae) was sampled as well as one representative of the genus *Psammotermes (*Rhinotermitidae). The phylogenetic analyses for the gene *COII* showed appropriate resolution, which was not the case for the genes *COI* and *12S*. Here sequencing of all samples was difficult and the phylogenetic trees did not give appropriate

resolution for all species (Fig. 2, Appendix 3, Fig. S1 and S2). This similarly applied for the other phylogenetic methods used.

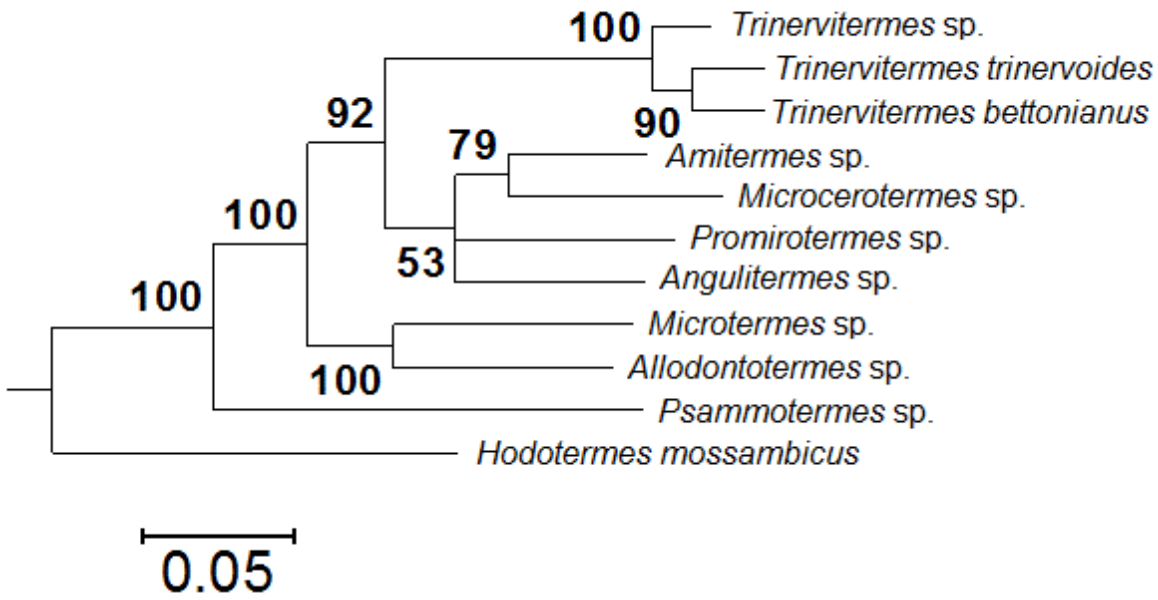

Figure 2. Input Bayesian phylogeny for Phylocom based on the gene cytochrome oxidase II using MrBayes v3.1.2. Analysis was done with 10^7 generations, as well as a number of chains=4, sample frequency=1000 and a finalizing burn-in of 2500.

Phylogenetic community structure

There were no significant signals of overdispersion or clustering within local communities. The NRI indices ranged from 0.21 to 1.12. They never deviated from random communities generated with the 'independent swap' algorithm (always $p > 0.05$). Species richness per plot did not correlate with NRI either (Spearman-rank correlation: NRI: $r= 0.313$, $p = 0.545$) (Fig. 3).

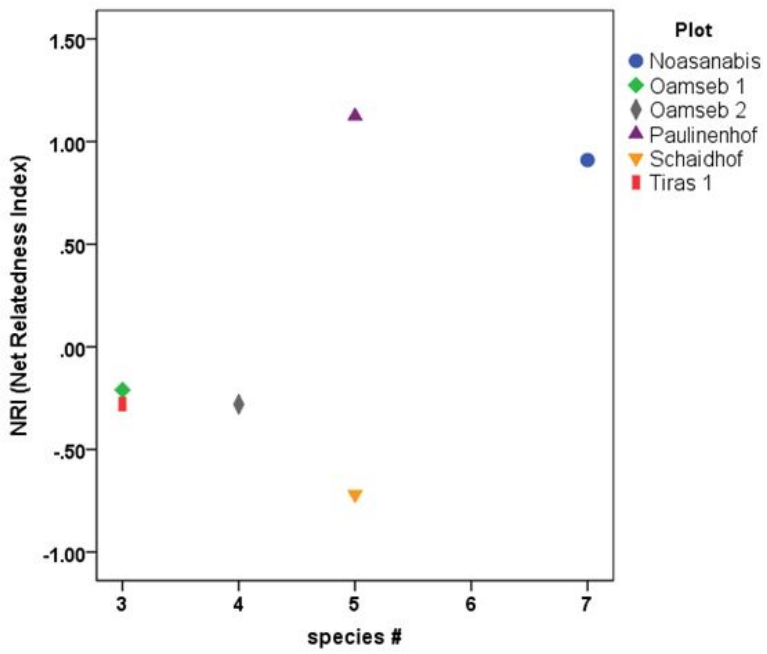

Figure 3. Indices of the phylogenetic community structure using the null model independent swap with the abundance data showing the NRI for all plots with the number of species per plot. The number of species did not correlate significantly with the NRI.

Comparison between study sites

The compositional similarity between plots varied, with the Sorensen index ranging from 0.40 to 1.00, the Bray-Curtis index ranging from 0.19 to 0.74 (Appendix 3, Fig. S3 and S4) and the PhyloSor index ranging from 0.53 to 1.00 (Appendix 3, Fig. S5). The Sorensen and Bray-Curtis indices correlated significantly with the PhyloSor indices (Spearman-rank correlation: Sorensen: $r = 0.742$, $p = 0.002$; Bray-Curtis: $r = 0.717$, $p = 0.003$). The PhyloSor and Sorensen index showed that the community pairs located in the arid, southern region were more similar to each other compared to the remaining community pairs. Tiras1 and Oamseb1, with a PhyloSor and Sorensen index of 1, were significantly more similar with regard to phylogenetic composition than expected by chance and had identical species composition (Appendix 3, Fig. S3 and S5, Table S2). Community pairs Tiras1 / Oamseb2 and Oamseb1 / Oamseb2 had PhyloSor values of 0.89 and Sorensen index value of 0.86. The remaining community pairs had index values ranging from 0.53 – 0.75 (PhyloSor index) and 0.40 – 0.67 (Sorensen index). The geographical distance between plots did not significantly correlate with

ß-diversity (Mantel-test: Sorensen index: r= -0.144, P=0.611; Bray-Curtis index: r = -0.050, p = 0.861) or phylogenetic ß-diversity (Mantel-test: r = -0.341, p = 0.205) (Appendix 3, Fig. S6).

Environmental variables

The observed pairwise correlations between plots did not correlate significantly before and after including mean annual precipitation with the phylogenetic correlations (always $p > 0.05$) (Fig 4a, b). Further, the change in occurrence correlations, when including mean annual precipitation, did not significantly correlate with the pairwise phylogenetic correlations ($p > 0.05$) (Fig 4c), indicating that it is not a major variable influencing species co-occurrences.

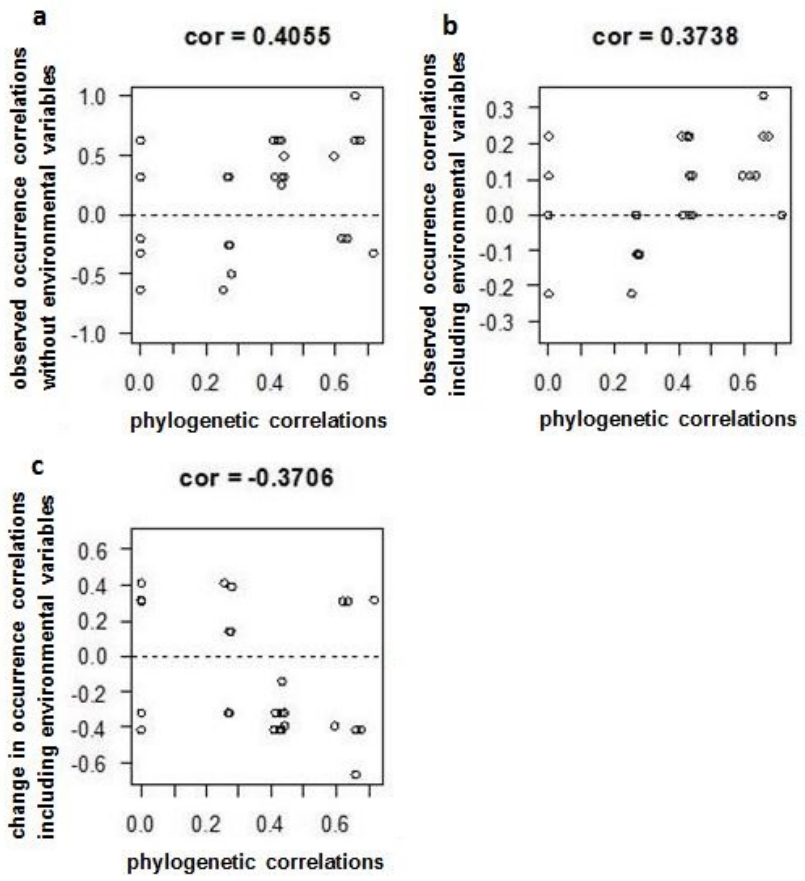

Figure 4. Influence of environmental factors on community structure. Shown are correlations of pairwise species co-occurrence and pairwise phylogenetic correlations a) without environmental variables, b) including environmental variables, and the c) change in species co-occurrence once environmental variables are taken into account. There were no significant results a) without and b) with environmental variables included ($P > 0.05$). Also c), the changes in correlation were not significant either ($P > 0.05$).

Discussion

Local community assembly

This study aimed at uncovering processes that structure termite communities in Namibia at a local scale, along a climatic gradient (Appendix 3, Table S3). We did not find evidence that habitat filtering or interspecific interactions play major roles in structuring these communities locally.

The highest termite diversity is located in African tropical forests (Eggleton et al., 1994; Davies et al., 2003). Compared to forests, savannahs harbour much lower species diversity. In West African savannahs at least 20 species were identified, mostly fungus-growing Macrotermitinae (Hausberger et al., 2011). This is higher than the uncovered regional species pool of 11 species from nine genera in this study (Appendix 3, Table S2). This might be due to the more arid conditions in Namibia as previous studies revealed less species under drier conditions (de Bello et al., 2006; Traill et al., 2013). For Namibia, a total of 17 termite genera have been identified (Jürgens et al., 2010). This is considerably more than what we found, but our study covered a smaller area and did not include all vegetation zones (e.g. woodland savannah). We concentrated on analysing local community assembly, which supplements the work of Jürgens et al. (2010), which monitored regional species occurrence and distribution. When comparing overlapping regions between both studies we had similar species occurrences (Appendix 3, Table S2).

This is the first study investigating the phylogenetic community structure of southern African termite communities and explicitly testing their composition against a null model of random assemblages. Termites are mainly sessile organisms in that the colonies stay on one site over many years. Therefore, they may be more prone to certain local environmental conditions and interspecific competition than highly mobile species that can (temporarily) escape unsuitable conditions, for example birds (Canales-Delgadillo et al., 2012; Harmon-

Threatt et al., 2013). Nest building in termites can be beneficial, in that it makes them less sensitive to abiotic environmental conditions. However, our results did not reveal significantly clustered or overdispersed communities according to the NRI, indicating a random component to local species assembly.

It has been shown that the opposing forces of habitat filtering and interspecific competition can counteract one another (Lessard et al., 2009), resulting in seemingly neutral communities. In order to test for such effects the environmental regression analyses were done that tested for and 'statistically' removed environmental effects to reveal potentially hidden patterns of competition (Kembel et al., 2010). Assuming that rainfall is the major environmental factor in arid regions, including mean precipitation still could not reveal such a hidden pattern. For other tropical species, a variety of assembly patterns have been found, ranging from phylogenetic overdispersion to phylogenetic clustering along an environmental gradient (Graham et al., 2009; Webb, 2000; Gòmez et al., 2010; Cavender-Bares et al., 2004). Several reasons may explain these differences such as the studied taxon, its ecological requirements and sampling effort as well as the geographic history and conditions of the respective region. Sampling effort could influence the results of community structure analyses as there might be a minimal diversity needed to detect a certain pattern. Other studies had a termite species diversity of around 20 species and here community structure was detectable, even in local sites harbouring only 3-5 species (Hausberger & Korb, 2015, 2016).

Community structure along the climatic gradient

The analysis of environmental variables showed that the effect of annual precipitation on community structure along the north / south gradient does not seem to be clear, despite the climatic gradient covered (annual precipitation in the north: 303 mm and south: 144 mm; Appendix 3, Table S3). This may be due to a small sample size and the fact that other factors influencing community structure may compensate for the low rainfall in the arid region. This

should be investigated in future studies. By contrast, other community studies have shown that broad-scale variation in climate, along latitudinal or altitudinal gradients, influences both the structure of species communities and the activity rates of certain species, which can modify species interactions and influence the degrees to which food resources are accessible (Lessard et al., 2011; Graham et al., 2009; Gòmez et al., 2010; Machac et al., 2011).

As the ß-diversity and phylogenetic ß-diversity of the sampling sites revealed that communities are more similar in the southern part of the sampling area, some environmental or historical processes seem to influence species assembly, although we did not find an effect of the rainfall gradient. Species diversity was higher in the northern area and next to a few other species, only *Trinervitermes* sp. and the 'desert'-species *Psammotermes* sp. were sampled frequently in the arid southern region. This is similar to what has been shown in previous studies (Coaton & Sheasby, 1972) and can be explained by the fact that *Trinervitermes* sp. are grass-feeders and occur more frequently in open grass savannahs with little other vegetation. Although more research is clearly needed, our study contributes to the identification of African termite species with the goal to understand their distribution and species assembly processes.

Acknowledgements

We thank the landowners in Namibia for allowing us to sample the termites on their land and Abbo van Neer for helping with field work, BIOTA South and its team for their assistance on-site, and the Ministry of Environment and Tourism of Namibia for the collection permit (2010: 1456/2010) and export permit (2010: 78091).

General Discussion

West African termite communities in savannah and forest ecosystems

The main goal of this study was to analyse diversity and community structure of West African termite communities in savannah and forest ecosystems using a standardized approach. We expanded our study by comparing protected/natural sites with disturbed sites that had been un-affected by strong anthropogenic disturbance since varying time periods (fallows in the savannah and teak plantations in the forest ecosystem), to reveal common principles and differences across ecosystems. Comparisons of savannah and forest species communities are generally rare, except for mammals and birds, which have been studied more widely (Ahumanda et al. 2011; Linzey & Kesner 2009; Porter et al. 2000). Therefore, this study contributes to the field of arthropod species community structure in African ecosystems.

The study conducted in the savannah ecosystem revealed that communities differed significantly in their compositional and phylogenetic similarity, depending on the respective habitat regime (Chapter 2), by unambiguously identifying the sampled termite species. Communities in protected habitats (Park) were more similar to each other, both compositionally and phylogenetically, than communities in the disturbed habitats (fallows). The communities in the Park seemed to have a habitat-specific species composition, result of a long 'assembly history' with relatively stable biotic and abiotic factors, while communities in the fallows seemed to experience a higher turnover of species due to the disturbance event, resulting in apparently less similar species compositions. Comparing fallows and protected sites showed intermediate similarity between these two habitat regimes. This was due to different species compositions of different aged fallows (Chapter 1).

Our results partially correspond with a similar savannah study in West Africa, looking at termite community assembly in Benin (Hausberger & Korb, 2016). As in our study,

protected sites were similar to each other but differed in similarity to those from disturbed village sites. Yet, disturbed sites in Benin were similar to each other and had very few termite species, probably due to disturbed sites being next to villages and including active agricultural fields, which our fallows lacked. In both studies, termite encounter rates were lower under disturbed than protected regimes. This also applied to our forest results and suggests that there is a general pattern: first species abundance declines with disturbance, then species numbers decline.

In the forest ecosystem the compositional and phylogenetic similarity were high among protected forest sites, but low between disturbed teak plantation sites, similar to the savannah (Chapter 2). However, the similarity between protected forest and teak plantations was low, while it was intermediate in the savannah, which is due to changes in species composition. In teak plantations most Nasutitermitinae disappeared, with three out of four *Trinervitermes* species missing. As *Trinervitermes* are grass-feeders and the teak mono-cultures are characterized by a complete absence of grasses on the ground, this result is not surprising.

In other forest studies there was a notable decline of soil-feeders with the transformation of forests into plantations and an increase in fungus-growing Macrotermitinae (Eggleton *et al*., 2002; Jones *et al.*, 2003). In our study, two Macrotermitinae (*M. bellicosus* and one *Odontotermes* species) disappeared in the plantations but one fungus-grower, *Pseudacanthotermes militaris*, was only found in the plantations, revealing an opposite pattern. These different effects of disturbance on termite community composition compared to other forest studies might be due to regional differences. Our species richness was rather low compared to tropical forests in central Africa or America, which have many more soil- and humus-feeders, especially Apicotermitinae. The fact that teak plantations are still forests, and not open areas like fallows or cultivated fields, may explain why we did not see an increase in Macrotermitinae with disturbance.

Comparing these two ecosystems savannah and forest, we can say that (i) as expected, there are more species and higher encounter rates in the forest than in the savannah, (ii) in neither ecosystem species richness or Net Relatedness Index (NRI), which can distinguish between random and non-random phylogenetic patterns in communities, changed significantly with time since disturbance, (iii) in both ecosystems the NRI did not differ between protected and disturbed habitat regimes with few signs of phylogenetic structuring in both regimes, (iv) in the teak plantations species richness declined compared to the protected forest, which was not the case in the fallows in the savannah, and (v) similarity in species composition between protected forest and teak plantations was low in comparison to Park and fallows in the savannah, which were intermediate. Nevertheless, species similarity in both ecosystems was low between disturbed sites, while it was high between protected sites.

Disturbance filters termite species

Disturbance has been an object of ecological research for decades. A hypothesis trying to explain how disturbance influences species communities is the 'intermediate disturbance hypothesis', first proposed by J. Connell (1978). It states that low levels of disturbance lead to low diversity of species through competitive exclusion and high levels of disturbance lead to low species diversity because few species are able to colonize disturbed sites. Local species diversity is supposed to be highest at intermediate levels of disturbance because both rapid colonizers and competitive species can co-exist (Roxburgh et al. 2004; Townsend & Scarsbrook, 1997; Wilkinson, 1999). Our results only partly support this hypothesis: The above mentioned results already show that disturbance affects and changes termite communities in West African savannah and forest ecosystems substantially. Our findings in Chapter 1 support these results as well as our hypothesis that strong anthropogenic disturbance selects for a subset of species, which are common crop pests in West Africa. We could show that disturbance is associated with environmental filtering, at least in the studied

savannah region, as vegetation type had an influence on compositional and phylogenetic species similarity and young fallows with a higher degree of disturbance had a different species composition than older fallows. The vegetation type ’field‘ was characterized by species which are known crop pests in West Africa, especially *Amitermes evuncifer*, *Ancistrotermes* sp., *Microtermes* spp. (Wood et al. 1980; Rouland-Lefèvre 2011; Cowie et al. 1989; Collins 1984). The question if the occurring species are pests because they are more resilient against disturbance or if selection as pests made them more resilient is difficult to answer. Some species occurred in both younger and older fallows, for example *Odontotermes* sp. and *Macrotermes subhyalinus*, implying that they are generalists which can cope better with disturbance. The grass-feeding *Trinervitermes* mainly occurred in older fallows and the protected Park. *Trinervitermes* have been identified as food-specialists (Sands, 1961), with each species foraging on a specific set of grasses, therefore occupying different food niches (Chapter 3). As grasses are commonly available in young fallows as well, limited food availability probably cannot account for their absence in young fallows, concluding that other traits/ factors make them less resilient against disturbance.

Against expectation, species richness did not increase with fallow age. It seems that a higher degree of disturbance in younger fallows creates a certain set of species and that this set of species then changes with decreasing disturbance in older fallows, but species richness itself is not affected by this. Surprisingly, the species composition of these older fallows was still a different one than the species composition of the Park sites, although the oldest fallows had an age of 12 years. This shows that anthropogenic disturbance seems to have long-term effects on termite species communities in African savannah regions. As termites are crucial for the preservation of savannah and forest habitats due to their positive influence on humification processes, soil fertility, bioturbation and water infiltration rates, disturbance quite surely will have a negative impact not only on all kinds of animals occupying these ecosystems, but also on humans living in these areas. As termite numbers decline, the

ecosystem services they provide will decline as well, with soil erosion and unfertility being the result, contributing further to demographic and political problems. To achieve a balance between termites and humans in West African savannahs and forests, this can be taken as a basis for future conservation schemes of African termite communities.

Food niche differentiation and community structure

A further question we wanted to investigate in this study is how these around 20 termite species do co-exist locally, although they seemingly have identical food requirements. Therefore, we tested if there is fine-scaled niche differentiation along the food axis, using $\delta^{15}N$ and $\delta^{13}C$ isotope analysis (Chapter 3). The results showed that closely related species either differed in their $\delta^{15}N$ and/or $\delta^{13}C$ signatures. By this we could confirm former studies mainly from forests and extend them to savannahs that the four recognized feeding groups can generally be distinguished by stable isotope signatures (Bourguignon et al., 2011; Tayasu, 1997, 1998). Compared to recent forest studies (Bourguignon et al., 2009, 2011), we measured considerably lower $\delta^{15}N$ values, which is not surprising, as we studied savannah assemblages, which lack many soil-feeders present in the forest. The high negative values are mainly due to the fungus-growers and partly also due to the grass-feeders. These groups are largely lacking in forests. $\delta^{13}C$ values in the savannah were similar to those found in the forest (Bourguignon et al., 2009). The study also confirmed the feeding group classification by Donovan et al. (2001). Both $\delta^{15}N$ and $\delta^{13}C$ values increased along the humification gradient, with feeding group II at the relatively non-humified end and group III and IV at the more humified end. Additionally, the results confirmed for the first time that grass-feeders (*Trinervitermes*) and fungus-growers (Macrotermitinae) actually lie outside the range of typical feeding group II species, although they have been classified as group II species in former studies. As these two groups naturally consist of closely related species and we could show that several *Trinervitermes* species and also several members of the Macrotermitinae do

co-exist in savannah habitats (Chapter 1 and 2), the question arises how these closely related species can co-exist without competing for the same foods. In former studies, fungus-growers are described to consume a broad range of dead plant material and no differentiation in food consumption has been identified (Donovan et al., 2001; Eggleton et al., 2001). Our data imply that this is not the case and that there is food niche differentiation among these closely related species. We even found a complementary pattern, in that fungus-growers which had similar $\delta^{13}C$ signatures differed in their $\delta^{15}N$ signatures and vice versa. For example, the four sampled *Microtermes* species all differed in their $\delta^{13}C$ signatures and the dominant mound builder, *Macrotermes bellicosus*, had lower $\delta^{15}N$ values than all other fungus-growers. Similarly, coexisting grass-feeding *Trinervitermes* species were separated along the $\delta^{13}C$ and $\delta^{13}N$ axis: *T. oeconomus*, which had a very broad range in its $\delta^{13}C$ spectrum, had much higher $\delta^{13}N$ values than its congeners, whereas the three other species clearly differed in their $\delta^{13}C$ signatures. This supports former studies that *Trinervitermes* species do have differing feeding preferences and behaviour, each species selecting a different set of grasses (Sands, 1961).

This fine-scaled niche differentiation of closely related species has been observed in other taxa as well. For example, oribatid and mesostigmatid mite species, a diverse group of soil microarthropods, have been shown to occupy different trophic niches and closely related taxa often had distinct isotope ratios suggesting that trophic niche partitioning facilitates coexistence of morphologically similar species (Schneider et al. 2004; Klarner et al. 2013). These studies for the first time documented strong trophic niche differentiation in decomposer microarthropods using stable isotope signatures, which was not expected beforehand, and showed that fine-scaled niche differentiation significantly contributes to the high species diversity in these soil animals, which seems to be the case for soil living termite species as well.

Analysis of phylogenetic patterns of feeding habits using the true phylogeny of the sampled savannah termites (Chapter 2) revealed that the more related the species are, the

more similar their diet appears to be. This was true for both $\delta^{15}N$ and $\delta^{13}C$ signatures. Phylogenetic clustering at the within genera and within subfamily level partly reflects the 'classical' food niche differentiation into grass-feeders and fungus-growers. At the between subfamily level there was phylogenetic overdispersion, which is in line with species from different subfamilies being less closely related and therefore occupying different niches along the humification gradient. This shows that feeding habits are phylogenetically conserved in termites. Nevertheless, our findings revealed that there are fine-tuned niche differences between closely related species.

It may be interesting to investigate if the symbiotic fungus *Termitomyces* plays a role in mediating such niche differentiation in closely related species, at least for the fungus-growers. *Termitomyces* is involved in the degradation of harvested plant material (C3 and C4 plants) (Poulsen et al. 2014; Nobre et al. 2010) to make it digestible for the termites. Studies have shown that different termite species can have distinct *Termitomyces* symbionts (Aanen et al. 2002), which may explain why most of our sampled fungus-growers had different $\delta^{13}C$ signatures. The fungal symbionts may contribute to the observed fine-tuned niche differentiation between coexisting savannah termites.

Comparison of West African and Southern African termite communities

Our study in southern Africa (Chapter 4), which we conducted in Namibia, showed quite interesting differences to our study in Togo, West Africa (Chapter 2). First, species richness was considerably lower in the sampled regions in Namibia than in the study regions in Togo, with 11 identified species in Namibia compared to 22 species in the savannah and 33 species in the forest in Togo. This indicates that there seems to be a 'species richness' - gradient from desert/arid regions to tropical savannahs to tropical forests, also indicated in other studies (Hawkins et al. 2003; Eggleton et al. 1994; Davies et al. 2003). Second, species composition differs between the two studied regions. In Namibia, communities consisted more of grass-

feeding *Trinervitermes* species as well as members of the lower termites, which were completely missing in the West African savannah and only little represented in the forest. *Trinervitermes* sp. are known feeding specialists, as they only consume a variety of grasses (Chapter 3), which occur more frequently in the dry habitats in Namibia with little other vegetation, making them a more dominant group here. Interestingly, the open savannah habitats we sampled in Togo, which had little vegetation cover and were therefore abundant in grasses, harbored many *Trinervitermes* species (Chapter 1), similar to the dry habitats in Namibia. We did not expect identical species composition between Togo and Namibia due to harsher environmental conditions and biogeography. The climate is much more arid in Namibia compared to West Africa, especially the Namib Desert, and occurring termite species have probably adapted to these conditions. Particularly the sampled lower termites are known to merely occur in these more arid regions, namely the Hodotermitidae and also *Psammotermes* sp., which is known as a 'desert'-species (Chapter 4). Strikingly, our results further showed that far more Macrotermitinae occurred in Togo than in Namibia. In Namibia we only sampled two members of the Macrotermitinae. In contrast, we sampled nine Macrotermitinae in the savannah and 11 in the tropical forest in Togo, showing that fungus-growers dominate in West African termite communities (Chapter 2) and thereby confirming previous studies as well (Hausberger et al. 2011; Hausberger & Korb 2015).

We could show that community structure along the climatic gradient studied in Namibia differed between the north and the south, although our results could not confirm that the analysed environmental variable ‘precipitation’ has a major influence on termite community structure (Chapter 4). This could be due to a small sampling size and other factors influencing community structure, which compensate for the low rainfall in the arid regions. Another thought might be that rainfall is much more unpredictable in the desert regions of southern Africa than in West Africa, with relatively constant dry and rainy seasons. Termite species may have adapted to these environmental conditions differently in both regions, with

species communities in Namibia therefore showing a more random pattern (Chapter 4) than communities in West Africa (Chapter 2).

Conclusion

We could reliably identify a total of 45 termite species in the sampled region of West Africa, covering the two main ecosystems here, savannah and forest, and 11 species in southern Africa. Anthropogenic disturbance was detected as a major influence to termite communities in West Africa, as it seems to select for a subset of termite species, which are common crop pests. We could also show that disturbance is associated with environmental filtering, which was obvious even after 10-12 years of regeneration after active agricultural land-use. Additionally, vegetation type had an influence as well, which it did not have in natural habitats. Interestingly, regardless of ecosystem type or disturbance gradient, local species richness always had a mean of around 10 species, which shows that deterministic processes do seem to structure species communities locally and the niche theory can be applied in West African termite communities. West African forests harbored the most species, followed by the savannah and then the arid regions in Namibia harboring far less species. In the southern African termite communities more random patterns were detected as well as deterministic processes, showing that here both theories have to be applied to explain termite community assembly. Stable isotope analyses contributed to answering the question how so many closely related termite species can coexist locally. Our findings imply that species similar with regard to $\delta^{15}N$ values generally differed in $\delta^{13}C$ values, and vice versa. We were able to distinguish fungus-growing and grass-feeding termite species from each other by $\delta^{15}N$ and / or $\delta^{13}C$ signatures, reflecting distinct feeding habits of coexisting species.

Outlook

This study can serve as a basis for future research in African termite community structure, which relies on proper and exact species identification. As human disturbance and destruction of natural habitats is increasing globally, more studies spanning more regions are advisable to derive general patterns and conclusions on termite community structure and assembly, to establish suitable conservation schemes.

Summary

In this study we wanted to investigate the community ecology of African termites and uncover possible mechanisms structuring these species communities. Termites are important ecosystem engineers, crucial for the maintenance of tropical biodiversity and ecosystem functioning, therefore we wanted to show how anthropogenic disturbance influences these termite communities. Using a cross-sectional approach, we studied termite community composition along a disturbance gradient from fields to 12-year-old fallows in a West African savannah. We could show that disturbance was associated with environmental filtering of termites from the regional species pool, maybe via its effect on vegetation type. The most heavily disturbed sites were characterized by a subset of termite species which are well-known pests of crop. This supports a model in which strong anthropogenic disturbance selects for termite pest species.

Additionally, we comparatively studied termite communities in the two major West African ecosystems, savannah and forest, both under natural settings and along disturbance gradients. Overall we found 33 species in the forest and 22 in the savannah. However, alpha diversity per site did not differ between both ecosystems with on average around ten species. For both ecosystems, species diversity did not decrease along the studied disturbance gradient but encounter rates did. In general, we found little evidence for strong community structuring mechanisms such as environmental filtering or interspecific competition in the natural habitats. Most local communities did not differ significantly from random assemblages of the regional species pool. Interestingly, only the disturbed sites in the savannah showed some sign of phylogenetic structuring, the teak plantation sites did not.

By using stable isotope analysis we could investigate how so many termite species with very similar feeding niches can coexist in an African savannah. We discovered that closely related species either differed in their $\delta^{15}N$ and /or $\delta^{13}C$ signatures, providing support

for our hypothesis that fine-scaled differentiation of the feeding niche exists between termites in the studied area that formerly have been classified as feeding on the same dead plant material. We were able to distinguish feeding groups with stable isotope analysis, as each feeding group had a specific $\delta^{15}N$ and $\delta^{13}C$ signature, supporting the classification of Donovan et al. (2001).

Comparatively, we tested whether southern African termite communities show signs of environmental filtering and / or competition along a rainfall gradient in Namibia. There was a regional species pool of 11 species and we found no evidence for phylogenetic structuring at the local scale. Rather, our results suggest that the assembly of the studied termite communities has as strong random component on the local scale, but that species composition changes along the climatic gradient. Interestingly, species richness and species composition was different to West African termite communities.

Zusammenfassung

Zielstellung dieser Arbeit war es die Gemeinschaftsökologie afrikanischer Termiten zu untersuchen, um mögliche Mechanismen aufzudecken, die diese Artengemeinschaften strukturieren. Termiten sind wichtige Ökosystem-Ingenieure, die für die Instandhaltung und das Funktionieren tropischer Biodiversität und Ökosysteme entscheidend sind. Deshalb wollten wir in dieser Arbeit zusätzlich untersuchen, wie anthropogene Störung Termitengemeinschaften beeinflusst. Wir analysierten die Zusammensetzung von Termitengemeinschaften entlang eines Störungsgradienten von Feldern bis zu 12 Jahre alten Brachen in einer westafrikanischen Savanne, indem wir einen Querschnittsansatz nutzten. Wir konnten zeigen, dass Störung mit Umwelt-Filterung von Termiten des regionalen Artenpools assoziiert war, möglicherweise durch dessen Effekt auf den Vegetationstyp. Die am stärksten gestörten Flächen zeichneten sich durch eine Untergruppe an Arten aus, welche bekannte Ernteschädlinge sind. Dies unterstützt ein Modell, in dem starke anthropogene Störung für Termiten selektiert, die Schädlinge sind.

Weiterhin haben wir die Gemeinschaftsstruktur der zwei bedeutenden westafrikanischen Ökosysteme, Savanne und tropischer Wald, vergleichend studiert. Einmal unter natürlichen Bedingungen sowie entlang eines Störungsgradienten. Insgesamt haben wir 33 Arten im Wald und 22 Arten in der Savanne identifiziert, jedoch hat sich die alpha-Diversität je Fläche mit im Durchschnitt zehn Arten zwischen den beiden Ökosystemen nicht unterschieden. In beiden Ökosystemen ist die Artendiversität entlang des Störungsgradienten nicht gefallen, jedoch ist die Begegnungsrate gesunken. Im Allgemeinen haben wir wenige Beweise für starke gemeinschaftsstrukturierende Mechanismen wie Umwelt-Filterung oder interartliche Konkurrenz in den natürlichen Habitaten gefunden. Die meisten lokalen Gemeinschaften unterschieden sich nicht signifikant von zufällig generierten Gemeinschaften

des regionalen Artenpools. Interessanterweise zeigten nur die gestörten Flächen in der Savanne leichte Anzeichen für phylogenetische Strukturierung, die im tropischen Wald nicht.

Durch stabile Isotopenanalysen konnten wir untersuchen, warum so viele Termitenarten zusammen vorkommen, die sehr ähnliche Nahrungsnischen besetzen. Es zeigte sich, dass sich nah verwandte Arten entweder in ihren $\delta^{15}N$ und /oder $\delta^{13}C$ Signaturen unterscheiden. Dies unterstützt unsere Hypothese, dass es eine feingradige Differenzierung von Nahrungsnischen zwischen den Termiten im untersuchten Gebiet gibt, obwohl diese Termiten zuvor alle als zu einer Nahrungsnische zugehörig beschrieben wurden. Die Nahrungsgruppen konnten mittels stabiler Isotopenanalyse voneinander unterschieden werden, da jede Gruppe eine bestimmte $\delta^{15}N$ und $\delta^{13}C$ Signatur aufwies, was die Klassifikation nach Donovan et al. (2001) unterstützt.

Vergleichende Untersuchungen von Termitengemeinschaften des südlichen Afrikas entlang eines Niederschlagsgradienten in Namibia zeigten einen regionalen Artenpool von 11 Arten. Es gab keine lokale phylogenetische Strukturierung, jedoch zeigten unsere Ergebnisse, dass die Zusammensetzung der untersuchten Termitengemeinschaften lokal eine starke zufällige Komponente hat, diese Artenzusammensetzung sich aber entlang des Niederschlagsgradienten verändert. Im Vergleich zu den westafrikanischen Termitengemeinschaften unterschieden sie sich in Artenreichtum und Artenzusammensetzung.

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Appendix

Appendix 1

Chapter 1 Supplementary Material

Genetic and phylogenetic analyses

DNA was isolated from the head of single individuals using a modified cetyltrimethyl ammonium bromide (CTAB)-protocol as described in Fuchs *et al.* (2003).

The gene *COII* was amplified using the primer pair Modified A-tLeu and B-tLys, *COI* was amplified using the primers HCO and LCO and the ribosomal gene *12S* was amplified using 12Sai_for/12Sbi_rev (Table S1). PCR were performed with the following cycle conditions for *COI* and *COII*: 94°C for 2 min; and then 35 cycles of 94°C for 1 min, 50°C for 1 min, 72°C for 1 min 15 sec and a final elongation step of 72°C for 7 min. For *12S* the cycle conditions were the same except for the annealing temperature, which was 55°C. PCR amplifications were purified using poly ethylene glycol (PEG) mix and sequencing was performed using BigDye Terminator v3.1 (concentration of 2:1, Applied Biosystems) with cycle sequencing conditions of 96°C for 1 min, then 30 cycles of 96°C for 30 sec, 50°C for 15 sec, and 60°C for 4 min on an ABI 3500 Genetic Analyser (Applied Biosystems).

To identify species, sequences for each gene were aligned separately using BioEdit (Hall 1999) and checked visually for missing or false bases at the nucleotide- as well as the amino acid level. Analyses were performed for each gene as in Hausberger et al. (2011). In short, we inferred phylogenies using (i) a Bayesian method with MrBayes (Huelsenbeck and Ronquist 2003) (10^7 generations, 25% discarded as burn-in), (ii) a maximum parsimony analysis (MP) with PAUP 4.0 (Swofford 1998) (heuristic search with 100 random addition replicates from random starting trees with TBR (tree bisection reconnection)), and (iii) a maximum-likelihood

(ML) analysis using RaxML (Stamatakis 2006). Nucleotide substitution models were selected with MrModeltest 2.3 (Nylander 2004). Posterior probabilities (Bayesian inference), decay values (MP) and bootstrap values (ML) were calculated to assess branch support.

Table S1. Primers with sequences and annealing temperatures for the genes *COI, COII, 12S*.

Gene	Primer	Sequence 5‘-3‘	Annealing temperature	Reference
COI	HCO	TAA ACT TCA GGG TGA CCA AAA AAT CA	50°C	Folmer et al. 1994
	LCO	GGT CAA CAA ATC ATA AAG ATA TTG G	50°C	Folmer et al. 1994
COII	Modified A-tLeu	CAG ATA AGT GCA TTG GAT TT	50°C	Inward et al. 2007
	B-tLys	GTT TAA GAG ACC AGT ACT TG	50°C	Inward et al. 2007
12S	12Sai_for	AAA CTA GGA TTA GAT ACC CTA TTA T	55°C	Simon et al. 1994
	12Sbi_rev	AAG AGC GAC GGG CGA TGT GT	55°C	Simon et al. 1994

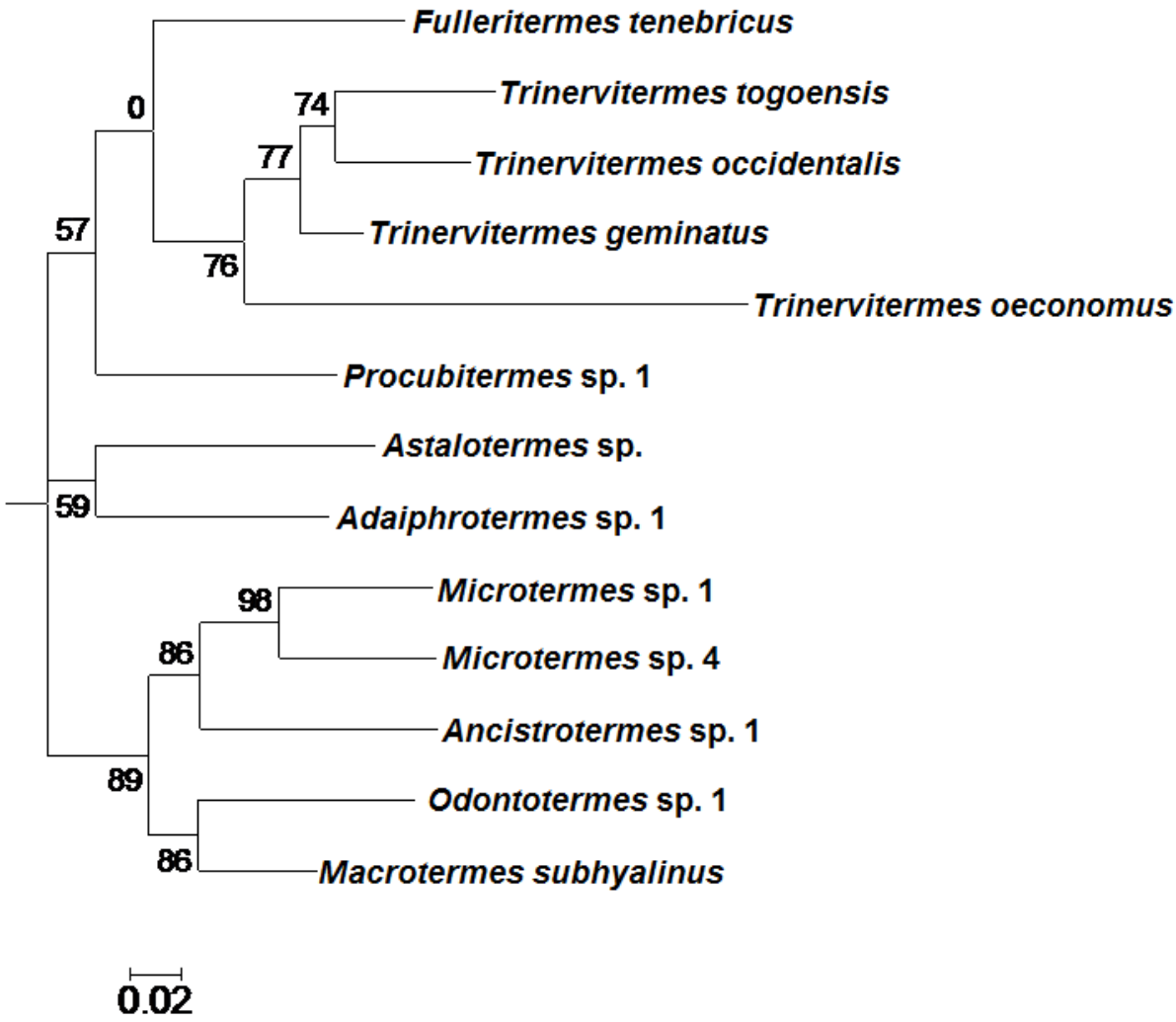

Figure S1. Bayesian phylogeny based on the gene cytochrome oxidase I using MrBayes v3.1.2. Analysis was done with 10^7 generations, number of chains=4, sample frequency=1000 and a finalizing burn-in of 2500. Due to primer binding problems during amplification, not all species are included. Numbers on nodes are the posterior probabilities calculated to assess branch support.

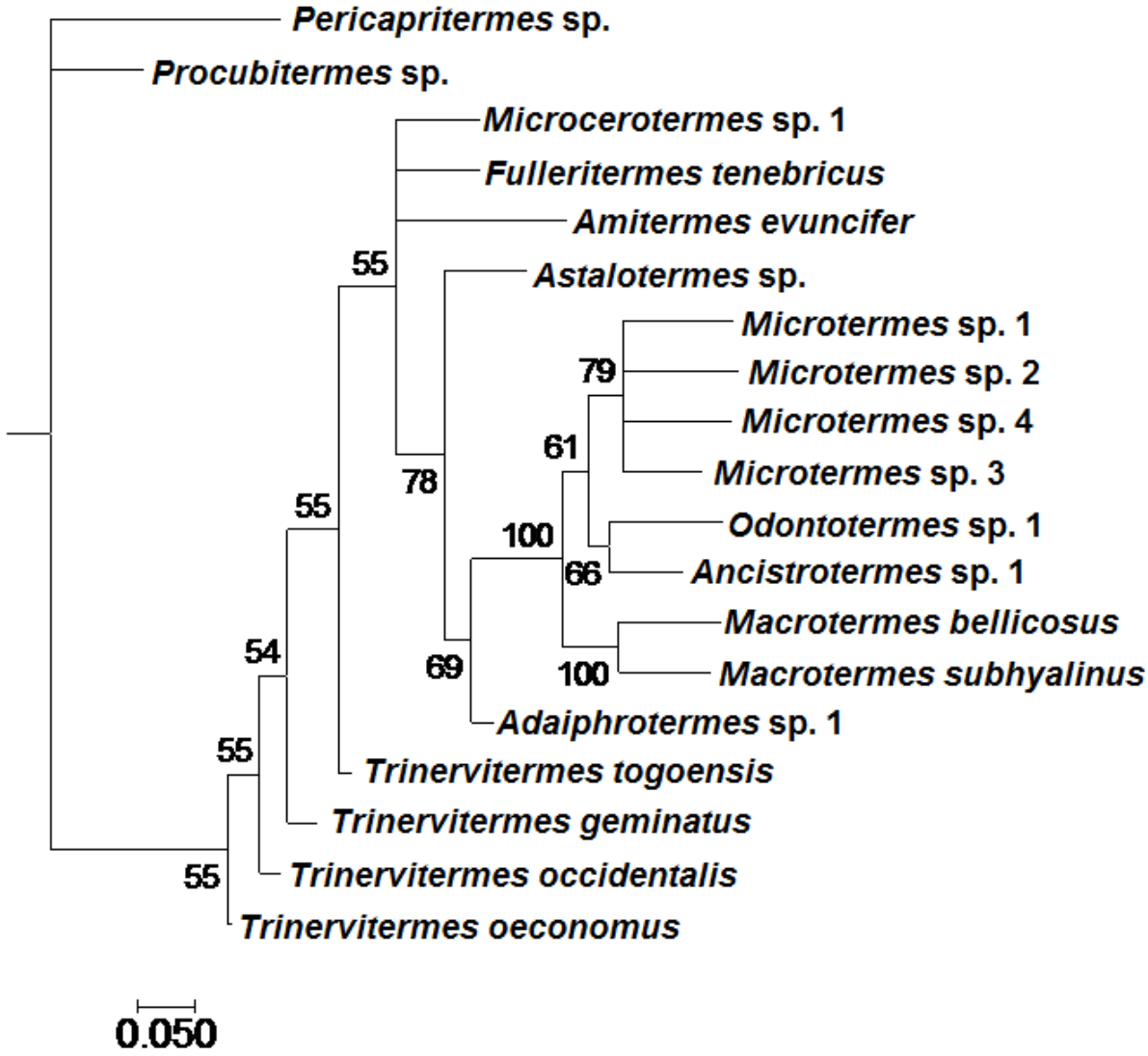

Figure S2. Bayesian phylogeny based on the ribosomal gene 12S using MrBayes v3.1.2. Analysis was done with 10^7 generations, number of chains=4, sample frequency=1000 and a finalizing burn-in of 2500. Due to primer binding problems during amplification, not all species are included. Numbers on nodes are the posterior probabilities calculated to assess branch support.

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Appendix 2

Chapter 2 Supplementary Material

Genetic and phylogenetic analyses

The gene *COII* was amplified using the primer pair Modified A-tLeu and B-tLys, *COI* was amplified using the primers HCO and LCO and the ribosomal gene *12S* was amplified using 12Sai_for/12Sbi_rev (Table S1). PCR was performed with the following cycle conditions for *COI* and *COII*: 94°C for 2 min; 35 cycles of 94°C for 1 min, 50°C for 1 min, 72°C for 1 min 15 sec and a final elongation step of 72°C for 7 min. For *12S* the cycle conditions were the same except for the annealing temperature, which was 55°C. PCR amplifications were purified using poly ethylene glycol (PEG) mix and sequencing was performed using BigDye Terminator v3.1 (concentration of 2:1, Applied Biosystems) with cycle sequencing conditions of 96°C for 1 min, then 30 cycles of 96°C for 30 sec, 50°C for 15 sec, and 60°C for 4 min on an ABI 3500 Genetic Analyser (Applied Biosystems).

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	LCO	GGT CAA CAA ATC ATA AAG ATA TTG G	50°C	Folmer et al. 1994
COII	Modified A-tLeu	CAG ATA AGT GCA TTG GAT TT	50°C	Inward et al. 2007
	B-tLys	GTT TAA GAG ACC AGT ACT TG	50°C	Inward et al. 2007
12S	12Sai_for	AAA CTA GGA TTA GAT ACC CTA TTA T	55°C	Simon et al. 1994
	12Sbi_rev	AAG AGC GAC GGG CGA TGT GT	55°C	Simon et al. 1994

Table S2. ß-diversity and phylogenetic ß-diversity indices for all study plot pairs in the natural and disturbed habitat regimes in the savannah.

Plot 1	Plot 2	Bray-Curtis	PhyloSor
L	M	0.677	0.762
L	N	0.451	0.718
L	O	0.193	0.605
L	P	0.569	0.672
L	R	0.643	0.730
L	S	0.644	0.687
L	T	0.441	0.722
L	U	0.596	0.868
L	W	0.122	0.387
L	2	0.391	0.887
L	3	0.367	0.758
L	5	0.115	0.496
L	B	0.503	0.764
L	C	0.275	0.741
L	D	0.591	0.726
L	E	0.475	0.697
L	F	0.562	0.798
L	G	0.496	0.779
L	H	0.491	0.706
L	I	0.36	0.672
L	K	0.569	0.811
L	Q	0.5	0.838
L	X	0.463	0.763
L	Y	0.512	0.720
L	Z	0.483	0.870
L	1	0.126	0.496
M	N	0.424	0.842
M	O	0.225	0.738
M	P	0.566	0.729
M	R	0.613	0.951

M	S	0.417	0.812
M	T	0.316	0.775
M	U	0.507	0.621
M	W	0.172	0.588
M	2	0.267	0.748
M	3	0.264	0.821
M	5	0.101	0.503
M	B	0.473	0.893
M	C	0.28	0.900
M	D	0.393	0.872
M	E	0.336	0.833
M	F	0.322	0.865
M	G	0.279	0.769
M	H	0.272	0.763
M	I	0.474	0.729
M	K	0.346	0.718
M	Q	0.416	0.897
M	X	0.382	0.922
M	Y	0.41	0.817
M	Z	0.342	0.775
M	1	0.129	0.503
N	O	0.288	0.771
N	P	0.427	0.666
N	R	0.453	0.800
N	S	0.429	0.758
N	T	0.529	0.918
N	U	0.542	0.681
N	W	0.268	0.627
N	2	0.385	0.722
N	3	0.427	0.771
N	5	0.159	0.533
N	B	0.41	0.845
N	C	0.202	0.750
N	D	0.593	0.844

N	E	0.477	0.805
N	F	0.393	0.818
N	G	0.33	0.621
N	H	0.389	0.708
N	I	0.303	0.666
N	K	0.542	0.780
N	Q	0.6	0.749
N	X	0.476	0.775
N	Y	0.527	0.662
N	Z	0.349	0.729
N	1	0.171	0.533
O	P	0.169	0.570
O	R	0.362	0.793
O	S	0.22	0.756
O	T	0.303	0.803
O	U	0.413	0.736
O	W	0.6	0.643
O	2	0.653	0.767
O	3	0.39	0.667
O	5	0.473	0.712
O	B	0.375	0.733
O	C	0.321	0.749
O	D	0.306	0.833
O	E	0.321	0.931
O	F	0.335	0.712
O	G	0.373	0.778
O	H	0.348	0.712
O	I	0.073	0.570
O	K	0.302	0.822
O	Q	0.248	0.716
O	X	0.331	0.771
O	Y	0.239	0.828
O	Z	0.357	0.692
O	1	0.514	0.712

P	R	0.496	0.688
P	S	0.549	0.798
P	T	0.404	0.677
P	U	0.509	0.643
P	W	0.212	0.175
P	2	0.252	0.576
P	3	0.366	0.724
P	5	0.042	0.145
P	B	0.452	0.733
P	C	0.413	0.703
P	D	0.523	0.687
P	E	0.379	0.589
P	F	0.487	0.780
P	G	0.388	0.675
P	H	0.329	0.822
P	I	0.63	1.0
P	K	0.408	0.628
P	Q	0.468	0.632
P	X	0.451	0.734
P	Y	0.469	0.726
P	Z	0.43	0.682
P	1	0.122	0.145
R	S	0.557	0.874
R	T	0.5	0.832
R	U	0.593	0.676
R	W	0.311	0.666
R	2	0.394	0.794
R	3	0.513	0.879
R	5	0.222	0.574
R	B	0.568	0.947
R	C	0.331	0.951
R	D	0.588	0.920
R	E	0.556	0.880
R	F	0.493	0.919

R	G	0.527	0.824
R	H	0.527	0.826
R	I	0.269	0.688
R	K	0.537	0.769
R	Q	0.481	0.857
R	X	0.561	0.971
R	Y	0.481	0.780
R	Z	0.516	0.829
R	1	0.213	0.574
S	T	0.593	0.797
S	U	0.488	0.749
S	W	0.177	0.461
S	2	0.3	0.676
S	3	0.462	0.848
S	5	0.058	0.389
S	B	0.586	0.926
S	C	0.281	0.820
S	D	0.68	0.796
S	E	0.596	0.758
S	F	0.625	0.894
S	G	0.654	0.790
S	H	0.682	0.943
S	I	0.341	0.798
S	K	0.518	0.733
S	Q	0.535	0.717
S	X	0.479	0.846
S	Y	0.654	0.738
S	Z	0.471	0.796
S	1	0.128	0.389
T	U	0.61	0.768
T	W	0.321	0.680
T	2	0.319	0.798
T	3	0.44	0.869
T	5	0.197	0.587

T	B	0.636	0.875
T	C	0.248	0.843
T	D	0.661	0.924
T	E	0.557	0.833
T	F	0.589	0.909
T	G	0.704	0.720
T	H	0.642	0.816
T	I	0.28	0.677
T	K	0.446	0.858
T	Q	0.346	0.693
T	X	0.475	0.865
T	Y	0.64	0.671
T	Z	0.483	0.820
T	1	0.161	0.587
U	W	0.338	0.455
U	2	0.462	0.920
U	3	0.474	0.700
U	5	0.331	0.552
U	B	0.615	0.707
U	C	0.304	0.687
U	D	0.5	0.769
U	E	0.394	0.739
U	F	0.517	0.741
U	G	0.523	0.809
U	H	0.505	0.766
U	I	0.343	0.643
U	K	0.504	0.848
U	Q	0.422	0.702
U	X	0.509	0.709
U	Y	0.523	0.673
U	Z	0.544	0.813
U	1	0.212	0.552
W	2	0.496	0.613
W	3	0.442	0.586

W	5	0.53	0.833
W	B	0.301	0.582
W	C	0.446	0.659
W	D	0.345	0.728
W	E	0.462	0.691
W	F	0.355	0.561
W	G	0.333	0.520
W	H	0.257	0.452
W	I	0.063	0.175
W	K	0.256	0.568
W	Q	0.242	0.541
W	X	0.374	0.644
W	Y	0.233	0.438
W	Z	0.365	0.517
W	1	0.426	0.833
2	3	0.577	0.738
2	5	0.5	0.683
2	B	0.275	0.744
2	C	0.452	0.803
2	D	0.444	0.871
2	E	0.419	0.840
2	F	0.446	0.774
2	G	0.441	0.835
2	H	0.352	0.692
2	I	0.118	0.576
2	K	0.515	0.868
2	Q	0.453	0.815
2	X	0.481	0.821
2	Y	0.362	0.711
2	Z	0.557	0.839
2	1	0.568	0.683
3	5	0.337	0.500
3	B	0.339	0.927
3	C	0.46	0.931

3	D	0.591	0.862
3	E	0.547	0.768
3	F	0.588	0.962
3	G	0.612	0.798
3	H	0.532	0.903
3	I	0.137	0.724
3	K	0.485	0.797
3	Q	0.519	0.762
3	X	0.571	0.912
3	Y	0.408	0.740
3	Z	0.645	0.895
3	1	0.34	0.500
5	B	0.19	0.497
5	C	0.302	0.568
5	D	0.198	0.635
5	E	0.222	0.749
5	F	0.227	0.482
5	G	0.306	0.617
5	H	0.217	0.382
5	I	0.023	0.145
5	K	0.328	0.736
5	Q	0.2	0.638
5	X	0.26	0.557
5	Y	0.108	0.540
5	Z	0.358	0.615
5	1	0.6	1.0
B	C	0.262	0.896
B	D	0.538	0.868
B	E	0.453	0.829
B	F	0.534	0.968
B	G	0.571	0.765
B	H	0.579	0.874
B	I	0.365	0.733
B	K	0.441	0.803

B	Q	0.353	0.798
B	X	0.48	0.919
B	Y	0.571	0.715
B	Z	0.474	0.870
B	1	0.116	0.497
C	D	0.333	0.929
C	E	0.36	0.838
C	F	0.491	0.929
C	G	0.366	0.872
C	H	0.244	0.839
C	I	0.325	0.703
C	K	0.422	0.779
C	Q	0.347	0.811
C	X	0.633	0.981
C	Y	0.338	0.791
C	Z	0.496	0.840
C	1	0.304	0.568
D	E	0.772	0.911
D	F	0.64	0.899
D	G	0.692	0.813
D	H	0.682	0.813
D	I	0.304	0.687
D	K	0.642	0.853
D	Q	0.53	0.790
D	X	0.561	0.948
D	Y	0.654	0.772
D	Z	0.586	0.818
D	1	0.209	0.635
E	F	0.576	0.807
E	G	0.595	0.778
E	H	0.609	0.718
E	I	0.186	0.589
E	K	0.552	0.896
E	Q	0.489	0.806

E	X	0.479	0.858
E	Y	0.559	0.825
E	Z	0.528	0.783
E	1	0.238	0.749
F	G	0.696	0.801
F	H	0.569	0.912
F	I	0.309	0.780
F	K	0.5	0.833
F	Q	0.474	0.775
F	X	0.647	0.950
F	Y	0.563	0.754
F	Z	0.6	0.903
F	1	0.228	0.482
G	H	0.716	0.808
G	I	0.202	0.675
G	K	0.521	0.814
G	Q	0.43	0.849
G	X	0.497	0.856
G	Y	0.579	0.821
G	Z	0.661	0.876
G	1	0.258	0.617
H	I	0.2	0.822
H	K	0.5	0.750
H	Q	0.432	0.706
H	X	0.4	0.863
H	Y	0.632	0.792
H	Z	0.6	0.846
H	1	0.139	0.382
I	K	0.383	0.628
I	Q	0.294	0.632
I	X	0.387	0.734
I	Y	0.337	0.726
I	Z	0.286	0.682
I	1	0.029	0.145

K	Q	0.531	0.792
K	X	0.571	0.799
K	Y	0.471	0.765
K	Z	0.579	0.900
K	1	0.274	0.736
Q	X	0.484	0.833
Q	Y	0.452	0.819
Q	Z	0.568	0.882
Q	1	0.239	0.638
X	Y	0.55	0.815
X	Z	0.597	0.861
X	1	0.273	0.557
Y	Z	0.55	0.760
Y	1	0.147	0.540
Z	1	0.291	0.615

Table S3. ß-diversity and phylogenetic ß-diversity indices for all study plot pairs in the protected and disturbed habitat regimes in the forest ecosystem.

Plot 1	**Plot 2**	**Bray-Curtis**	**PhyloSor**
A	B	0.587	0.632
A	C	0.52	0.603
A	D	0.441	0.703
A	E	0.408	0.634
A	H	0.588	0.745
A	I	0.412	0.697
A	K	0.489	0.676
A	L	0.494	0.583
A	M	0.553	0.624
A	O	0.358	0.518
A	R	0.406	0.665
A	S	0.705	0.601
A	P	0.419	0.497
A	G	0.631	0.79
A	F	0.363	0.386
A	T	0.279	0.664
B	C	0.708	0.832

B	D	0.465	0.599
B	E	0.463	0.552
B	H	0.546	0.849
B	I	0.611	0.87
B	K	0.59	0.704
B	L	0.662	0.846
B	M	0.59	0.899
B	O	0.235	0.801
B	R	0.277	0.811
B	S	0.566	0.677
B	P	0.488	0.641
B	G	0.56	0.653
B	F	0.198	0.664
B	T	0.169	0.827
C	D	0.609	0.57
C	E	0.545	0.53
C	H	0.594	0.702
C	I	0.674	0.725
C	K	0.557	0.681
C	L	0.59	0.7
C	M	0.587	0.75
C	O	0.155	0.647
C	R	0.188	0.783
C	S	0.486	0.524
C	P	0.466	0.648
C	D	0.426	0.549
C	F	0.248	0.671
C	T	0.183	0.694
D	E	0.482	0.685
D	H	0.665	0.629
D	I	0.534	0.544
D	K	0.481	0.652
D	L	0.478	0.527
D	M	0.608	0.529
D	O	0.135	0.483
D	R	0.132	0.607
D	S	0.417	0.576
D	P	0.379	0.303
D	G	0.426	0.613
D	F	0.188	0.32
D	T	0.14	0.501
E	H	0.492	0.603
E	I	0.464	0.582
E	K	0.419	0.745
E	L	0.454	0.552
E	M	0.417	0.527
E	O	0.173	0.518
E	R	0.184	0.612
E	S	0.367	0.484
E	P	0.434	0.481
E	G	0.376	0.59

E	F	0.249	0.404
E	T	0.138	0.584
H	I	0.616	0.812
H	K	0.581	0.755
H	L	0.632	0.821
H	M	0.659	0.838
H	O	0.086	0.706
H	R	0.163	0.758
H	S	0.445	0.657
H	P	0.376	0.617
H	G	0.469	0.765
H	F	0.251	0.638
H	T	0.145	0.748
I	K	0.724	0.658
I	L	0.685	0.809
I	M	0.722	0.859
I	O	0.101	0.793
I	R	0.154	0.843
I	S	0.595	0.72
I	P	0.461	0.689
I	G	0.495	0.68
I	F	0.172	0.63
I	T	0.145	0.768
K	L	0.73	0.699
K	M	0.72	0.745
K	O	0.091	0.734
K	R	0.148	0.801
K	S	0.613	0.607
K	P	0.425	0.51
K	G	0.498	0.594
K	F	0.2	0.549
K	T	0.152	0.702
L	M	0.781	0.836
L	O	0.114	0.704
L	R	0.191	0.756
L	S	0.588	0.842
L	P	0.461	0.615
L	G	0.536	0.612
L	F	0.265	0.844
L	T	0.253	0.746
M	O	0.162	0.851
M	R	0.256	0.884
M	S	0.678	0.669
M	P	0.442	0.632
M	G	0.577	0.628
M	F	0.278	0.654
M	T	0.269	0.89
O	R	0.58	0.857
O	S	0.384	0.662
O	P	0.336	0.628
O	G	0.687	0.594

O	F	0.118	0.52
O	T	0.667	0.79
R	S	0.612	0.671
R	P	0.132	0.639
R	G	0.445	0.634
R	F	0.181	0.583
R	T	0.575	0.796
S	P	0.204	0.562
S	G	0.335	0.68
S	F	0.18	0.655
S	T	0.424	0.595
P	G	0.469	0.671
P	F	0.268	0.725
P	T	0.119	0.678
G	F	0.178	0.468
G	T	0.504	0.671
F	T	0.111	0.5749

Appendix 3

Chapter 4 Supplementary Material

Genetic and phylogenetic analyses

DNA was isolated from the head of single individuals using a modified cetyltrimethyl ammonium bromide (CTAB)-protocol as described in Fuchs *et al.* (2003).

The gene *COII* was amplified using the primer pair Modified A-tLeu and B-tLys, *COI* was amplified using the primers HCO and LCO and the ribosomal gene *12S* was amplified using 12Sai_for/12Sbi_rev (Table S1). PCR were performed with the following cycle conditions for *COI* and *COII*: 94°C for 2 min; and then 35 cycles of 94°C for 1 min, 50°C for 1 min, 72°C for 1 min 15 sec and a final elongation step of 72°C for 7 min. For *12S* the cycle conditions were the same except for the annealing temperature, which was 55°C. PCR amplifications were purified using poly ethylene glycol (PEG) mix and sequencing was performed using BigDye Terminator v3.1 (concentration of 2:1, Applied Biosystems) with cycle sequencing conditions of 96°C for 1 min, then 30 cycles of 96°C for 30 sec, 50°C for 15 sec, and 60°C for 4 min on an ABI 3500 Genetic Analyser (Applied Biosystems).

To identify species, sequences for each gene were aligned separately using BioEdit (Hall 1999) and checked visually for missing or false bases at the nucleotide- as well as the amino acid level. Analyses were performed for each gene as in Hausberger *et al*. (2011). In short, we inferred phylogenies using (i) a Bayesian method with MrBayes (Huelsenbeck and Ronquist 2003) (10^7 generations, 25% discarded as burn-in), (ii) a maximum parsimony analysis (MP) with PAUP 4.0 (Swofford 1998) (heuristic search with 100 random addition replicates from random starting trees with TBR (tree bisection reconnection)), and (iii) a maximum-likelihood (ML) analysis using RaxML (Stamatakis 2006). Nucleotide substitution models were selected with MrModeltest 2.3 (Nylander 2004). Posterior probabilities (Bayesian inference), decay values (MP) and bootstrap values (ML) were calculated to assess branch support.

Table S1. Primers and primer sequences with annealing temperatures for the genes *COI, COII, 12S*.

Gene	Primer	Sequence 5‘-3‘	Annealing temperature	Reference
COI	HCO	TAA ACT TCA GGG TGA CCA AAA AAT CA	50°C	Folmer et al. 1994
	LCO	GGT CAA CAA ATC ATA AAG ATA TTG G	50°C	Folmer et al. 1994
COII	Modified A-tLeu	CAG ATA AGT GCA TTG GAT TT	50°C	Inward et al. 2007
	B-tLys	GTT TAA GAG ACC AGT ACT TG	50°C	Inward et al. 2007
12S	12Sai_for	AAA CTA GGA TTA GAT ACC CTA TTA T	55°C	Simon et al. 1994
	12Sbi_rev	AAG AGC GAC GGG CGA TGT GT	55°C	Simon et al. 1994

Table S2. GenBank accession numbers of *COI, COII* and *12S* sequences for the analyzed specimens and potential species as shown in the phylogenetic trees.

species	sample ID	*COI*	*COII*	*12S*
Allodontotermes sp.	P_T7_Du1	MF555694	MF555600	MF554681
Allodontotermes sp.	Oa2_R4_4	-	MF555606	-
Allodontotermes sp.	*Oa1_T2_S1*	-	MF555608	-
Allodontotermes sp.	Pau_R3_1	-	MF555610	-
Allodontotermes sp.	Sch_R4_2	-	MF555612	-
Allodontotermes sp.	Tir2_R4_3	-	MF555613	-
Allodontotermes sp.	Tir2_T10_S2	-	MF555614	-
Amitermes sp.	Sch_S3_1	MF555695	MF555615	-
Amitermes sp.	Noa_T5_S2	-	MF555652	MF554682
Angulitermes sp.	Noa_T3_S2	MF555689	MF555617	MF554672
Hodotermes mossambicus	Ti3_X9M	MF555661	MF555644	
Hodotermes mossambicus	Tri2_X4_M	-	-	MF554678
Hodotermes mossambicus	Ga2_X1_1	MF555676	MF555645	
Hodotermes mossambicus	Ga2_X2M	MF555688	MF555646	MF554670
Microcerotermes sp.	Pa_T6_S2	MF555693	MF555616	MF554671
Microtermes sp.	P_T1_W1	MF555683	MF555595	MF554659
Microtermes sp.	P_T2_W1	MF555684	MF555596	MF554660
Microtermes sp.	P_T6_S1	-	MF555597	MF554661
Microtermes sp.	P_T9_W2	MF555687	MF555598	MF554662
Microtermes sp.	Noa_T6_W1	-	MF555599	-
Microtermes sp.	P_T8_S1	MF555685	MF555601	MF554663
Microtermes sp.	P_T9_W1	MF555686	MF555602	MF554664
Microtermes sp.	Noa_T10_S1	MF555680	MF555603	MF554665

Microtermes sp.	Noa_T2_S1	-	MF555604	-
Microtermes sp.	Noa_T3_S1	-	MF555605	-
Microtermes sp.	Noa_T9_W1	MF555679	MF555607	MF554683
Microtermes sp.	Pa_T9_W4	-	MF555609	-
Microtermes sp.	Pau_R5 _1	MF555692	MF555611	MF554679
Microtermes sp.	Noa_T10_W1	MF555681	MF555649	MF554684
Microtermes sp.	Noa_T10_W2	MF555682	-	MF554666
Microtermes sp.	Noa_T10_W3	-	MF555650	-
Microtermes sp.	Noa_T5_S1	-	MF555651	-
Microtermes sp.	Noa_T6_S2	-	MF555653	-
Promirotermes sp.	N43	MF555660	MF555655	MF554673
Psammotermes sp.	Ti3_X5M	-	MF555641	MF554675
Psammotermes sp.	Ti_Ro1_1	-	MF555642	-
Psammotermes sp.	Ti2_T6_1St	MF555696	MF555647	MF554676
Trinervitermes bettonianus	P15	MF555657	MF555627	MF554656
Trinervitermes bettonianus	P19	MF555658	MF555628	MF554657
Trinervitermes bettonianus	P20	MF555659	MF555629	MF554658
Trinervitermes bettonianus	P11	MF555666	MF555648	MF554674
Trinervitermes sp.	Ti1_X1M	MF555670	MF555635	-
Trinervitermes sp.	Tri2_X1_M	-	-	MF554677
Trinervitermes sp.	Ti2_X12M	MF555674	MF555637	-
Trinervitermes sp.	Ti2_X9M	MF555675	MF555643	-
Trinervitermes trinervoides	Noa_T8_S1	MF555690	MF555618	MF554680
Trinervitermes trinervoides	Oa1_1	MF555662	MF555619	-
Trinervitermes trinervoides	Oa1_42	MF555668	MF555620	-
Trinervitermes trinervoides	Oa1_57	MF555669	MF555621	-
Trinervitermes trinervoides	Oa2_10	MF555672	MF555622	-
Trinervitermes trinervoides	Oa2_34	MF555663	MF555623	-
Trinervitermes trinervoides	Oa2_80	MF555691	MF555624	MF554669
Trinervitermes trinervoides	P_S10_2	MF555671	MF555625	-
Trinervitermes trinervoides	Sch_T10_S2	MF555656	MF555626	-
Trinervitermes trinervoides	N2	MF555664	MF555630	-
Trinervitermes trinervoides	N11	MF555665	MF555631	-
Trinervitermes trinervoides	Sch16	MF555667	MF555632	-
Trinervitermes trinervoides	Sch60	-	MF555633	-
Trinervitermes trinervoides	Sch77	MF555673	MF555634	MF554668
Trinervitermes trinervoides	Ti1_S9_1	-	MF555636	-
Trinervitermes trinervoides	Ti2_X14M	-	MF555638	-
Trinervitermes trinervoides	Ti2_X18M	-	MF555639	-
Trinervitermes trinervoides	Ti2_X1M	-	MF555640	-
Trinervitermes trinervoides	Oa1_S10_2	MF555677	MF555654	MF554667

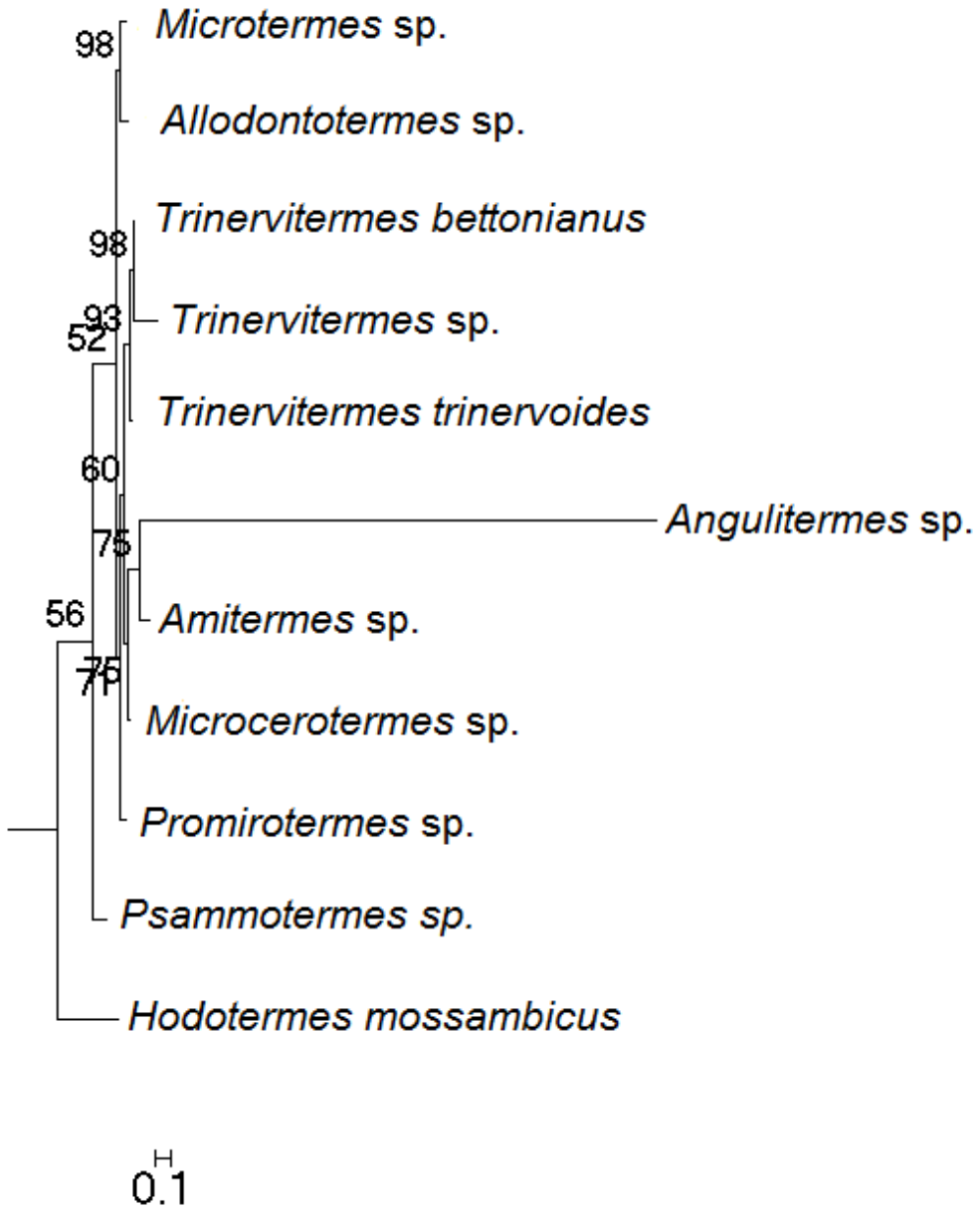

Figure S1. Bayesian phylogeny for the ribosomal mitochondrial gene *12S*.

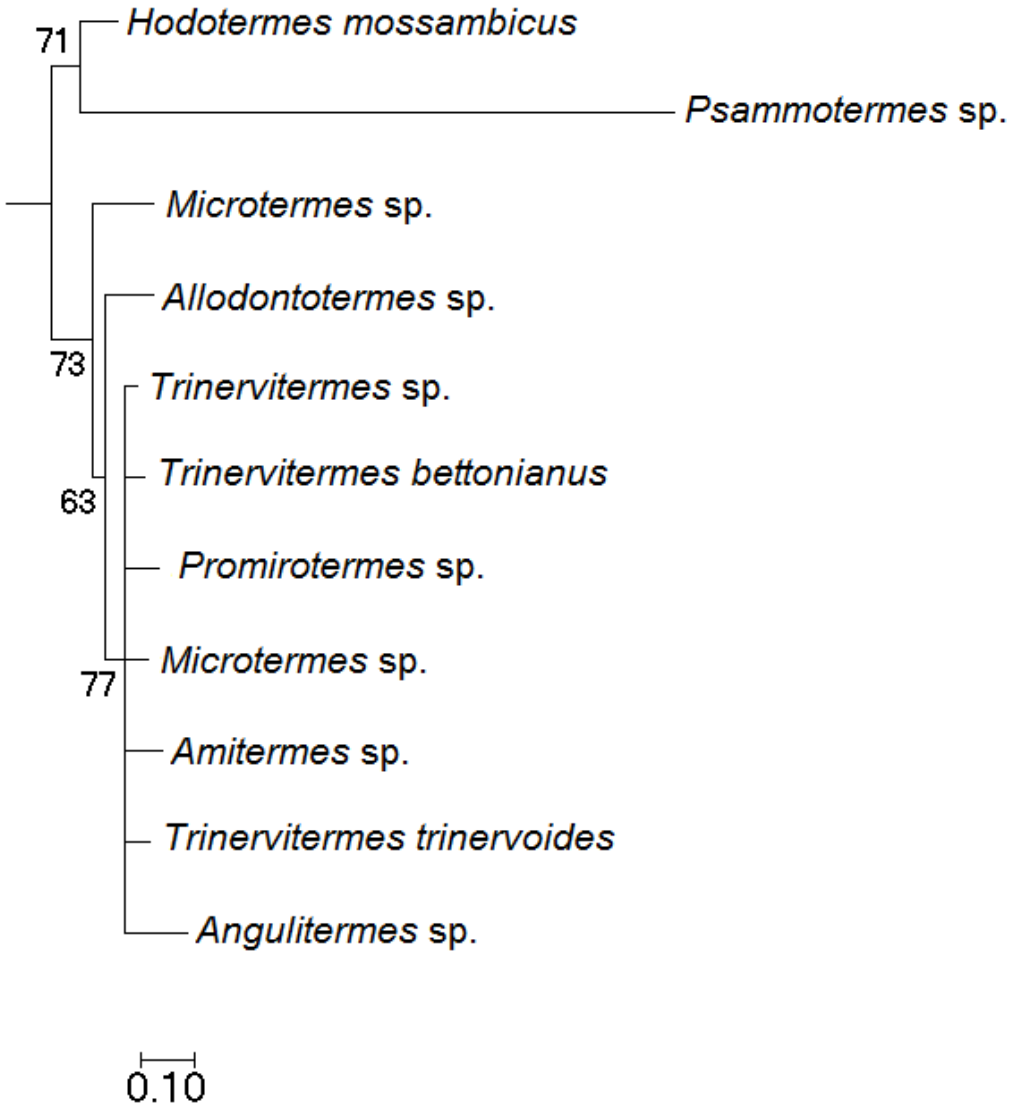

Figure S2. Bayesian phylogeny for the mitochondrial gene *COI* (*cytochrome oxidase I*).

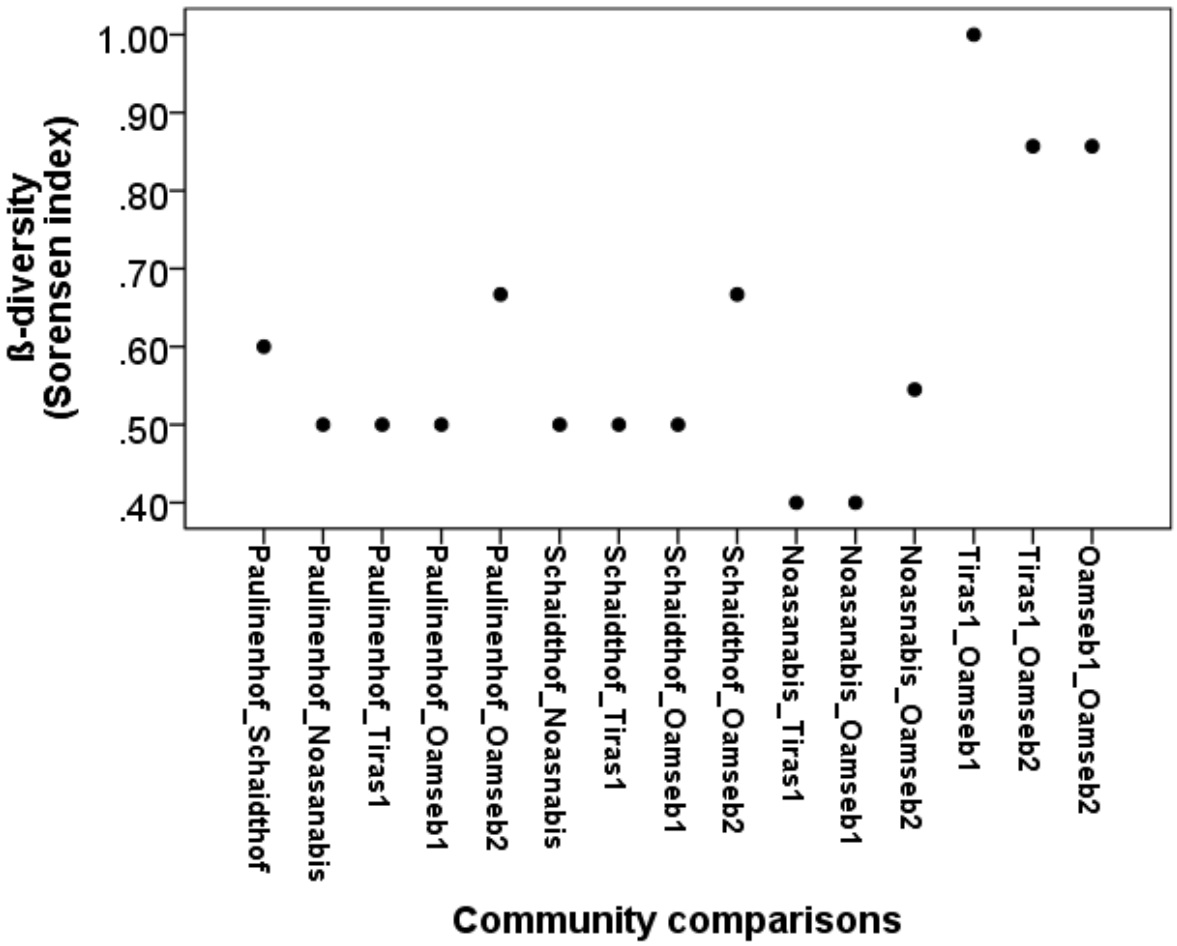

Figure S3. Quantification of the compositional similarity (ß-diversity) between all localities using the Sorensen index. High values indicate high similarities between plots with regard to species composition and low values the reverse.

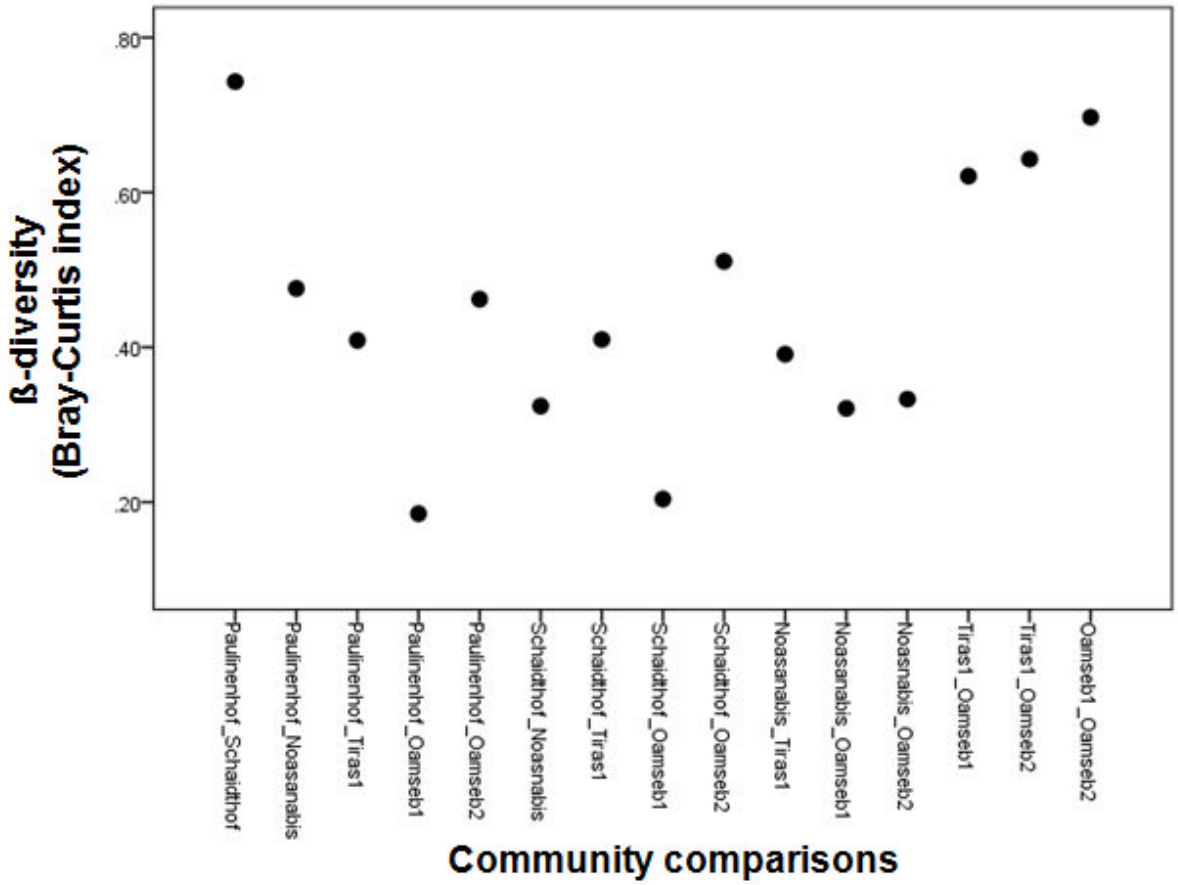

Figure S4. Quantification of the compositional similarity (ß-diversity) between all localities using the Bray-Curtis index. High values indicate high similarities between plots with regard to species composition and low values the reverse.

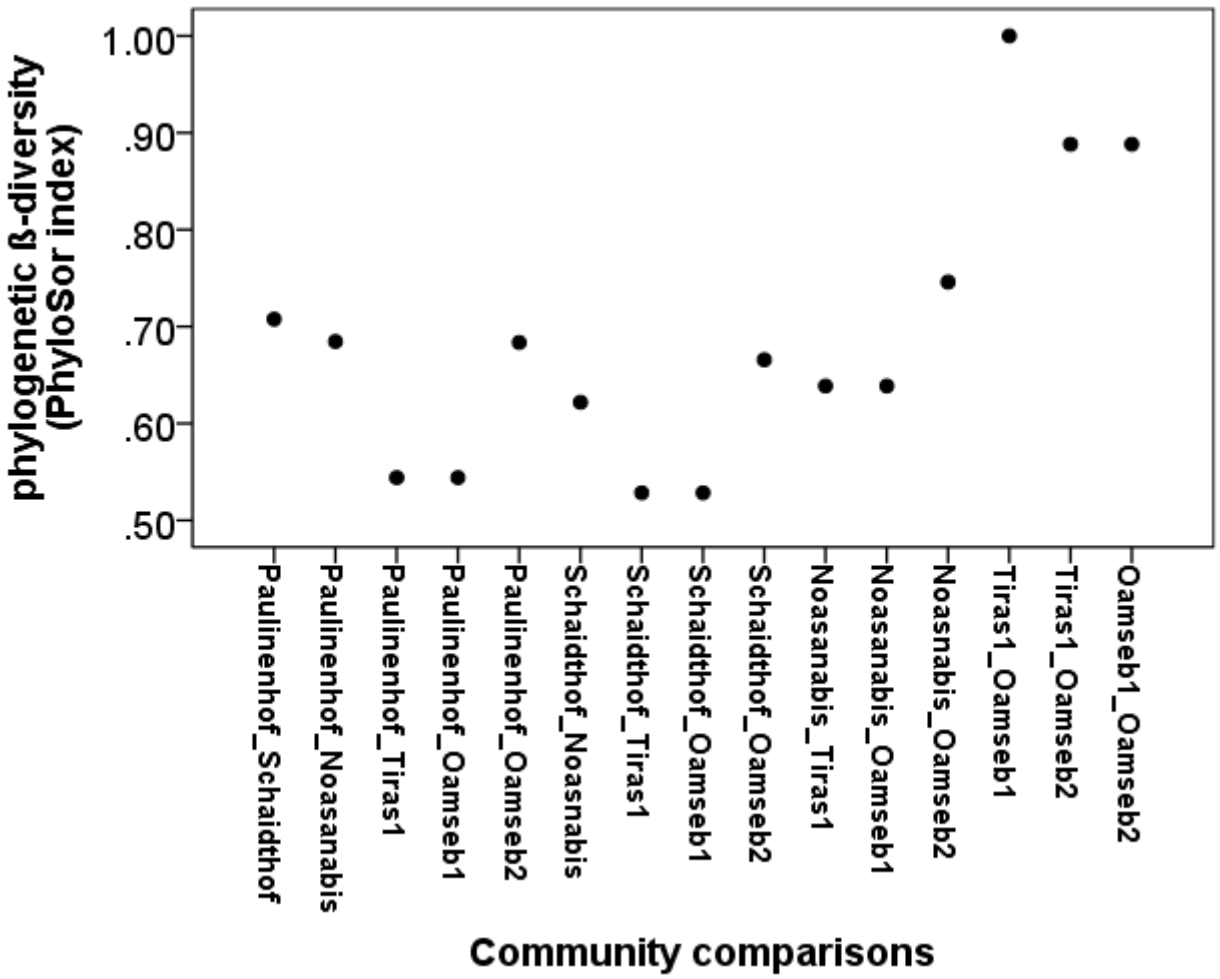

Figure S5. PhyloSor index for community pairs to measure phylogenetic ß-diversity, which gives the fraction of branch-length shared between two communities. Using null model 'independent swap', which randomizes the community data matrix with the independent swap algorithm, maintaining species occurrence frequency and sample species richness.

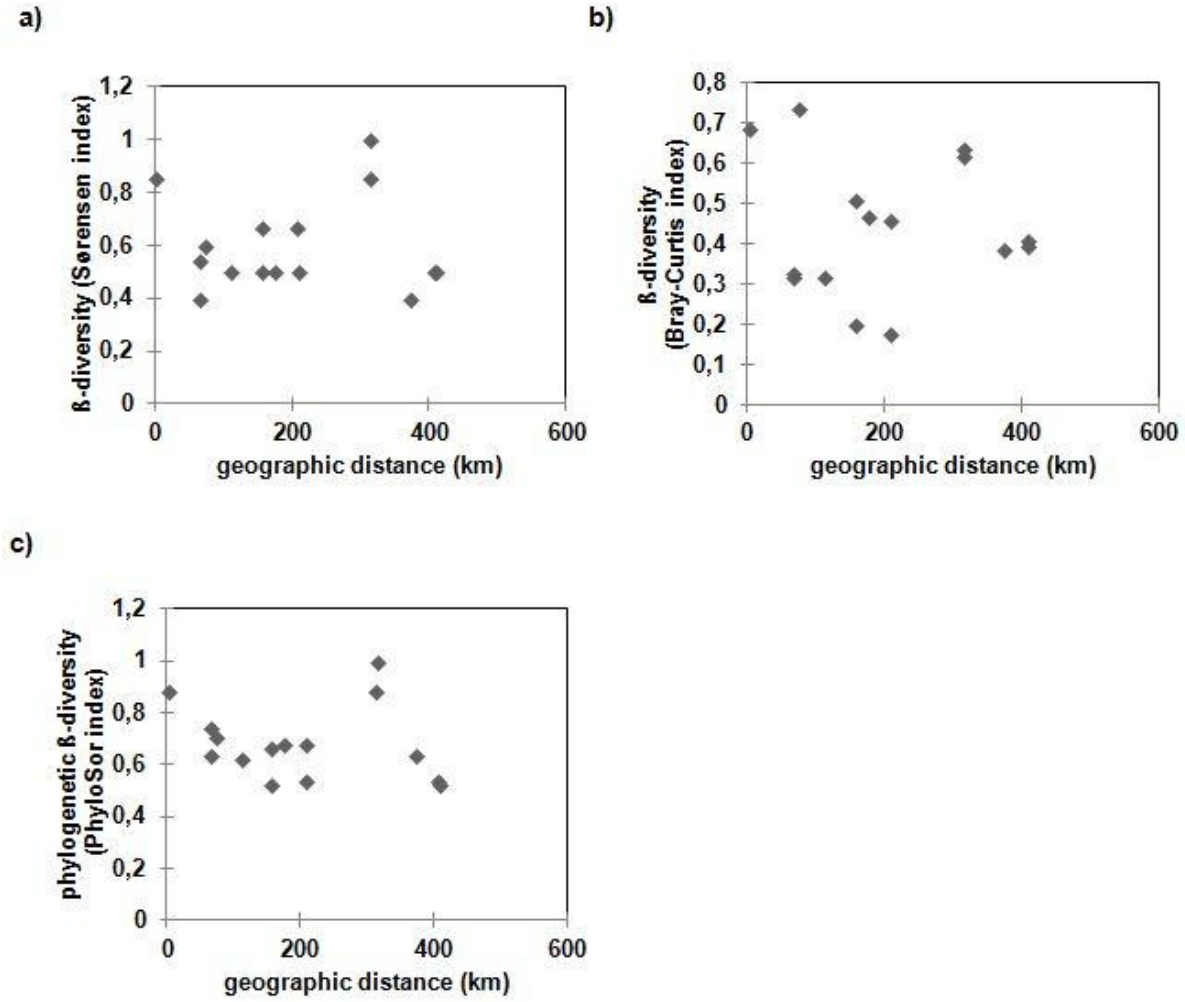

Figure S6. Correlation to detect geographic distance correlates with a) ß-diversity (Sorensen index), b) ß-diversity (Bray-Curtis index) and c) phylogenetic ß-diversity (PhyloSor index). Results show no significant correlation between geographic distance and ß-diversity / phylogenetic ß diversity.

Table S3. Community data matrix with species abundances for each of the six communities. Species are shown in first column and plots in first line of the table. In the last column for the Jürgens *et al.* data: 1 = present and 0 = absent in the sampled areas.

Species/Plots	**Paulinenhof**	**Schaidhof**	**Noasanabis**	**Tiras1**	**Oamseb1**	**Oamseb2**	**Jürgens *et al.* 2010**
Trinervitermes sp.	0	0	0	0	0	0	1
Trinervitermes trinervoides	4	4	5	6	6	4	1
Trinervitermes bettonianus	5	4	0	7	1	3	1
Amitermes sp.	0	1	1	0	0	0	1
Promirotermes sp.	0	0	1	0	0	0	0
Angulitermes sp.	0	0	1	0	0	0	1
Microcerotermes sp.	1	0	0	0	0	0	0
Microtermes sp.	5	0	9	0	0	0	1
Allodontotermes sp.	5	5	1	0	0	7	1
Psammotermes sp.	0	0	4	11	27	18	1
Hodotermes mossambicus	0	1	0	0	0	0	1

Table S4. Environmental characteristics of each sampling site in Namibia. Vegetation density: medium dense = thornbush savannah / higher trees; open = open shrubland / grassland.

Plot	**Mean annual precipitation (mm)**	**Mean annual temperature (°C)**	**Soil type**	**Vegetation density**
Paulinenhof	392	17.9	sandy	medium dense
Schaidthof	303	19.3	sandy	medium dense
Noasanabis	260	19.7	silt/sandy	open/medium dense
Oamseb 1	247	19.8	dry sand	open
Oamseb 2	249	19.8	dry sand	open
Tiras 1	144	15.3	stony/dry sand	open

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Erklärung über die Eigenständigkeit der erbrachten wissenschaftlichen Leistung

gem. § 8 Abs. 2 Buchstabe b der Promotionsordnung der Fachbereiche Physik, Biologie/Chemie und Mathematik/Informatik der Universität Osnabrück

Ich erkläre hiermit, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte sind unter Angabe der Quelle gekennzeichnet.
Bei der Auswahl und Auswertung folgenden Materials haben mir die nachstehend aufgeführten Personen in der jeweils beschriebenen Weise entgeltlich / unentgeltlich geholfen.

1. Prof. Dr. Judith Korb stand als Betreuerin bei allen Phasen der Arbeit beratend zur Seite und unterstützte bei der Datenanalyse und dem Verfassen der Manuskripte.
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Weitere Personen waren an der inhaltlichen und materiellen Erstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich hierfür nicht die entgeltliche Hilfe von Vermittlungs- bzw. Beratungsdiensten (Promotionsberater oder andere Personen) in Anspruch genommen. Niemand hat von mir unmittelbar oder mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

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Ort, Datum Unterschrift

Erklärung über etwaige frühere Promotionsversuche

gem. § 8 Abs. 2 Buchstabe g der Promotionsordnung der Fachbereiche Physik, Biologie/Chemie und Mathematik/Informatik der Universität Osnabrück

Hiermit bestätige ich, dass ich die vorgelegte Dissertation bisher weder im In- noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt habe.

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