Termite responses to long term burning regimes in southern African savannas: patterns, processes and conservation

by

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I, ……Andrew Byron Davies…………………………………………… declare that the thesis/dissertation, which I hereby submit for the degree ……M.Sc. Entomology……………………….. at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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Termite responses to long term burning regimes in southern African savannas: patterns, processes and conservation

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Abstract

Termites are considered to be major ecosystem engineers in tropical and sub-tropical environments, and fire in savanna systems is regarded as a major and necessary disturbance for the maintenance of biodiversity. However, most fire ecology studies have focused on vegetation dynamics with little attention given to other taxa, especially invertebrates. This thesis has addressed several aspects of savanna termite ecology. First, based on a review of studies examining the relationship between fire ecology and termites, I found that few broad conclusions can be made based on the published literature. Hence little is known on the interactions between termites and ecological processes such as fire. Leading on from this, several recommendations are provided in the thesis for future research to improve ecological understanding of savannas and the dynamics that structure these systems. Second, savanna termite responses to long-term burning regimes were investigated across four distinct savanna types along a rainfall gradient in South Africa using comprehensive sampling protocols. This was achieved using experimental burning plots which have been in place in the Kruger National Park (KNP) since 1954 as well as sites in Hluhluwe-iMfolozi Park. Termite communities were found to differ significantly between these savannas with higher diversity at Pretoriuskop, a mesic savanna but not the wettest. Termite diversity was lowest at the most arid site (Mopani) but certain feeding groups peaked at Satara, a savanna with intermediate rainfall. Differences between these savannas are attributed to broad underlying changes in net primary productivity, temperature and soil type, with the role of mammalian herbivores also being considered. Seasonality was also examined and it was found that termite activity peaks in the wet and transitional seasons and is significantly lower in the dry season. Considering different fire regimes, termites, in general, were found to be highly resistant to burning, but assemblage composition was affected, this being more pronounced at the mesic savanna where fire has more effect on vegetation. These assemblage changes are linked to changes in vegetation structure caused by fire. Finally, termite ecology is often constrained by sampling difficulties and a lack of sampling protocols in savannas. A comparison of two often used sampling methods, baiting and active searching, was conducted across the savanna types studied. The efficiency of sampling method varied along the rainfall gradient and a single method was not the best for all savanna types. In mesic savannas, active searching (an often neglected sampling method in savannas) was most effective at sampling termite diversity while baiting was more effective in arid savannas, although this method is biased toward wood-feeding termites from feeding group II. Baiting also provides a better measure of termite activity than active searching. I demonstrate that termite communities differ significantly with savanna habitat and their responses to long-term burning regimes differ between these habitat types. Although termite communities were found to be quite resistant to burning, the degree of resistance differed with savanna type and management policies in protected areas and elsewhere need to take this into account when formulating conservation policies. Similarly, sampling methods differ in their efficiency at different sites which needs to be considered when designing sampling protocols in order to accurately reflect the biodiversity present.

Keywords: fire ecology, Hluhluwe-iMfolozi Park, invertebrates, Kruger National Park, long-term burning regimes, rainfall gradient, sampling protocols, savanna, seasonal differences, termites

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Disclaimer

Chapters 2, 3 and 4 of this thesis have been prepared for submission to different scientific journals. Therefore, styles and formats may vary between all chapters of this thesis and some overlap in content may occur throughout the thesis to secure publishable entities. For ease of reading, tables and figures have been placed on separate pages at the end of each chapter.

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Chapter 1: Introduction

Rationale and background

Fire is an often observed phenomenon in ecosystems across the world, with up to 40% of the earth's land surface consisting of fire-prone systems (Chapin *et al.* 2002), including grasslands, boreal forest, mediterranean shrublands and savannas. Although much control of ecosystem functioning is attributed to climatic factors and resource availability, fire is a very real, yet underestimated, driver of processes related to such functioning (Bond *et al.* 2005). It is analogous to herbivory in many aspects, acting as a 'generalist herbivore' consuming vast amounts of grass and tree biomass and in turn modifying vegetation structure and composition (Bond & Keeley 2005). In savannas in particular, it has been attributed a pivotal role in maintaining the co-existence of trees and grass (Higgins *et al.* 2000; van Langevelde *et al.* 2003) and has also been shown to influence other aspects of ecology such as grazing patterns (Archibald & Bond 2004; Archibald *et al.* 2005; Parrini & Owen-Smith 2009), nutrient cycling (Hobbs *et al.* 1991; Van de Vijver *et al.* 1999) and aboveground net primary productivity (Buis *et al.* 2009).

Savannas are considered to be highly variable and diverse ecosystems (House *et al.* 2003) and as a result fire plays differing roles of importance in these systems. In arid savannas, climatic variables often set limits to the amount of canopy cover because there is insufficient moisture to form a closed canopy system. However, where rainfall is sufficient for this to happen, fire and other disturbances such as herbivory are thought to limit woody cover and thus maintain a savanna structure of trees and grass (Bond & Keeley 2005; Sankaran *et al.* 2005). Effects of fire on other ecosystem processes and potentially fauna are therefore expected to differ somewhat in different savanna types.

Knowledge on faunal responses to fire is, however, limited. This was highlighted in a review by Parr and Chown (2003) who critiqued the literature on fire and fauna studies in southern Africa and found it to be limited. Certain groups of animals, notably reptiles, amphibians and invertebrates were strikingly under represented in fire studies. In addition to this, the authors suggested that most of the current studies are incomparable due to vastly different experimental approaches and poor reporting. Furthermore, many of the studies were observational reports and few were based on long-term burning experiments, focussing rather on once off fire events which are quite different to fire regimes. If ecologists and managers of conservation areas are to better understand the role of fire, more studies, based on sound experimental design, need to be conducted, especially in relation to long-term burning regimes (Parr & Chown 2003; Chapter 2).

This is of much relevance in relation to invertebrates. Although a fair amount of work has investigated insect responses to fire (see Swengel (2001) for a review), little of this is specifically related to savannas globally or to the southern Africa region (Parr & Chown 2003). Yet insects form the bulk of species diversity and biomass on earth and are critically important for ecosystem functioning around the globe (Wilson 1991) and therefore cannot be ignored when seeking to understand ecological processes or planning conservation objectives.

One such insect group is termites (Blattodea: Termitidae), which are of great ecological importance in the tropics and sub-tropics. They are considered to be ecosystem engineers in that they modify the mineral and organic composition of soils, as well as affecting soil drainage (Jones *et al.* 1994; Konaté *et al.* 1999). They also improve soil infiltration rates and porosity, while decreasing bulk density (Mando *et al.* 1996). In tropical forests and savannas, termites are considered to be the dominant arthropod decomposer (Collins 1981; Holt 1987; Schuurman 2005) and in African savannas have been shown to have a biomass comparable to ungulates and mega herbivores (Dangerfield *et al.* 1998). As decomposers, their role in nutrient cycling and distribution can also not be ignored (Holt & Coventry 1990; Konaté *et al.* 1999; Lepage *et al.* 1993; Scholes 1990).

Termitaria constructed by termites have also been shown to affect the ecological dynamics of savannas in a variety of ways (see e.g. Fleming and Loveridge (2003) on how *Macrotermes* mounds provide habitat for small mammals). Moe *et al.* (2009) found a significantly higher number of woody plant and forb species occurring on mounds compared to the surrounding matrix, which suggests that mounds can increase the patchiness and heterogeneity of savanna vegetation by forming nutrient hotspots. By concentrating nutrients, termitaria also provide key resource areas including quality forage that is intensely used by browsers and grazers (Grant & Scholes 2006; Mobæk *et* *al.* 2005). The presence of this forage may enable the persistence of herbivore species within a landscape that would otherwise offer lower forage quality.

Despite their importance in these ecosystems, knowledge on termites is limited, with even basic natural history information lacking for many species (Dangerfield & Schuurman 2000; Dawes-Gromadzki 2003). Taxonomically, many genera are also in need of revision (Uys 2002), and many new species are surely awaiting discovery and description. Standardised sampling protocols, especially for savannas, are also lacking (Dawes-Gromadzki 2003) which contributes to the problem. In terms of the effects of fire on termites, much the same scenario arises, with little data or comparable studies (see Chapter 2 for a review and suggested future research directions). But if we are to better understand savannas and effectively manage conservation and agricultural land within them, more knowledge on interactions between fire (an often used management tool) and termites (a critically important organism) is necessary.

Objectives

The objective of this study was to enhance the scientific knowledge and understanding of termite-fire interactions in southern African savannas. To this end sampling and analysis of termite communities subjected to different long-term burning regimes was conducted using sites in two South African reserves, Kruger National Park (22° 25' - 25° 32' S and 30° 50' - 32° 02' E (hereafter KNP) and Hluhluwe-iMfolozi Park (28° 01' - 28° 25' S and 32° 15' - 32° 26' E (hereafter HiP)). Since effects of fire on vegetation, and likely fauna, vary in savannas of differing climatic and other abiotic variables (Sankarran et al. 2005, Bond and Keeley 2005), these interactions were tested in four different savanna types situated along a rainfall gradient. In addition, several methods and techniques were used to adequately sample the termite communities, allowing an additional investigation of sampling method efficiency to be conducted, with the aim that this will enhance future studies related to termite ecology and diversity.

Study area

The KNP is the largest protected area in South Africa, covering an area of 1 948 528 ha (van Wilgen *et al.* 2007) while HiP is considerably smaller at approximately 90 000 ha

(Archibald *et al.* 2005), but still one of South Africa's largest parks. Both parks are located in the eastern part of the country and have a sub-tropical climate with a distinct summer rainfall pattern. Although highly variable throughout the park, the existing fire regime in KNP is generally characterised by a concentration of fires during the late dry season (late winter), with a mean fire return interval of 4.5 years (van Wilgen *et al.* 2000) At HiP, fire regimes have been highly variable with a shorter mean fire return interval of 3.8 years, although this is highly skewed toward shorter return intervals, the median being only 1.3 years (Archibald *et al.* 2005).

Between 1948 and 1956, the fire management policy in the KNP was aimed at reducing the impacts of fire (van Wilgen *et al.* 2007), but in 1953 an uncontrolled fire burnt approximately a quarter of the park (Biggs *et al.* 2003). This raised concerns over the impacts of fire on the flora and fauna of the park and in response to this a series of experimental burn plots was established in 1954 spanning much of KNP's latitudinal gradient (Fig. 1). This experimental burn plot trial therefore provides an ideal platform to examine questions related to long-term burning regimes and rainfall seeing that it has been in place for several decades and is situated along a rainfall gradient of approximately 450 mm to 700 mm. Consequently, it has become an invaluable savanna burning experiment, and although initially established to test effects of fire on vegetation, the experiment has since been used to study many other aspects of savanna ecology and fire interactions including faunal responses (see van Wilgen et al (2007) for a review of the experiment).

The KNP experiment was set up in four of the major vegetation types in the park, within the Mopani, Satara, Skukuza and Pretoriuskop areas (Fig 1), and within each of these vegetation types it was replicated four times in the form of strings consisting of 12 – 14 plots, each of which are subjected to a different burning regime. These burning regimes consist of different season (dry, wet and transitional) and frequency (from annual through to sexennial) combinations and importantly, each string has a control plot which is prevented from burning (see Fig. 2 for more information on the different burning regimes used in this study). Each plot measures approximately 380 x 180 m (7 ha) and is protected from each adjacent plot by a single fire break. Each string (replicate) is in turn protected from the surrounding vegetation by a double fire break road (Biggs *et al.* 2003).

For this study, I made use of only three of the four KNP vegetation types available because the fourth set of plots (the Skukuza plots) are located across differing soil types (Venter 1999) which could possibly have led to confounding results. Moreover, I made use of only three of the four available strings of plots (replicates) in each vegetation type seeing that the fourth replicate is on a different soil type to the other three (Venter 1999) and therefore considered to be unrepresentative and was not utilised. Thus three replicates, situated 10 – 20 km apart, were chosen in three vegetation types.

In order to extend the rainfall gradient, I also sampled termites at HiP, where rainfall is approximately 900 mm. However, no such burning experiment exists here and so fire records were utilised in order to match up sites with similar fire histories to those of the burn plots in KNP. Even though there is not such a neat experiment in HiP, it was considered useful to add to the study because the higher rainfall enabled me to asses termite communities in a more mesic savanna. Here, three sites of each burning regime, as described in Figure 2, were selected to match the replication used in KNP, with the exception of the burning regime used to match the triennial August burns as an adequate third site was not found. Although these sites were initially chosen in order to test effects of different fire regimes on termites, it was decided to only use the HiP sites in combination with the KNP sites to test for differences in termite communities across savanna types (i.e., the overall rainfall gradient component of the study), due to uncertainty in the HiP fire histories and thus uncertain conclusions been drawn.

Within these two parks, the study was therefore carried out in four distinct savanna vegetation types, Mopane woodland (Mopani area of the northern KNP), *Acacia* savanna (Satara area of the central KNP), *Terminalia* woodland (Pretoriuskop area of the southern KNP) and mesic *Acacia* savanna (Hluhluwe section of HiP), arranged along this rainfall gradient. The three replicates used in the Mopani section of KNP were Tsendse (23°41′S 31°31′E), Mooiplaas (23°34′S 31°27′E) and Dzombo (23°26′S 31°22′E); the replicates used in the Satara region were N'wanetsi (24°26′S 31°51′E), Marheya (24°32′S 31°46′E) and Satara (24°24′S 31°45′E); and the replicates in the Pretoriuskop area were Kambeni (25°15′S 31°26′E), Numbi (25°13′S 31°20′E) and Shabeni (25°12′S 31°23′E). In HiP, all sites were located in the northern Hluhluwe section of the reserve. The following four burning regimes were selected in each of the vegetation types: August annual, August triennial, December triennial and the unburnt control plot (Fig. 2). These were, as best as possible, matched in HiP with sites of similar fire history. August burns represent late winter fires which are at the end of the dry season and are intense, hot fires while December burns represent early summer fires at the beginning of the wet season and are cooler, less intense fires. The use of these burning regimes enabled me to test the effects of fires of differing season (late dry and early wet), frequency (annual and triennial) and intensity (hot dry season fires and cool wet season fires) (Fig. 2).

The Mopani plots were situated in the Mopane shrubveld, which is a mopane (*Colophospermum mopane* J. Kirk ex J. Léonard) dominated habitat with few other woody species present (Low & Rebelo 1996). The mean annual rainfall is 450 to 500 mm and the area ranges in altitude from 300 to 340 m a.s.l. (Gertenbach 1983). In the Satara region, the plots were situated in a mixed knobthorn *Acacia nigrescens* Oliv. and marula *Sclerocarya birrea* (A. Rich. Hochst.) savanna in the sweet lowveld bushveld (Low & Rebelo 1996). The area ranges in altitude from 240 to 320 m a.s.l. and has a mean annual rainfall of 550 mm (Gertenbach 1983). The Pretoriuskop region is sour lowveld bushveld, consisting of open tree savanna dominated by silver clusterleaf (*Terminalia sericea* Burch. ex DC), but bushwillow (*Combretum collinum* Fresen.) is also common (Low & Rebelo 1996). The region has a mean annual rainfall of 700 mm and the altitude varies from 560 to 640 m a.s.l. (Gertenbach 1983). The sites situated in HiP were located within Natal lowveld bushveld, dominated by various acacia species, notably *A. tortilils* and *A. karoo*, but several other species are also common (Low & Rebelo 1996). The mean annual rainfall for the entire park is 600 to 1000 mm and the altitude ranges from 40 to 750 m a.s.l. (Archibald *et al.* 2005), with the Hluhluwe region being in the wetter and higher altitude range of the park. Both the Mopani and Satara regions have basalt-derived clay soils while the Pretoriuskop region has granite-derived sandy soils (Gertenbach 1983). At Hluhluwe the underlying geology is predominantly sandstone and shale resulting in sandy soils (Archibald *et al.* 2005).

Structure of the thesis

Following this introduction, Chapter 2 provides a review of current knowledge on termite-fire interactions. I show that currently general conclusions cannot be drawn and provide suggestions for future research. Building on this, Chapter 3 examines the effects of long-term burning regimes on termite diversity and activity. Chapter 4 makes use of some of the sampling methods used in Chapter 3 to asses the efficiency of sampling methods and how this may change across savanna types situated along the rainfall gradient. The thesis ends with a general conclusion of the overall thesis findings in Chapter 5, with reference to management and conservation implications.

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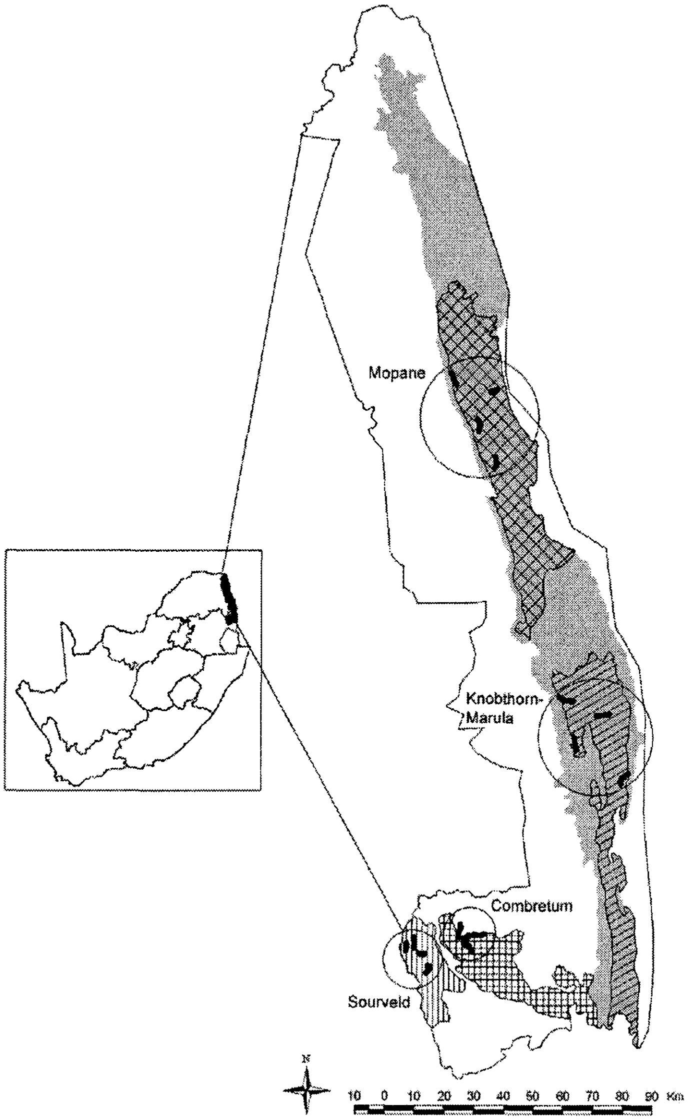

Figure 1: Location of the replicates of the experimental burning plots in the Kruger National Park, South Africa. Hatched and striped areas indicate the four major vegetation types the experiment is located within while the unshaded area represents granitic based geology while the shaded area shows the basalt areas. Taken with permission from van Wilgen *et al.* (2007)

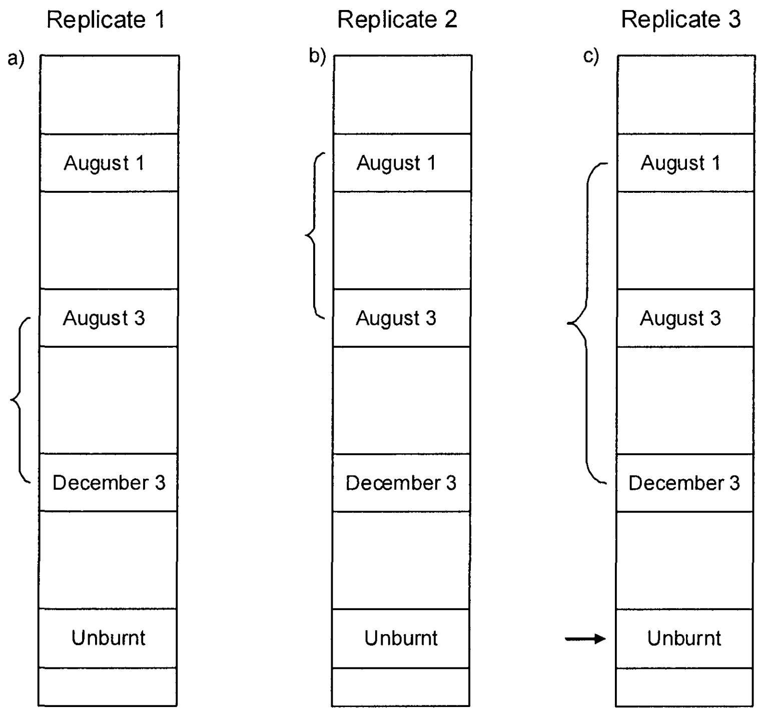

Figure 2: A schematic diagram of the experimental design that was followed in each savanna type. Four burning regimes, replicated three times, were sampled in each savanna type in order to examine a) different fire seasons (late winter and early summer), b) fire frequencies (annual vs. triennial), and c) burnt plots vs. long unburnt plots. Fire intensity was also assessed along a gradient of very hot intense fires at triennially burnt August plots to cool low intensity fires at triennially burnt December fires.

Chapter 2

Termites and fire: current understanding and future research directions for improved savanna conservation

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Abstract

Termites are considered to be major ecosystem engineers in tropical environments. However, they are often neglected and under studied, especially in grassy systems. The interaction between termites and fire ecology is one example of this. Given the importance of both fires and termites in savanna systems, it is critical for an improved ecological understanding of savanna biodiversity that the interaction between them is better understood. In this paper, we highlight the lack of published literature on fire ecology and invertebrates in austral systems, with particular focus on termites. We review the six studies conducted in savannas spanning the southern hemisphere which investigate this interaction, summarizing their findings and limitations. We suggest areas of future research related to fire and termites which will improve our ecological understanding of savannas and the dynamics that structure these systems.

Keywords: burning regimes, invertebrates, research directions, savanna, termites.

Importance of fire and invertebrates

While tropical savannas and grasslands typically attract less attention than temperate systems (see e.g. Gaston *et al.* 1998 and references therein indicating the general lack of biological data at low latitudes), they represent one of the dominant biomes of the southern hemisphere, and indeed the world, with savannas covering an estimated 12.5% of global land area and over half of Africa and Australia, 45% of South America and 10% of India and Southeast Asia (Scholes & Archer 1997). Fire is considered one of the most important disturbances in these grassy systems being both frequent and widespread across Australian, African and South American savannas (Bond & Keeley 2005). The exceptional diversity and biomass of invertebrates has been long recognized, as has their functional importance in ecosystem services across the globe (Wilson 1987). Fire and invertebrates are thus key components determining the functioning and dynamics of savannas (Parr *et al.* 2004, van Wilgen *et al.* 2007), as well as other systems around the world (e.g. boreal forests – McCullough *et al.* 1998).

Yet, generally scientists, and more especially conservation managers, have a poor understanding and limited predictive capacity of the way in which invertebrate communities respond to fire and the implications for diversity and functioning in savanna systems. This was highlighted for the southern hemisphere by Parr & Chown (2003) who reviewed fire and invertebrate studies in southern Africa. A search on Web of Science using the keywords ‘insect*’ and ‘Africa’ with either ‘fire*’ or ‘burning’ revealed that since the review by Parr & Chown (2003) only three additional papers and one book chapter dealing with fire and invertebrates in Africa have been published (Parr *et al.* 2004; Axmacher *et al.* 2006; Uys *et al.* 2006; Underwood & Christian 2009); this indicates little has changed since 2003. Similarly and for the same time period, work conducted at the global scale is also limited in its contribution to our broader understanding of the ecological processes involved when studying fire and invertebrate interactions. The lack of knowledge on invertebrates and fire is thus an important shortcoming to understanding how savanna systems are structured and function, and also when managing for the conservation of biodiversity, especially since savannas are often subject to intense fire management (van Wilgen *et al.* 2007).

In tropical and sub-tropical areas, including savannas, termites are considered key ecosystem engineers, altering the mineral and organic composition of soils, their hydrology, drainage (Jones *et al.* 1994) and infiltration rates (Mando *et al.* 1996), as well as influencing decomposition, nutrient cycling and distribution (Holt & Coventry 1990; Scholes 1990; Lepage *et al.* 1993; Konaté *et al.* 1999). Their vast biomass alone makes them an important consideration in tropical and sub-tropical ecology (Josens 1983) and they are considered the dominant arthropod decomposer in tropical forests and savannas (Collins 1981; Holt 1987; Schuurman 2005). Termites are also a diverse and varied group comprising of several functional groups, including wood feeders, grass harvesters and soil feeders (Josens 1983). Although it is somewhat surprising that relative to other invertebrate groups termite work is scarce with even basic natural history information lacking for many species (Dangerfield & Schuurman 2000; Dawes-Gromadzki 2003), this is likely because there are sampling and taxonomic difficulties associated with the group (Josens 1983).

Here I use examples of studies conducted in savannas across the globe to highlight what I see as a critical research gap: the lack of published information on the interactions between termites specifically (Blattaria: Termitidoidae) and fire. Furthermore, I propose that if protected areas in savannas are to uphold their mandate of conserving biodiversity in its entirety, then a better ecological understanding of interactions between fire and termites is crucial for achieving this. The aims of this paper are therefore to highlight what I perceive as a paucity of studies on the topic, to demonstrate that critical information is still lacking, and to look towards potential future research directions. I compare studies from several continents and suggest ways in which the termite fauna of these continents could vary in their response to fire and some resultant ecological implications of this, particularly for the southern hemisphere.

Current knowledge status

Since fires in savannas are frequent, and that in these systems they represent a disturbance that is often controlled (e.g. determining season, fire size and frequency, Govender *et al.* 2006), it is important to have basic information on how burning influences diversity and processes within savannas. Basic research questions that will advance ecological understanding of termite-fire interactions include: what is the effect of different fire regimes (e.g. fires of differing frequency, season and intensity) on termite diversity and activity? How do the effects of repeated fires vary from single fires? And, how do different functional groups of termites respond to variation in burning regimes, e.g. are grass harvesters, for example, more susceptible than other groups?

Following on from this and given the importance of fire and the role of termites in savannas it is concerning that to our knowledge, only six studies focusing on fire-termite interactions in savannas have been published to-date: Trapnell *et al.* (1976), Benzie (1986), Ferrar (1982), DeSouza *et al.* (2003), Dawes-Gromadzki (2007) and Traore & Lepage (2008). These constitute four from Africa, and one each from South America and Australia. Even when other biomes are included, there has only been one additional study conducted on fire and termites in the southern hemisphere, this in the Mediterranean-type vegetation in Western Australia (Abensperg-Traun & Milewski 1995). Although I acknowledge the scientific value of these studies, an understanding of the effects of fire on termites is, to-date, clearly limited in scope and geographic coverage, with large areas such as east Africa and India being poorly studied. Single studies in Australia, South America and southern Africa also cannot be seen as a true representation of fire–termite interactions on these continents due to the high levels of variability within and across savanna landscapes and at larger scales (e.g. continental and sub-continental scales).

Of the six studies conducted in savanna ecosystems, three dealt with fire regimes (Trapnell *et al.* 1976; Benzie 1986; Traore & Lepage 2008) and three with single fire events (Ferrar 1982; DeSouza *et al.* 2003; Dawes-Gromadzki 2007). The three studies dealing with fire regimes (all conducted in Africa) considered only two extreme regimes: that of fire exclusion and of annual burns. In all three, only mound building termites were considered and the experiments in the Trapnell *et al.* (1976) and Benzie (1986) studies were not replicated. Results were complementary for the two studies carried out in west Africa (Benzie 1986; Traore & Lepage 2008); in both these studies *Trinervitermes* mound densities decreased significantly under fire treatment, and *Macrotermes* and *Cubitermes* mounds remained unaffected by fire. However, in the study by Trapnell *et al.* (1976), mound densities of *Cubitermes* termites increased under fire treatment, with no results for other genera reported. The latter study was conducted on plots which had been subjected to experimental burning for much longer (23 years) than the Benzie (1986) and Traore & Lepage (2008) studies (3 and 10 years respectively). Difference in habitat (Zambian miombo woodland and west African guinea and Sudanian woodland), and likely also species, may explain some differences in the results for *Cubitermes* mound density changes, but no clear patterns can be detected with such limited data.

Of the three studies which investigated effects of a single fire event on termites, one was conducted in Africa, one in Australia and the other in South America. The Australian study (Dawes-Gromadzki 2007) was replicated and all functional groups were considered along with other soil macroinvertebrate fauna. Termite abundance was found to decrease significantly after fire was applied to the experimental sites (this despite the relatively low intensity of the fires), but effects on species richness were less apparent. In South America (DeSouza *et al.* 2003), fire had no effect on the termite assemblages but the relatively coarse level of resolution may have masked any species-level effects and experimental replication was poor. The African study was conducted in a savanna area of South Africa (Ferrar 1982), and was an opportunistic study after a low intensity fire burnt a study area being used to look at more general termite ecology. Cellulose baits consisting of toilet rolls were laid out on the site post fire to sample termites present over time as the vegetation recovered from the fire. The results of the study show that termite attack of the baits was much reduced compared with similar sites which had not been burnt. Ferrar (1982) concluded that this was probably the result of the protective grass cover being removed by the fire, leading to greater insolation and desiccation of the soil, making it unfavourable for termites, however, no pre-fire data were available. The study documents a slightly delayed increase in termite activity post-fire, although this post-fire time interval is not given.

The above studies suggest that fire can have a significant effect on termite densities and activity levels, especially it seems when the extremes of fire treatment are examined, that of fire exclusion and annual burning. However, even though some invertebrate groups have shown resilience to burning and others have not (see Swengel 2001 for a review on insect responses to fire), I propose that there are insufficient studies to provide a clear picture of the relationship between fire ecology and termites, particularly because only extreme fire regimes have been studied. Fire exclusion and continuous annual burning are both unrealistic and arguably unnatural management options for savannas, and since these are the only two regimes investigated, the above studies are somewhat limited in their contribution to our understanding of fire ecology. Furthermore, the four African studies focused only on one suite of termites – mound builders in west and central Africa (Trapnell *et al.* 1976; Benzie 1986; Traore & Lepage 2008) and wood feeders attracted to cellulose baits in southern Africa (Ferrar (1982). Experimental replication was also limited in three of these four studies, with suitable replication only occurring in the Traore & Lepage (2008) study. The South American study did take more functional groups into consideration, but here replication was again poor and the study had a course taxonomic resolution. The Australian study avoided both these problems, but only gives us a snapshot of the ecological process of termite recovery after fire since it was based on a single fire event and termites were only sampled once after the fire (after two weeks). Finally, the range of responses detected from these studies means that general patterns at this stage are impossible to detect.

Future research directions

In order to improve current knowledge on fire-termite interactions, and consequently savanna ecology, I highlight the urgent need for further research and recommend that it should especially be focused on long term experiments. Research on long term burning regimes in addition to single-fire events is important because the effects of single-fire events can be markedly different to those from repeated burning (Parr & Chown 2003); the effects of fire regimes on biodiversity need to be understood in order to implement ecologically relevant fire management strategies. In addition, a wider range of fire regimes spanning different intensities (e.g., seasons) and frequencies need to be investigated rather than only fire exclusion and annual burns which are not realistic or practical to implement. At the same time, it is also important to better understand the ecological impacts of single fire events since accidental or anthropogenic unnatural fires occur frequently in savannas across the globe. To this end, studies of single fire events will be valuable especially where accompanied with pre-fire data.

Another aspect of termite ecology which warrants urgent attention is that of their diversity. Because the studies to date focus on a limited suite of functional groups the ecological effects of fires at the assemblage level are unclear. I predict that the various functional groups will respond differently to repeated burning events. For example, wood feeding termites may be more likely to be affected by intense fires or repeated burning which consume large amounts of dead wood. Although no data are available for African savannas, in Australian savannas, on average 27 % of standing dead wood is consumed per low intensity fire (Fensham 2005); this figure is likely to be significantly higher with more intense fires. In contrast, less severe fires which only remove the grass layer may be more likely to affect grass harvesters. This may potentially result in a shift in functional groups under different fire regimes which may have a significant influence on system functioning.

Interactions between termites and fire on different continents are expected to differ somewhat. In African savannas, for example, these interactions are expected to differ from those elsewhere due to the high diversity of ungulates and the resultant effects they have on ecosystem functioning. These effects include maintaining a balance between grass and woody biomass and increasing the rate of nutrient cycling (Du Toit & Cumming 1999), a process also critical to and facilitated by termites and their ecology. The large degree of savanna spatial heterogeneity in Africa which is driven by variations in rainfall, topography and soil fertility (Du Toit & Cumming 1999) could provide many opportunities to study termite fire interactions in differing habitats. These studies would also be useful to understanding savanna ecology elsewhere, since many processes operating in African savannas are common to savannas elsewhere and this could lead to worthwhile comparisons being drawn between continents; similarities include high seasonality and the importance of fire in these systems (Bourlière & Hadley 1983).

Since termites originated in African rainforests (Aanen *et al.* 2002), this may also lead to differences in response to fire between Africa and other continents due to consequent higher termite diversity. Evolutionary history could also be used to explain findings on other continents because traits carried over to these continents could be ancestral and evolved under African conditions. Similarly, the biogeographic origin of different species could possibly be used to predict responses of species to fire. For example, there may be a range of savanna-adapted genera that are less affected by fire compared to genera that have a forest-oriented biogeographic history such as

Ancistrotermes and indeed most of the *Apicotermitinae* subfamily (Eggleton *et al.* 2002). These forest-associated genera may be more susceptible to frequent fires that open up woody vegetation and alter microclimatic conditions and food availability. Climatic variables may also be of importance in predicting termite responses since more arid areas have been shown to be more resilient to fires than mesic areas with regards to other invertebrates (see e.g., Parr *et al.* 2004 for ants). Much work needs to be conducted before these hypotheses, related specifically to termites, can be supported or falsified.

Another avenue of future research could focus on how termites might, in turn, influence fire patterns in savannas. Termites are herbivores which often forage sporadically in a patchy pattern dependent on environmental conditions (Wood 1978). This could have important implications for fire spread in savannas; for example, areas where harvester termites have removed grass provide short-grass patches which could prevent the spread of fire and create unburnt refuges for other taxa to utilize. Understanding of this relationship could provide answers to how termites as herbivores interact with fires to shape savannas.

I hope that this paper will inspire future work on termites and fire ecology, despite the difficulties associated with it. Knowledge at a species, as opposed to generic, level would be especially helpful in providing a more complete picture of responses and ecological implications. Although this is not an easy task given the state of termite taxonomy, understanding how fire ecology and termites interact is of critical importance for improved ecological understanding and furthermore for ensuring effective management and conservation of savanna ecosystems.

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Chapter 3

Savanna termite responses to long-term burning regimes

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Abstract

Fire in savanna systems is regarded as a major and necessary disturbance for the maintenance of biodiversity. However, most fire ecology studies have focused on vegetation dynamics with little attention given to other taxa, especially invertebrates. Termites are considered to be major eco-system engineers in savannas, but are often neglected due to sampling and taxonomic difficulties. Hence very little is known on the interactions between termites and ecological processes such as fire. But if we are to conserve biodiversity, interactions between ecological processes and drivers need to be well understood. I made use of a long-term burning experiment initiated in 1954 in the Kruger National Park, as well as sites in Hluhluwe-iMfolozi Park, South Africa, to test the effect of different fire regimes on termite assemblages. I sampled across four distinct savanna types situated along a rainfall gradient, and across three seasons. Termites were comprehensively sampled using a variety of methods in order to sample a large suite of functional groups. Assemblages differed significantly across savanna types with higher levels of diversity in mesic sites. Diversity was lowest at the most arid site but certain feeding groups peaked at Satara, a savanna with intermediate rainfall. Differences between these savannas are attributed to broad underlying changes in net primary productivity, temperature and soil type, with the role of mammalian herbivores also being considered. Seasonality was also examined and it was found that termite activity peaks in the wet and transitional seasons and is significantly lower in the dry season. Termites were overall highly resistant to fire, but assemblage composition was affected, this being more pronounced with increasing annual rainfall. Assemblage changes are linked to changes in vegetation structure caused by fire. Vegetation is little affected by fire in drier areas, but in wetter areas fire plays a major role in shaping its structure and composition, this same pattern seems to be reflected with termites. Although managers can afford to place more emphasis on other taxa when deciding on a burning policy, in mesic savannas more caution should be exercised.

Keywords: assemblage composition, conservation, fire ecology, invertebrates, resistance

Introduction

Fire is a frequent and widespread disturbance in African savannas, where it acts like a generalist herbivore modifying vegetation structure and composition (Bond and Keeley 2005) and facilitates the co-existence of trees and grass (Higgins et al. 2000, van Langevelde et al. 2003). Fire has also been shown to influence grazing patterns (Archibald and Bond 2004, Archibald et al. 2005, Parrini and Owen-Smith 2009), nutrient cycling (Hobbs et al. 1991, Van de Vijver et al. 1999) and aboveground net primary productivity (Buis et al. 2009).

Although the effects of fire on savanna vegetation are well documented (see e.g. Bond 1997, van Wilgen et al. 2003, van Wilgen et al. 2007), for animals, and especially invertebrates, knowledge is scarce (Parr and Chown 2003, Parr et al. 2004, Chapter 2). This is concerning since fire is used extensively in savanna systems across the globe as a management tool for livestock farming, and often to achieve conservation goals in protected areas (Biggs et al. 2003, van Wilgen et al. 2004, Andersen et al. 2005). Few studies have been conducted on invertebrates, and results thus far have been mixed, with some studies concluded that fire does have some affect on invertebrates (Ferrar 1982, Zieger et al. 1998) while others (Parr et al. 2002, Parr et al. 2004) found fire to have little affect. Furthermore where studies have been carried out, they have focused predominately on single fire events or burning regimes which do not reflect natural regimes. Experiments which make use of long-term burning regimes that more closely resemble natural fires are thus likely to provide more meaningful ecological understanding and allow more informed management decision-making (Parr and Chown 2003).

Sankaran et al. (2005) introduced the idea that African savannas tend to be either stable or unstable depending on the mean annual precipitation (MAP) received. That is, below a threshold MAP of ~650mm savannas are considered to be more stable, with disturbances such as fire and herbivory having little effect on woody vegetation cover. However, savannas with a MAP greater than ~650mm are considered to be unstable because they have enough moisture to potentially form closed canopy forests. In these areas, disturbances such as fire and herbivory are crucial for maintaining an open canopy that allows grasses to grow, and thus these disturbance types play critical roles in determining woody vegetation structure and composition. Whether the effect of these disturbances can also significantly influence the fauna remains to be formally examined. However, if faunal response to fire is linked to changes in vegetation structure, as has been suggested (Catling et al. 2001, Parr et al. 2004), I would expect limited or no response in arid, more stable savannas and a significantly greater response in more mesic savannas (>650 mm). Results from a study by Parr et al. (2004) looking at fire effects on ant assemblages across savanna systems suggested this may indeed be the case: in low rainfall ('stable') savannas there was little or no change in ant richness, abundance and composition with burning, whereas in higher rainfall ('unstable') savannas responses were greater. I aimed to test this idea more fully by determining how termite communities responded to fire at a range of savanna sites along a rainfall gradient. I investigated long term burning regimes across this rainfall gradient which encompassed both 'stable' and 'unstable' African savannas. Effects of fire were thus investigated at, and compared between, savannas of markedly different rainfall patterns.

Termites (Blattodea: Termitidoidae) are an invertebrate group which has been largely neglected in terms of fire research (see Chapter 2), even though they are considered to be ecosystem engineers and crucial to savanna system functioning (Jones et al. 1994). They are capable of altering soil composition and hydrology, as well as drainage (Jones et al. 1994) and infiltration rates (Mando et al. 1996). Termites are also considered to be the dominant invertebrate decomposer in tropical forests and savannas (Collins 1981, Holt 1987, Schuurman 2005), and thus also play an important role in nutrient cycling and distribution (Holt and Coventry 1990, Scholes 1990, Lepage et al. 1993, Konaté et al. 1999). Although termites are notoriously difficult to sample comprehensively, especially in savannas, understanding how they are affected by fire in savanna systems is critical for a more effective understanding, and conservation, of those systems.

The aims of this study were to investigate how termite diversity (richness, abundance and composition) and activity (i) vary between major savanna habitats situated along a gradient of increasing MAP; (ii) vary with season, and (iii) are influenced by long-term burning regimes. I will test whether termite responses to fire can be fitted within the stable-unstable savanna conceptual framework. This is the most comprehensive study to date on savanna termites not only in terms of the spatial and temporal extent of the study but also in the diversity of sampling methods employed.

Methods

Study site

The study was conducted in four distinct savanna vegetation types along a rainfall gradient in two of South Africa's major reserves: Kruger National Park (KNP, 22° 25' - 25° 32' S, 30° 50' - 32° 02' E) and Hluhluwe-iMfolozi Park (HiP, 28° 01' - 28° 25' S, 32° 15' - 32° 26' E). These parks are located in the eastern part of the country and experience a sub-tropical climate with a distinct summer rainfall pattern. The existing fire regime in KNP is generally characterised by a concentration of fires during the late dry season (late winter), with a mean fire return interval of 4.5 years, although this does vary substantially throughout the park (van Wilgen et al. 2000). In HiP, fire regimes have been highly variable with a shorter mean fire return interval of 3.8 years, although this is highly skewed toward shorter return intervals, the median being only 1.3 years (Archibald et al. 2005) (for more details on these parks see Archibald et al. 2005 and van Wilgen et al. 2007).

In KNP termite sampling was carried out in three dominant savanna vegetation types in the park using a large-scale (spanning *ca.* 250 km), long-term burning experiment established in 1954 (Biggs et al. 2003, van Wilgen et al. 2007). Within each savanna type, sampling took place on a series of burn plots (7 ha each in size), replicated three times. Replicates within a savanna type are situated 10 – 20 km apart. The three savanna types consisted of Mopani woodland (Mopani area of the northern KNP), *Acacia* savanna (Satara area of the central KNP) and *Terminalia* woodland (Pretoriuskop area of the southern KNP). In order to test the effects of fire season (late dry and early wet), frequency (annual and triennial) and intensity (hot, dry season fires and cool, wet season fires), four burning regimes were selected within each replicated plot namely August annual, August triennial, December triennial and the unburnt control plot. August burns represent late winter fires which are at the end of the dry season and are intense, hot fires while December burns represent early summer fires at the beginning of the wet season and are cooler, less intense fires.

Because no such experiment exists in HiP, fire map records were used to identify sites in the landscape with fire histories that, as best as possible, match those of the burn plots in KNP. Despite using only fire histories, this savanna site was investigated because it is in a higher rainfall area and thus provides a more mesic savanna for comparison. Three sites of each burning regime were selected in mesic *Acacia* savanna (Hluhluwe section of HiP) to match the replication used in KNP, with the exception of the burning regime used to match the triennial August burns where only two sites were selected at HiP as an adequate third site was not found. Because there is less certainty about the fire histories of the selected HiP plots, they were later excluded from any fire ecology analyses, and instead only used for overall savanna comparisons. The total rainfall gradient represented by the four savanna types (i.e. KNP and HiP combined) ranged from 450 mm (Mopani woodland in KNP) to 900 mm (mesic *Acacia* savanna in HiP) (see Supplementary material S1 for more information on the replicated sites in each of the four habitat types).

Termite sampling

Termites were sampled using a variety of methods in order to sample all feeding groups adequately: cellulose baits, active searching, and mound counts. Sampling was conducted in three seasons during 2008 and early 2009: March to May 2008 (the austral autumn, transitional season), June to September 2008 representing the dry season (the austral winter), and November 2008 to February 2009 representing the wet season (the austral summer).

During each season, 40 cellulose baits in the form of toilet paper rolls (500-sheet single-ply, unscented - hereafter referred to as baits) were placed on each plot (see Le Fage et al. 1973). They were arranged in a grid of five by eight baits, spaced five metres apart at the centre of each plot to prevent edge effects. Half (20) of the baits were placed directly on the soil surface, any litter present was brushed aside to ensure direct contact was made with the soil and the base of the bait (Dawes-Gromadzki 2003). These baits were wrapped around the middle with packaging tape to prevent unravelling and secured to the soil surface using an aluminium tent peg placed through the centre gap of each bait. The other half of the baits were buried below the soil surface at a depth of approximately

2 cm which ensured they were adequately covered with soil. Each line of eight baits consisted of four buried and four surface baits with the position of the baits alternated. Baits were checked for termites, and termite attack assessed, after predetermined intervals of 7 (5 days during the wet season), 14, 28 and 56 days. At each of these time intervals, five surface and five buried baits were removed, and any termites present were sampled (at least ten of each caste were sampled when present to ensure a representative sample, Uys 2002). The baits were then scored according to the intensity of attack (IA). This involved giving each bait a score of one to six according to how much of the bait had been consumed, which was assessed visually. Baits which were completely intact with no evidence of termite activity were assigned a value of 0, subsequent to this baits were scored according to the following scale: 1 = 1 – 25% consumed, 2 = 26 – 50% consumed, 3 = 51 – 75% consumed, 4 = 76 – 99% consumed and 5 = 99 – 100% consumed (Dawes-Gromadzki 2003). Baits which had been disturbed by vertebrates or otherwise affected (e.g. no longer in direct contact with the soil surface or completely destroyed) were excluded from analysis.

During the transitional and dry seasons, two belt transects of 50 by 2 metres were walked by two people in each plot, during which any termite activity was noted and termite searching was conducted. In addition, any course woody debris (CWD) found along the transects was sampled and later weighed and searched thoroughly for termites. During the wet season, representing peak termite activity (Dawes-Gromadzki and Spain 2003), this method was augmented to be a modified version of the standardised belt transect method described by Jones & Eggleton (2000) (see Supplementary material S2 for more information on this modified method). Two 50 by 2 metre belt transects were laid out on each plot, with each sub-divided into ten 5 x 2 metre blocks and each block searched for a period of ten person minutes. During this time period the entire block was searched for termites; this included excavating soil and searching dead wood, termite nests and other microhabitats. Vegetation up to a height of one metre was searched.

Mound counts were conducted during the dry season of 2008. Two blocks of 50 by 50 metres were laid out on each plot and searched thoroughly by three people for any mounds present. These mounds were then broken open to sample any termites found. The dry season was selected for this because grass cover at this time is less dense, allowing more effective searching.

Termite Identifications

Termite samples were identified at the Natural History Museum, London, U.K., the University of Pretoria and the National Collection of Insects, Pretoria, South Africa. Specimens were identified to species were possible using soldier castes whenever available (when soldiers were not present, workers were used). Where this was not possible, genera were separated into morphospecies (e.g. for *Odontotermes*), and where even this was problematic the specimens were pooled to genus (this occurred, for example, with the genera *Microtermes, Microcerotemes* and *Astalotermes*). Many termite genera are in need of taxonomic revision (Uys 2002) and it was considered better to treat these taxa at a genera level only instead of risking the possibility of finding differences in community assemblages when species thought to be different were actually the same. Although I refer to 'species' throughout the manuscript, due to the above taxonomic constraints, this refers to genera in cases where a genus could not be easily split into its constituent species. A reference collection will be lodged with the National Collection of Insects, Pretoria.

Environmental data

A variety of methods were used to quantify and describe the vegetation present on each plot. The percentage cover of each vegetation type was assessed using twenty 1-m^2 quadrats placed ten metres apart in a 5 x 4 grid. The percentage cover of grass, bare ground, dead grass and leaf litter, forbs, woody vegetation, dead wood, dung and rock was estimated for each quadrat and the percentage of canopy cover was also estimated. Data on the dominant grass and tree species for each plot were provided by South African National Parks (KNP) and the Zululand Tree Project (HiP).

Temperature readings were recorded using iButtons at selected sites which provided a representation of the various burning regimes. A single iButton was placed on each site for the most centrally located string of plots in each savanna type during each season and also on two sites for each adjacent string. In HiP, a similar setup was followed. At these sites, temperature readings were recorded at hourly intervals. Soil type and associated data were provided by South African National Parks.

Analyses

Species accumulation curves were constructed in EstimateS for each savanna type in order to asses sampling adequacy (Gotelli and Colwell 2001). This was achieved by using the nonparametric incidence coverage estimator (ICE) (Chazdon et al. 1998), Chao 2, Jack 2 and Michaelis-Menten richness estimators (Colwell and Coddington 1994), all estimators recommended for small sample sizes (Colwell and Coddington 1994, Magurran 2004). If the sample-based rarefaction curves and these estimators converge closely at the highest observed species richness, this observed richness can be considered representative (Longino et al. 2002, Magurran 2004). Multiple estimators were used to asses sampling adequacy because each one is influenced differently by species abundance data and it is difficult to determine which one is the least biased as it involves factors such as community evenness and sampling intensity (Brose et al. 2003). This analysis showed that sampling was incomplete at Satara and Pretoriuskop, but satisfactory at the other sites. However, although sample-based rarefaction curves (i.e. observed richness) together with the richness estimators started flattening off for most study regions (Supplementary materials, Fig. S3), typically they did not reach an asymptote (based on singleton and doubleton values), especially at Satara. Additionally, when each season's species richness estimates were considered separately, an asymptote was not reached. I therefore opted to use the raw species richness values in subsequent analyses because the estimators were considered unreliable and hence the observed richness values were considered to be the best available estimate of richness.

Observed species richness and overall abundance (the latter was only obtained for the wet season sampling) were compared between the savanna types, seasons and burning regimes using one-way analysis of variance (ANOVA) when data were parametrically distributed. Where data were non-parametrically distributed and could not be easily transformed, appropriate non-parametric tests were applied such as a Kruskal-Wallis ANOVA. Due to difficulties associated with collecting and counting all termites found at a bait or in a block of a belt transect, the number of encounters for each method was considered as a surrogate for termite abundance. Abundance is defined as the total number of encounters for each termite species in a transect or grid of baits. An encounter is an occurrence of a population of termites of one species at one point (bait or block of transect) (Davies et al. 2003).

Termites were classified into feeding groups based on the classification of Donovan et al. (2001), which places termites into four groups dependent on the humification of the feeding substrate, which is a measure of the stage of decomposition this feeding substrate is in and ranges from living plants and trees to organic material in the soil (Donovan et al. 2001). Group I comprises the non-termitids, all of which feed on dead wood and grass; Species in groups II-IV are all Termitidae. Group II has a range of feeding habits, which include dead wood, grass, leaf litter and micro-epiphytes; group III feed in the organic rich upper soil layers (broadly 'humus-feeders'); and group IV contains the true soil-feeders which ingest mineral soil. Different termite feeding groups have different ecological roles and so understanding how these groups differ between savanna types, seasons or burning regimes is important ecologically.

Differences in termite assemblage composition, based on the data collected for each sampling method respectively, were analysed between savanna types, seasons and burning regimes using multivariate analyses in Primer v. 5.2 (Clarke and Gorley 2001). Bray-Curtis similarity matrices of the data were constructed in order to asses overall compositional differences. The data were square root transformed before similarity matrices were constructed in order to weight common and rare species equally (Clarke and Warwick 2001).

Analysis of similarity (ANOSIM, Clarke 1994) was used to test if there were significant differences between the assemblages; this is a non-parametric permutation procedure applied to rank similarity matrices which underlie sample ordinations (Clarke and Warwick 2001, Parr et al. 2004), in which a significant global R-statistic of close to one indicates distinct differences between the assemblages compared. Negative values of R indicate that there are more differences between sites of the same treatment than between treatments, and R can take on any value between -1 and 1.

The R-value itself is not unduly affected by the number of replicates in a sample, however, the significance level of this R-statistic is. This can result in a situation where the R-value is, for example, very low, which indicates that assemblages are barely separable, but this value may be significantly different from zero, perhaps leading to an interpretation that the assemblages in question are indeed different. However, this significance level is more a reflection of a high number of replicates or samples, and the R-value is of greater importance for interpretation (Clarke and Warwick 1994, Parr et al. 2004). The opposite may also be true with an R-value being close to one. Similarity percentage analysis (SIMPER) from Primer (Clarke and Warwick 2001) was then conducted on the wet season data in order to identify which species were contributing most to differences between these assemblages.

Termite activity levels were also assessed and compared between savanna types and burning regimes indirectly as a percentage of the baits attacked as well as the intensity of attack on these baits. These data were compared using ANOVA where the data were normally distributed. For data which could not be easily transformed, non-parametric tests, Mann-Whitney U and Kruskal-Wallis ANOVA were applied to the data. Since animal disturbance resulted in a different number of baits been available for termite sampling, the number of encounters and richness values obtained were corrected for the number of baits per site (the number of encounters or species were divided by the number of baits present, giving the number of encounters or species per bait, and this total multiplied by 40 for each site, giving the number of encounters or species per 40 baits).

Results

Across savanna habitats and seasons

Species richness and abundance

Termites from 18 genera and 5 subfamilies were collected during the study; the genus *Anenteotermes* being recorded from South Africa for the first time (Appendix A). When data from all sampling methods and seasons were pooled, there was a significant difference in species richness across the four savanna habitats (ANOVA, $F_{3,43} = 5.016$, $P < 0.005$). Mopani had significantly lower species richness (mean of 4.50 species plot^{-1}, SE = 0.47) than Satara and Pretoriuskop. Satara (mean of 6.75 species plot^{-1}, SE = 0.39) and Pretoriuskop (mean of 7.08 species plot^{-1}, SE = 0.48) had higher richness while Hluhluwe had an intermediate species richness (mean of 5.27 species plot^{-1}, SE = 0.81).

An examination of species feeding groups indicates however, that termites at Mopani and Satara differ to those at the mesic sites (Pretoriuskop and Hluhluwe): Feeding group II dominates the assemblage at Mopani and Satara, whereas the mesic sites are more evenly split between Feeding groups II and III, with Feeding Group IV also being present (Fig. 2).

Using bait data, there is a significant seasonal effect on observed species richness in all savanna types except Mopani (Kruskal-Wallis ANOVA, $H_{2,27} = 1.584$, $P > 0.05$) with the wet season, in general, being most species rich (Fig. 3, see also Appendix A). Termite abundance also differed significantly across the four savannas (Fig. 4a; ANOVA, $F_{3,43} = 14.488$, $P < 0.000001$), with the highest number of encounters at Satara. Considering active searching data, Mopani had significantly fewer occurrences compared with the other three savannas (Fig. 4a; ANOVA, $F_{3,39} = 4.049$, $P < 0.05$).

Assemblage composition

Considering all possible comparisons across savanna types (pair-wise tests), analysis of similarity (ANOSIM) revealed differences in termite assemblages between savannas were most pronounced in the wet season compared to those in the dry and transitional seasons (Table 1). Pair-wise tests between Mopani and Pretoriuskop contributed most to the overall assemblage differences across seasons followed by Satara vs. Pretoriuskop.

Frequency of attack

For all seasons the highest percentage of baits attacked was at Satara (Fig. 5a, ANOVA, $F_{3,43} = 15.089$, $P < 0.000001$; $F_{3,43} = 83.988$, $P < 0.000001$; $F_{2,33} = 12.526$, $P < 0.0001$ for the wet, dry and transitional seasons respectively), and was highest in the wet and transitional seasons and lowest in the dry season for all savannas (Fig. 5a, ANOVA, $F_{2,33} = 5.445$, $P < 0.01$; $F_{2,33} = 28.442$, $P < 0.000001$; $F_{2,33} = 25.828$, $P < 0.000001$; Mann-Whitney U, $U = 16.500$, $P < 0.01$ for Mopani, Satara, Pretoriuskop and Hluhluwe respectively). Post-hoc Tukey HSD tests revealed that while the reduction in frequency of attack from the wet to the dry season was significant for all the savanna types examined, it was especially pronounced at the more mesic sites (Pretoriuskop and Hluhluwe) (Fig. 5a).

Intensity of attack

In all three seasons, the intensity of termite attack was significantly higher at Satara than in the other savannas, which showed very similar intensity levels (however see Mopani when all seasons are combined where the IA is significantly higher than that at Hluhluwe) (Kruskal-Wallis ANOVA, $H_{3,779}$ = 87.048, P < 00001, $H_{3,691}$ = 91.059, P < 00001, $H_{2,592}$ = 73.194, P < 00001, $H_{3,2062}$ = 219.079, P < 00001 for the wet, dry, transitional and all seasons pooled respectively, Fig 5b).

Intensity of attack also differed significantly across seasons at all four sites (Mopani: Kruskal-Wallis ANOVA, $H_{2,503}$ = 19.054, P < 0005; Satara: Kruskal-Wallis ANOVA, $H_{2,604}$ = 55.543, P < 00001; Pretoriuskop: Kruskal-Wallis ANOVA, $H_{2,634}$ = 107.996, P < 0001; Hluhluwe: Mann-Whitney U, U = 8757.5, P < 0.000005), with the dry season having significantly lower levels of attack than the wet and transitional seasons which did not differ from each other (except at Mopani where the transitional season does not differ from either the wet or dry seasons) (Fig. 5b).

Fire effects

Species richness and abundance

There were few clear differences in species richness and occurrence of termites across different fire regimes within each savanna type (Figs. 1, and 4b & c for richness and occurrence respectively). For species richness, the only significant difference was at Pretoriuskop where the August 3 plot had more termite species than the August 1 plot. In terms of the effect of fire on termite abundance, there were only two significant differences, one at Mopani for the AS data (wet season), where the December 3 plot has significantly more termites than the August 1 and Unburnt plots (Fig.4b) and one at Pretoriuskop for the bait data (wet season) where the August 1 plot has significantly more termites than the Unburnt plot (Fig. 4c).

Assemblage composition

When examining differences in termite assemblage composition with burning regime, the results vary with sampling method. For the active searching data, assemblage composition differences between the burning regimes become less pronounced as sites become more mesic: there are three pairs of regime that differ significantly at Mopani (Unburnt vs. August 2, December 3 vs. August 1 and August 2), two at Satara (Unburnt vs. August 1 and August 3) and only one at Pretoriuskop (August 3 vs. August 1) (Table 2). In contrast, when the bait data are considered, differences become more pronounced as sites become more mesic: there are three pairs of regime differences at Pretoriuskop (Unburnt vs. August 1 and December 3, December 3 vs. August 1), one at Satara (December 3 vs. August 1) and none at Mopani. During the dry season, assemblage composition is unaffected by burning regimes, and the transitional season also produces few differences, with the exception being at Mopani (Table 2).

ANOSIM reveals significant difference in assemblage composition with sampling method (active searching and baits) at Mopani and Pretoriuskop ($R = 0.601$, $p = 0.001$ and 0.498, $p = 0.001$ for Mopani and Pretoriuskop respectively). The differences are less pronounced at Satara ($R = 0.247$, $p = 0.001$). The sites where the assemblages are more dissimilar are also the savanna types which show more differences in assemblage response to fire, suggesting that different suites of termites (i.e. Feeding Groups) sampled by the different methods respond differently to fire (Table 3). Active searching targets a broader range of Feeding Groups while baits attract Feeding Group II primarily. In addition, using active searching along the rainfall gradient demonstrated there is a shift in Feeding Group with savanna type: Feeding Group III and IV were sampled primarily at Pretoriuskop, while at Mopani only Feeding Group I and II were sampled. SIMPER showed that most differences were driven by FG II, indicating differences in abundances are more important, however, this did vary with savanna type and sampling method (Supplementary material, Table S4).

Frequency and intensity of attack

There is no significant difference in the percentage of baits attacked by termites between burning regimes at any of the four savanna types in any of the three seasons. However, with intensity of attack, in KNP the response to burning regime becomes more pronounced as sites become more mesic (Fig. 6); there is no difference in termite attack between any of the burning regimes at Mopani (Fig. 6a), compared with one difference found in Satara (Fig. 6b) and three differences found at Pretoriuskop (Fig. 6c).

Environmental variables

Data for the environmental variables are shown in Table 3. Grass cover generally increased as fire intensity and frequency decreased as did canopy cover. Bare ground showed the opposite relationship, increasing with fire intensity and frequency. Temperatures decreased with increasing rainfall and latitude.

Discussion

Diversity across savanna habitats

Termite diversity differed significantly along the rainfall gradient in terms of species richness, abundance and assemblage composition. This corresponds to extensive variation in rainfall, vegetation and soil type. In semiarid areas such as South Africa, precipitation sets limits to net primary productivity (NPP), giving rise to a strong association between these two variables (see O'Brien 1998, O'Brien et al. 2000, van Rensburg et al. 2002). It is therefore reasonable to assume that changes in rainfall result in changes in NPP across the study sites, with corresponding impacts on termite diversity, as predicted by species-energy theory (see Rosenzweig and Abramsky 1993, Wright et al. 1993). Indeed, Mopani (the most arid site, and presumably with the lowest NPP) had significantly lower species richness and abundance than all other sites. This is in keeping with Eggleton et al. (1994), who found a moderately strong relationship between NPP and termite diversity within biogeograpic regions.

Although termite diversity is highest in the warm, wet tropics (Eggleton et al. 1994, Eggleton 2000), I found species richness was highest at Pretoriuskop, before declining at Hluhluwe, the wettest site. Although Hluhluwe has the highest rainfall, the higher elevation and generally increased cloud cover and mist at this site result in lower temperatures than those along the gradient further north, perhaps explaining to some extent the decrease in species richness. Termites are susceptible to temperature changes (Ueckert et al. 1976, Ohiagu 1979, Smith and Rust 1994, Korb and Linsenmair 1998), and soil-feeders are reported to be excluded by low temperatures (Bignell and Eggleton

2000, Donovan et al. 2002, Palin et al. in press), hence a decrease in diversity and proportion of soil feeders (relative to Pretoriuskop) at Hluhluwe. Independent of burning regimes, interactions between rainfall, NPP and temperature thus seem important for termite diversity responses in savannas.

The clearest trend across the investigated rainfall gradient is that the termite assemblage changes, especially in functional group composition. Because soil feeders are especially susceptible to habitat desiccation and require malleable, carbon-rich soils (Bignell and Eggleton 2000) they tend to be excluded from drier sites; none were sampled at Mopani and although a few species occurred at Satara their abundances were relatively low. Throughout the tropics closed canopy forest has a higher diversity of termites, this is likely to be due to environmental stability and resource availability in tropical rain forests (Eggleton et al. 1994, Eggleton 2000). Similarly, savannas with higher rainfall and more canopy cover are likely to be more favourable for termites. It is therefore unsurprising that the mesic sites (Pretoriuskop and Hluhluwe) have higher levels of termite diversity. Eggleton et al. (1995) and Eggleton et al. (1996) found that in tropical forests when disturbance occurs which opens up the canopy, there is a decrease in termite diversity, particularly of soil feeders (FG III and IV). The absence of these FGs in the drier savanna sites would suggest that this pattern is also evident on the landscape scale.

Variation in soil type across the savanna types (clay at the two drier sites and sandy soils at the mesic sites) is also likely to influence termites since they are considered to be soil animals (Holt and Lepage 2000). Termites have a profound affect on soil characteristics (see Holt and Lepage (2000) for a review), and are, in turn, strongly influenced by soil properties (see Lee and Wood (1971) for a review). Close inspection of the assemblages sampled suggests that sites with a similar broad soil type are more similar, and this factor cannot be ignored when seeking to understand why these termite communities differ. The ability of mound building and subterranean termites to construct mounds and tunnels respectively is influenced largely by the clay, silt and sand content of soils (Lee and Wood 1971). Changes in these ratios observed in this study will no doubt affect termite diversity.

Only the driest site, Mopani, had significantly lower abundance when considering the active searching data (mirroring the species richness results). When baiting data are considered, Satara (low to intermediate rainfall) stands out with significantly higher abundance than all other sites. Because baiting attracts termites primarily from Feeding Group II, my results suggest that at Satara these termites dominate, being replaced by other FGs as rainfall increases, perhaps as a result of competition with fungi in wetter savannas (Aanen and Eggleton 2005) Termite activity (primarily from baiting and hence a reflection of FG II) reflected this same pattern, with significantly higher levels of attack frequency and intensity at Satara. As the range of humification of the feeding substrate decreases, humivorous termites (FG III and IV) disappear and are replaced by fungus-growers and wood-feeders (FG II); a pattern which has been shown previously in African and Asian savannas (Buxton 1981, Bignell and Eggleton 2000). Satara also has comparably higher mammalian herbivore densities than the other study sites, resulting in higher concentrations of dung in these areas. This higher dung concentration may lead to higher nutrient concentrations in the soil as well as to more available food for termites, which feed on drier dung material, especially termites from FG II (Freymann et al. 2008). The processing of dung material by termites may in turn facilitate nutrient cycling, increasing plant productivity (and possibly grass nutrient quality) making the area more favourable for herbivores, thus creating a positive feedback loop. Similar patterns have been documented by Gosling (*unpublished*) in Hluhluwe-iMfolozi Park: higher levels of termite activity (of FG II) were recorded in the drier iMfolozi region than the mesic Hluhluwe. At iMfolozi, herbivore densities are also higher, presumable providing more nutrients for the termites. The feedback link between herbivore and termite densities remains, however, to be tested.

Seasonal effects

The higher levels of termite activity and species richness during the wet and transitional seasons follows the general trend for insect activity (Wolda 1988) and similar findings for termites recorded elsewhere (e.g. west Africa: Ohiagu (1979), Western Australia: Abensperg-Traun (1991), northern Australia: Dawes-Gromadzki and Spain (2003), but see Dibog et al. (1998) where tropical forest termites in Cameroon were largely unaffected by seasonality). This is likely to be a reflection of greater food and moisture availability during the wet season and the effect extends into the transitional season due to a lag effect on vegetation growth and also because this season may be better suited to termite foraging than the wet season (e.g. see Dawes-Gromadzki and Spain 2003). Those authors recorded higher levels of termite activity during the transitional season and deduced that this was because of heavy monsoonal rainfall in northern Australia during the wet season, causing soil to become waterlogged and hence unsuitable for termite foraging. Dibog et al. (1998) also found a negative relationship between termite activity and rainfall, especially within a two day period following a rainfall event, and concluded that this was possibly due to flooding of termite subterranean galleries. In this study, the mesic savanna at Pretoriuskop showed higher activity levels during the transitional season, possibly also due to waterlogging of soils and above-ground seepage during the wet season, which was apparent during sampling. In the more xeric savanna sites, activity and diversity peaked during the wet season rather than the transitional and is probably because waterlogged soils and flooding are not common features here, nor the rainfall enough to have a pronounced lag effect into the transitional season, suggesting that termites have an optimal rainfall range for activity, being inactive when conditions are excessively wet or dry. Unfortunately, transitional season data are unavailable for Hluhluwe.

Being soft-bodied and susceptible to desiccation, termites are also likely to move deeper into the soil during dry periods, becoming biologically inactive and less likely to be sampled with baiting or active searching. During the wet season, as the upper horizons of the soil become moister, termites move up in the profile and become more susceptible to sampling, thereby increasing recorded activity levels.

Fire effects

This study used long-term burning regimes, a broader range of fire treatments and a wider variety of sampling methods than previous studies (Chapter 2). This enabled us to assess fire effects on the entire termite assemblage. Termites have subterranean habits and are protected from the direct effects of fire, so the effects of repeated burning are thus likely to be primarily indirect, through changes to vegetation structure and resource (food) availability.

Overall, termite assemblages in this study showed striking resilience to fire: species richness and abundance showed few significant differences across burning regimes, although there were some differences between burning treatments at Pretoriuskop. This is in keeping with a previous study carried out on savanna ant assemblages using the same experimental burning plots (Parr et al. 2004), as well as studies elsewhere on savanna insect responses to burning (Andersen et al. 2003, Andersen et al. 2005) and for biodiversity more broadly (Parr and Andersen 2006). My results contrast, however, with studies on termites and fire from elsewhere (see Chapter 2 for a review). The contrast with other studies is likely to be because most previous studies focused solely on mound-builders and sampled only extremes of fire regimes (annual and unburnt) (e.g. Benzie 1986, Traoré and Lepage 2008).

While little response to burning was detected when examining species richness and abundance, at the assemblage level some patterns could be detected. This aspect of termite diversity has not been investigated previously within long-term burning regimes. Additionally, my study revealed that the sampling method used also had an effect on the termite responses recorded, indicating that different suites of termites (sampled by different methods) respond differently to fire; it may thus be difficult to get a full understanding of the effect of fire on termites unless a variety of sampling methods are employed.

When active searching (which samples the entire range of Feeding Groups, although still has a seasonal bias) was used, more pronounced differences in assemblage composition between fire treatments were recorded at the drier sites than the wettest (Pretoriuskop). Since soil feeding termites are more susceptible to desiccation and disturbance than other groups (Eggleton et al. 1995, 1996), at arid sites they may better be able to survive on unburnt sites which have more canopy and grass cover. Indeed *Promirotermes* spp., and *Astalotermes* spp., both FG III, were found almost exclusively on unburnt plots at Satara. However the presence of FG I termites (*Hodotermes mossambicus*) at the most arid site (Mopani) may have biased results here; those termites were only sampled at the December 3 plot and tend to occur in a patchy, sporadic fashion (*personal observation*). These grass harvesters contributed 10 % of the dissimilarity between the December 3 and August burns and did not occur on other fire plots. These results should also be treated with some caution as active searching has been little tested in arid savannas (Chapter 4, but see Zeidler et al. (2004) for a comparison with baiting) and its success is likely to be closely associated with the occurrence of rainfall events in those environments. If sampling had occurred on another day, *H. mossambicus* may well have not been sampled.

However, when the bait data are considered, responses to fire at the assemblage level differ more strikingly along the rainfall gradient. Baiting targets Feeding Group II, the most dominant, diverse and widespread feeding group in savannas and thus probably the most important from a functional perspective. My results suggest that for these termites, burning has differing levels of effect across the savanna habitats, and that effect is probably dependent on vegetational effects. At the arid Mopani site, there are negligible effects; here, FG III and IV are absent and vegetation is little affected by fire, resulting in few differences in the overall habitat and hence no measurable effect on termite composition.

In contrast, as rainfall increases, fire has a more pronounced effect on the vegetation (Parr et al. 2004), and the effect on termite diversity and activity becomes concomitantly more noticeable. At Pretoriuskop, the most striking differences are between unburnt and intense (August) fires, as well as between frequent, intense fires (August 1) and cool, less frequent fires (December 3). Since baiting does not generally attract soil feeders, these differences are likely to be attributed to differences in relative occurrences of termite species. Indeed, the differences between these plots are driven predominantly by the genus *Microtermes*, which is present on all plots but is most abundant on burnt (especially frequently burnt) plots. This would support the idea of FG II termites been excluded by soil feeders as burning regimes become less frequent and intense, allowing the humification of the feeding substrate to increase and the subsequent dominance of FG III and IV (Buxton 1981, Bignell and Eggleton 2000) where they can compete with fungi (Aanen and Eggleton 2005), indeed more termites from FG III and IV were present on unburnt plots (mean per plot) in the present study.

At the wettest site (Pretoriuskop), there is also a significant trend of more termites and activity with increasing fire intensity, and especially frequency. As discussed above, previous studies have found that as aridity increases (Eggleton et al. 1995, 1996) and the subsequent humification of the feeding substrate decreases (Buxton 1981, Bignell and Eggleton 2000), humivorous termites are excluded and replaced with fungus-growers and wood-feeders (which are attracted to baits). It would appear that fire has a similar effect in these mesic savannas, opening up the canopy for increased desiccation of the substrate, allowing fungus-growers and wood feeders of Feeding Group II to replace soil feeding termites, possibly as a result of fungus-growing termites being able to outcompete fungal decomposers in more desiccated environments where soil-feeders cannot survive (Aanen and Eggleton 2005). Also of importance here are the increased activity levels on annually burnt plots, which are possibly linked to vertebrate herbivore densities. Herbivores are likely to favour grazing on burnt plots due to higher forage potential and visibility (Wilsey 1996, Archibald and Bond 2004, Parrini and Owen-Smith 2009). This could result in a positive-feedback loop as more dung will be available here, both as food for termites (of FG II) and for increased soil nutrients which may influence termite distributions (Crist 1998).

Conclusions

Sampling termites from a variety of methods, although important in order adequately to sample all Feeding Groups, makes it difficult to draw broad conclusions because different data sets cannot always be combined. In addition, different termite feeding groups seem to react differently to fire, again making conclusions difficult.

However, there are distinct differences along the rainfall gradient, in terms of both termite diversity across savanna types and termite responses to fire. While diversity increases with rainfall so do responses to the long-term burning regimes. Although, termite communities were, overall, highly resilient to fire, the greatest effects were observed at Pretoriuskop (the most mesic site investigated) in terms of species richness, abundance, assemblage composition and activity levels (in terms of the dominant FG).

Re-visiting the concept suggested by Sankaran et al. (2005) of stable and unstable savannas dependent on rainfall, in this study Mopani and Satara would represent stable savannas and Pretoriuskop an unstable savanna. Sankaran et al. (2005) argue that fire has increased effect in unstable savannas in terms of vegetation structure and canopy cover, and my results indicate that faunal responses seem to follow this same pattern, at least with regard to termites, especially those attracted to baits.

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Table 1: Analysis of similarity (ANOSIM) for termite assemblages between four savanna habitats, across three seasons. For the dry and transitional seasons, presence/absence data were used (data from active searching and baits combined), and for the wet season abundance data were used (data from the two sampling methods analysed separately). AS = active searching. Baits = cellulose baits. The R-statistic is a measure of similarity of assemblages, the closer this value is to 1, the more dissimilar assemblages are (Clarke & Warwick 2001). *P* is considered significant at the α-level of 0.05. Highlighted values are those above or equal to 0.250 which are considered to be markedly dissimilar (Clark and Warwick 2001).

	Wet (AS)		Wet (baits)		Dry		Transitional	
	R	P	R	P	R	P	R	P
Global R	**0.433**	0.001	**0.397**	0.001	**0.271**	0.001	0.116	0.009
Paired savanna comparisons								
Mopani vs. Satara	**0.398**	0.005	**0.420**	0.001	0.185	0.012	0.074	0.141
Mopani vs. Pretoriuskop	**0.798**	0.001	**0.434**	0.001	**0.393**	0.001	0.191	0.004
Mopani vs. Hluhluwe	**0.376**	0.002	**0.287**	0.002	0.203	0.006		
Satara vs. Pretoriuskop	**0.445**	0.001	**0.574**	0.001	**0.326**	0.001	0.074	0.074
Satara vs. Hluhluwe	**0.300**	0.001	**0.401**	0.001	**0.389**	0.001		
Pretoriuskop vs. Hluhluwe	**0.339**	0.001	0.242	0.011	**0.262**	0.004		

Table 2: Analysis of similarity (ANOSIM) for termite assemblages between four burning regimes at three savanna habitats and during three seasons. For the dry and transitional seasons, presence/absence data were used (data from active searching and baits combined), and for the wet season abundance data were used (data from the two sampling methods analysed separately). AS = active searching. Baits = cellulose baits. The R-statistic is a measure of similarity of assemblages, the closer this value is to 1, the more dissimilar assemblages are (Clarke and Warwick 2001). *P* is considered significant at the α-level of 0.05. Highlighted values are those above or equal to 0.250 which are considered to be markedly dissimilar (Clark and Warwick 2001).

	Wet AS	Wet baits	Dry	Transitional
Site	R	R	R	R
Mopani				
Global R	0.229	− 0.145	− 0.205	0.205
Unburnt vs. August 1	0.000	0.000	− 0.111	0.241
Unburnt vs. August 2	**0.250**	0.074	− 0.148	**0.296**
Unburnt vs. December 3	0.000	− 0.111	− 0.093	0.241
December 3 vs. August 1	**0.750**	− 0.296	− 0.315	− 0.222
December 3 vs. August 2	**0.750**	− 0.259	− 0.407	**0.407**
August 2 vs. August 1	− 0.500	− 0.222	− 0.315	**0.500**
Satara				
Global R	0.137	0.031	− 0.012	− 0.096
Unburnt vs. August 1	**0.481**	0.000	− 0.130	0.204
Unburnt vs. August 3	**0.259**	− 0.111	− 0.093	0.000
Unburnt vs. December 3	0.148	− 0.148	− 0.037	− 0.148
December 3 vs. August 1	0.241	**0.333**	− 0.074	− 0.130
December 3 vs. August 3	− 0.037	− 0.111	− 0.315	− 0.074
August 3 vs. August 1	− 0.444	0.074	− 0.130	− 0.370
Pretoriuskop				
Global R	0.074	0.170	− 0.150	− 0.069

Unburnt vs. August 1	0.000	**0.259**	0.056	0.000
Unburnt vs. August 3	0.148	− 0.259	− 0.481	− 0.093
Unburnt vs. December 3	− 0.185	**0.296**	− 0.352	− 0.074
December 3 vs. August 1	0.074	**0.630**	0.130	− 0.111
December 3 vs. August 3	0.185	0.148	0.130	− 0.074
August 3 vs. August 1	**0.296**	0.074	− 0.481	− 0.111

Table 3: Mean percentage values for vegetation and overhead canopy cover as well as mean temperature readings recorded during the wet season at each savanna type and burning regime. G = grass, DGL = dead grass litter, DLL = dead leaf litter, BG = bare ground, F = forbs, WV = woody vegetation, DW = dead wood, R = rock and D = dung.

	Percentage Cover										
Site	G	DGL	DLL	BG	F	WV	DW	R	D	Canopy cover	Temperature
Mopani	**26.49**	**15.05**	**6.99**	**46.09**	**0.84**	**0.66**	**2.14**	**0.35**	**1.38**	**1.53**	**32.78**
Unburnt	35.68	20.85	10.10	28.53	0.48	1.10	1.70	0.18	1.40	2.88	
December 3	31.30	15.03	6.30	42.65	0.53	0.55	2.20	0.10	1.35	1.20	
August 3	16.33	12.85	5.60	57.70	1.95	0.53	2.80	0.75	1.50	0.48	
August 1	22.68	11.48	5.95	55.50	0.40	0.48	1.88	0.38	1.28	1.58	
Satara	**34.83**	**12.08**	**0.88**	**45.56**	**2.75**	**1.40**	**0.73**	**0.33**	**1.43**	**1.36**	**29.82**
Unburnt	47.78	26.48	1.73	15.73	3.62	2.22	0.08	0.47	1.89	3.18	
December 3	43.35	10.92	0.72	40.73	1.35	1.22	0.48	0.30	0.93	1.72	
August 3	34.68	8.93	0.65	48.85	2.89	1.27	0.87	0.22	1.65	0.50	
August 1	13.52	1.97	0.42	76.93	3.17	0.90	1.50	0.35	1.25	0.05	
Pretoriuskop	**45.73**	**13.18**	**5.59**	**28.92**	**2.23**	**1.67**	**0.56**	**0.64**	**1.48**	**7.43**	**24.78**
Unburnt	42.03	16.05	10.68	21.55	3.48	2.00	0.20	1.83	2.20	21.03	
December 3	53.43	22.10	7.30	12.15	2.23	0.93	0.48	0.23	1.18	2.15	
August 3	56.78	13.53	2.83	22.05	1.45	1.75	0.50	0.33	0.80	2.75	
August 1	30.70	1.05	1.55	59.93	1.78	2.00	1.05	0.20	1.75	3.78	
Hluhluwe	**50.44**	**5.61**	**7.00**	**23.72**	**5.06**	**2.25**	**4.76**	**1.09**	**0.22**	**14.45**	**23.45**

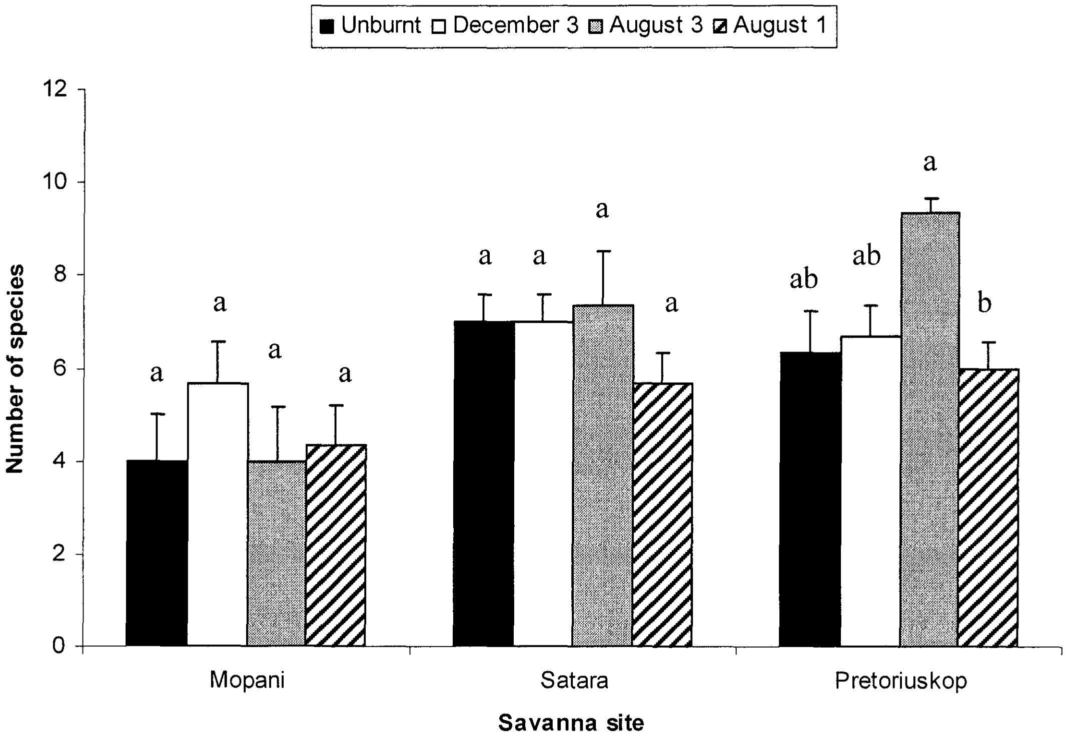


Figure 1: Mean (± 1 SE) observed termite species richness for each burning regime across three savanna types for all methods and seasons combined. Symbols denote significant differences. Letters denote sites which are the same statistically within a savanna habitat, differences are considered significant at the α-level of 0.05.

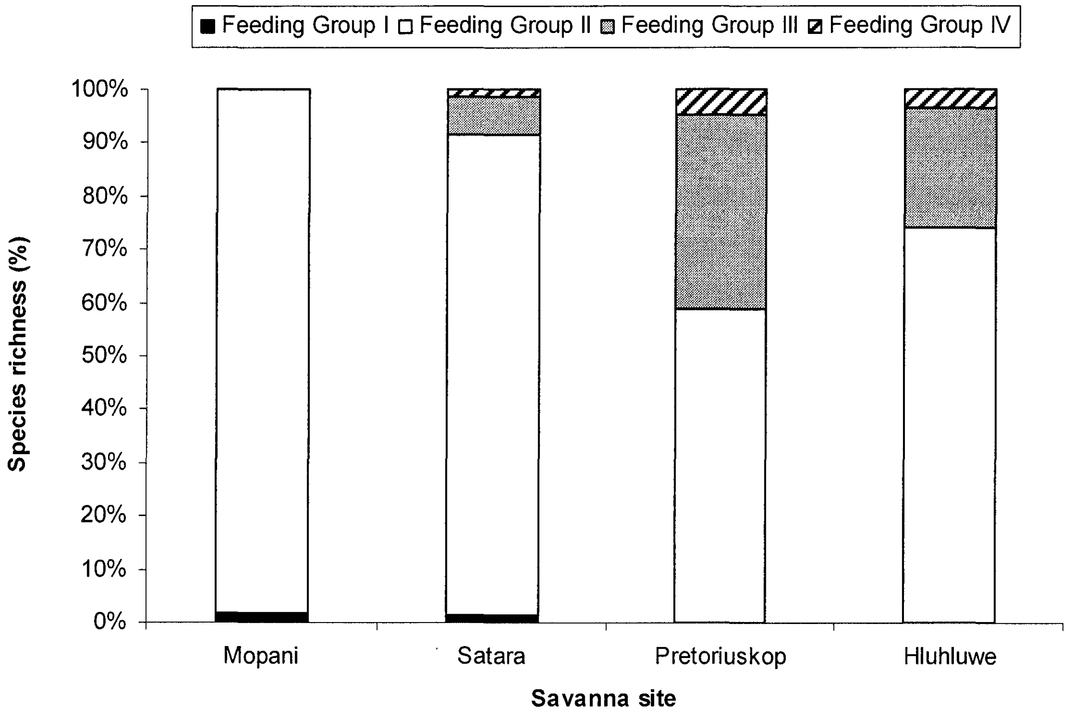


Figure 2: The relative contribution (measured as a percentage) each feeding group makes to the termite assemblage. Data are from all seasons and all sampling methods. Feeding group I comprises the lower termites which feed on dead wood and grass; group II is made up of Termitidae with a range of feeding habits which include dead wood, grass, leaf litter and micro-epiphytes; group III feed in the organic rich upper soil layers and are also Termitidae; and group IV contains the true soil-feeders which ingest mineral soil, again all Termitidae.

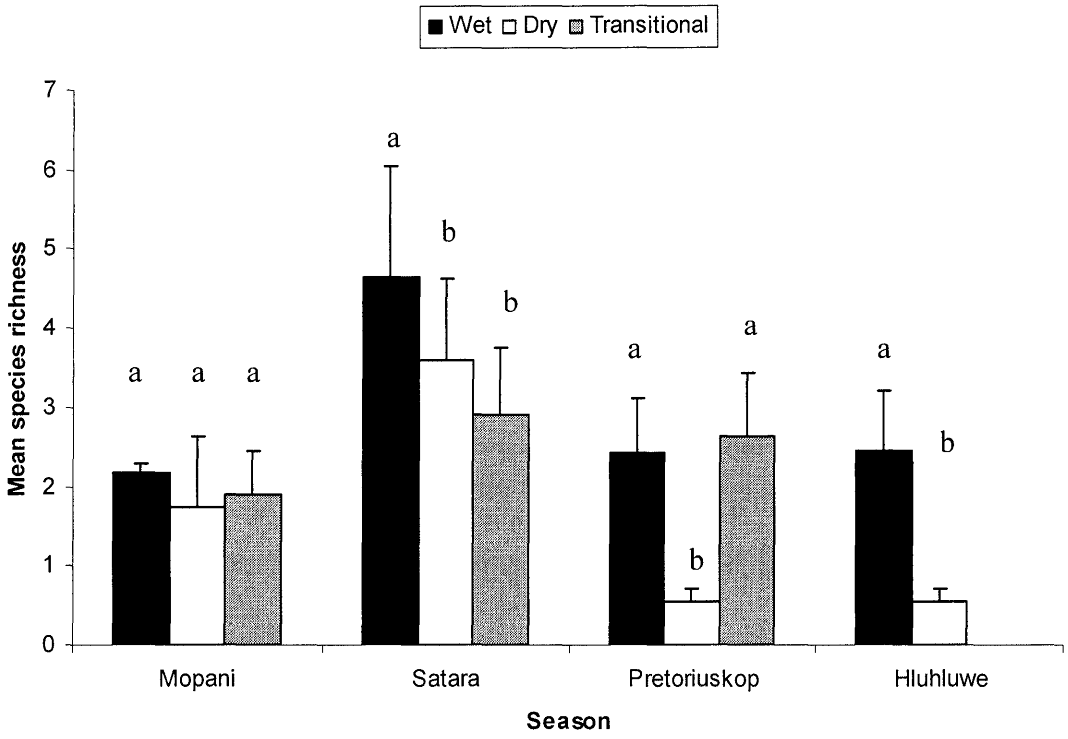
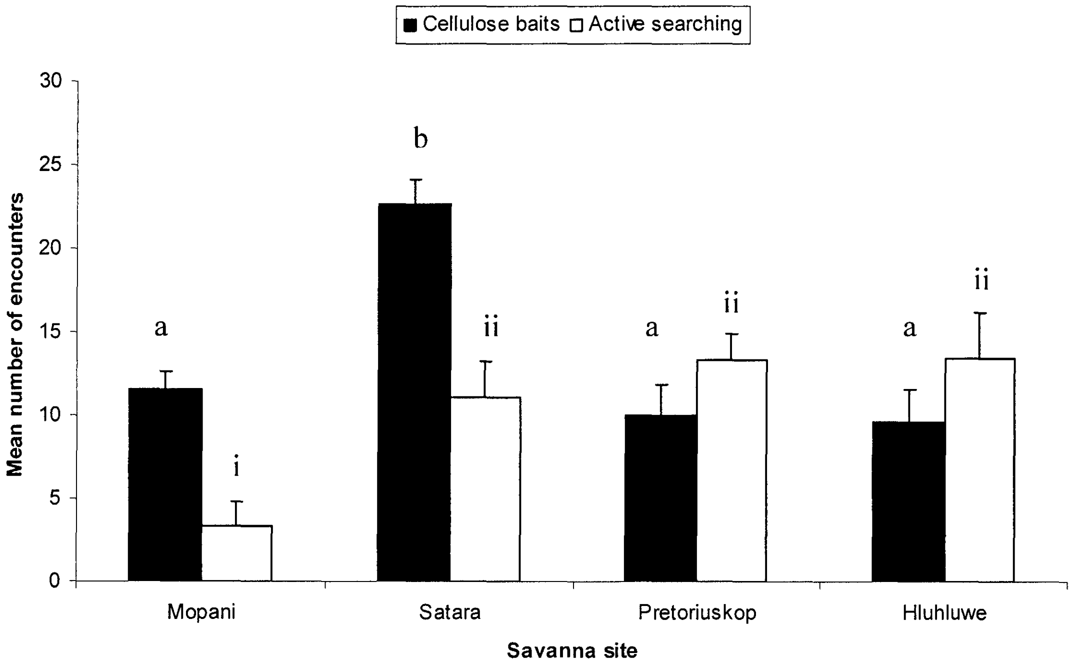
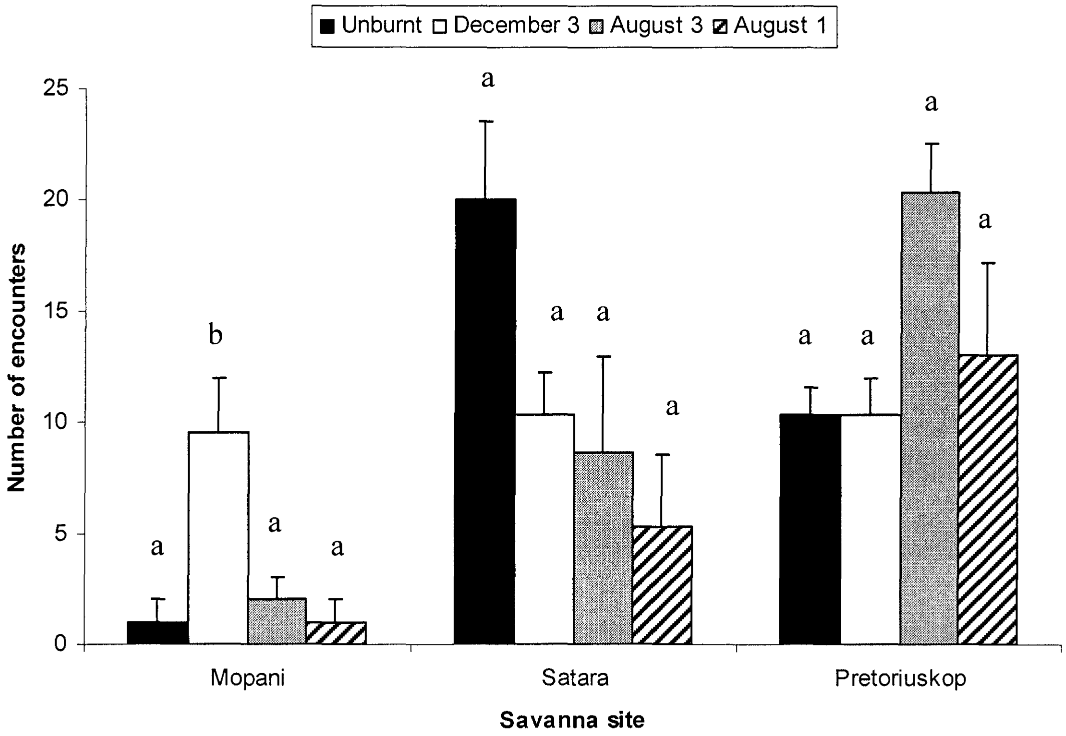


Figure 3: Mean (± 1 SE) observed termite species richness recorded at paper baits (both buried and on the surface) across three seasons and four savanna types. Letters denote sites which are the same statistically within one savanna habitat; differences are considered significant at the α-level of 0.05.

a.


■ Cellulose baits □ Active searching
Mean number of encounters
30
25
20
15
10
5
0
a
i
b
ii
a
ii
a
ii
Mopani
Satara
Pretoriuskop
Hluhluwe
Savanna site

b.


■ Unburnt □ December 3 ▨ August 3 ▨ August 1
Number of encounters
25
20
15
10
5
0
a
b
a
a
a
a a
a
a a
a
a
Mopani
Satara
Pretoriuskop
Savanna site

c.

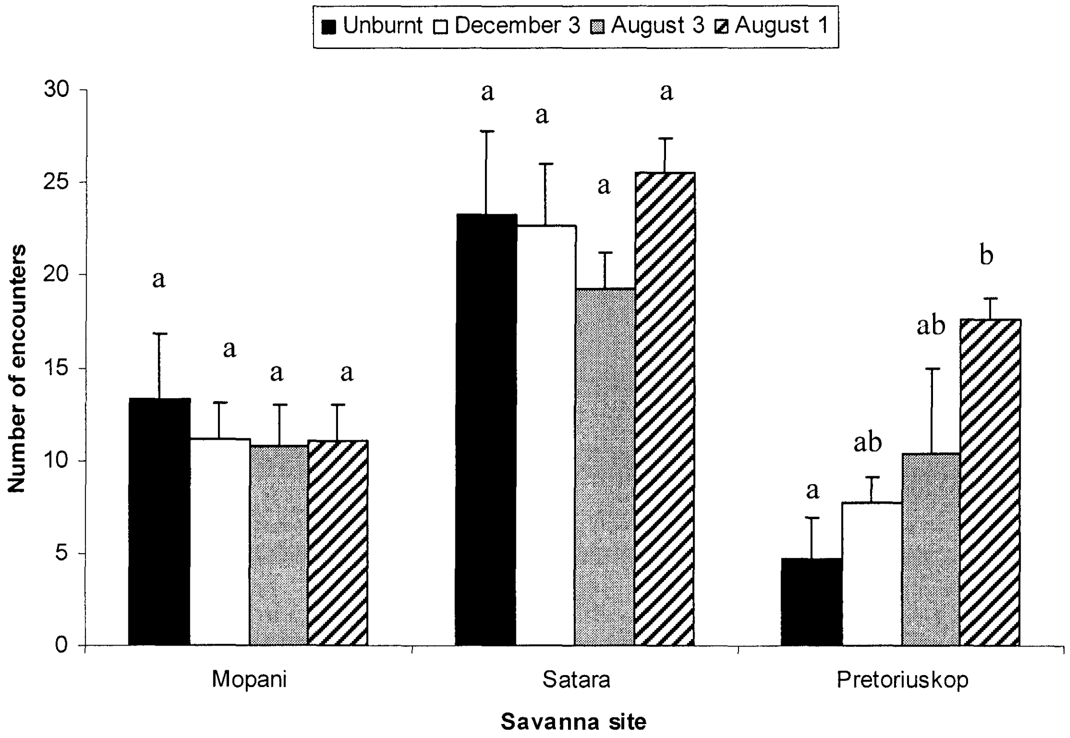


Figure 4: Overall termite abundance a) between savanna types for each wet season method separately and for b) active searching data and c) cellulose baits between burning regimes at each savanna type during the wet season. Letters denote sites which differ significantly within the respective savanna habitat, with differences being considered significant at the α-level of 0.05.

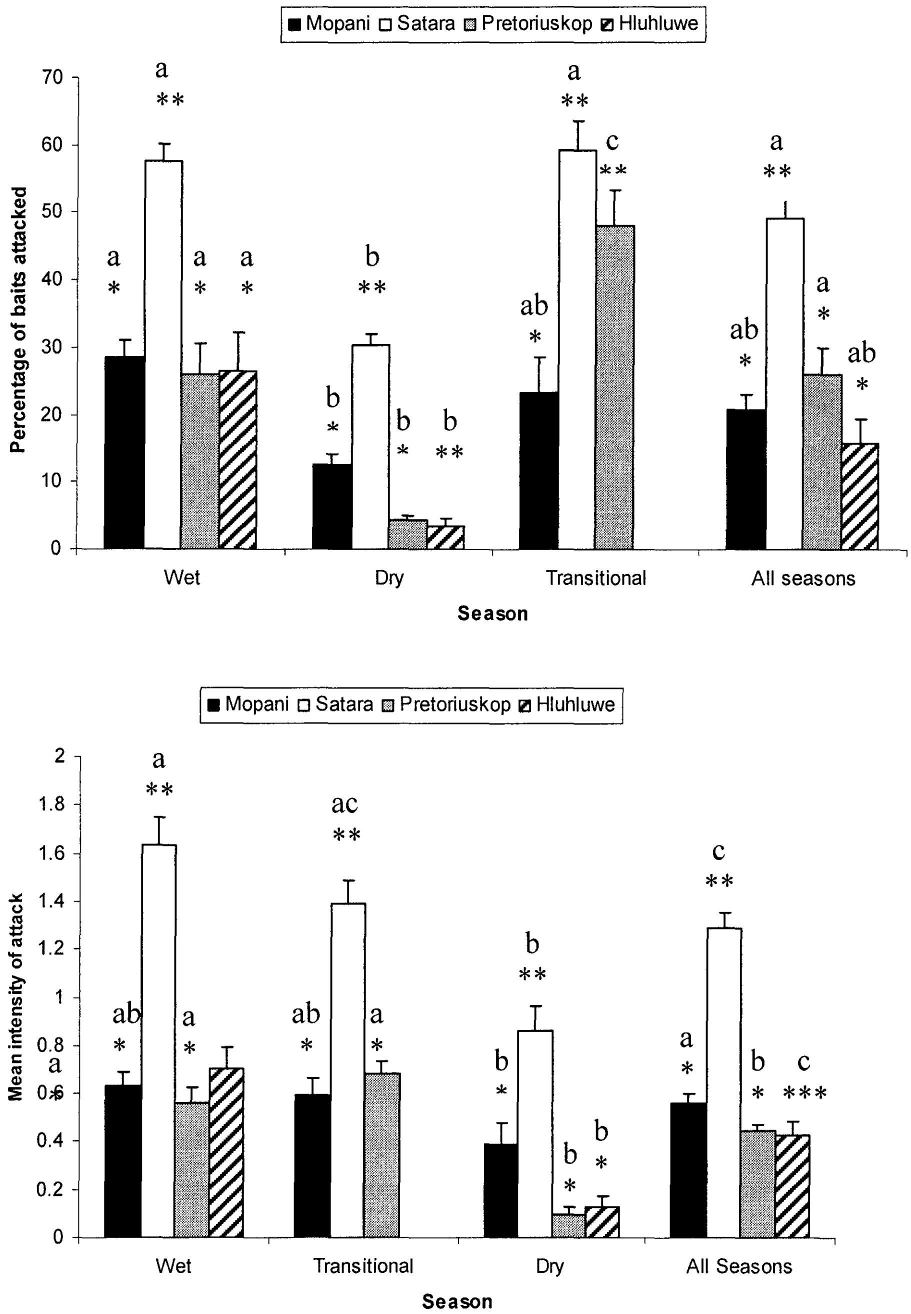
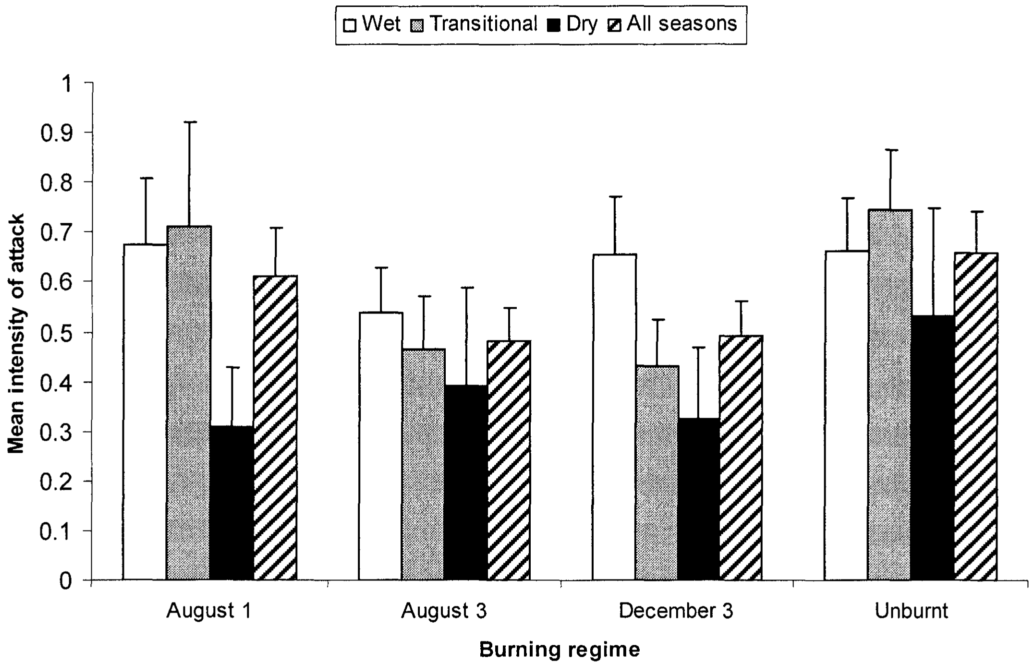
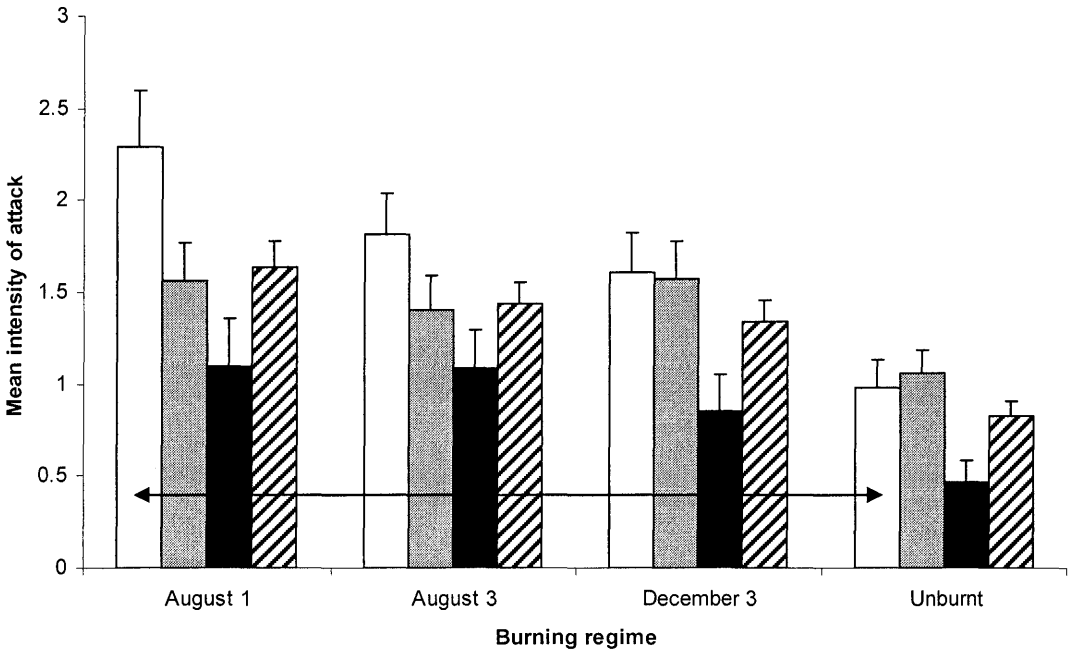


Figure 5: Mean (± 1 SE) a) frequency and b) intensity of termite attack recorded at paper baits (both buried and on the surface) at four savanna sites and across three seasons. An asterisk denotes significant differences between savannas in a given season and letters denote significant seasonal differences within savanna sites, differences are considered significant at the α-level of 0.05.

a.


□ Wet ▨ Transitional ■ Dry ▨ All seasons
Mean intensity of attack
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
August 1
August 3
December 3
Unburnt
Burning regime

b.


Mean intensity of attack
3
2.5
2
1.5
1
0.5
0
August 1
August 3
December 3
Unburnt
Burning regime

c.

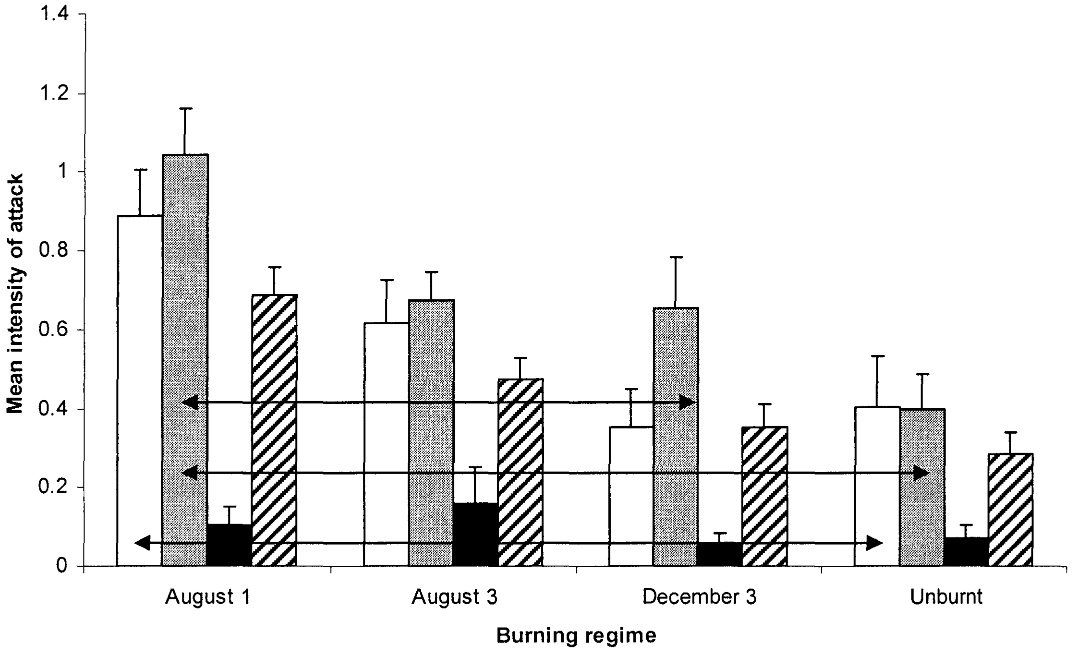


Figure 6: Mean (± 1 SE) intensity of termite attack recorded at paper baits (both buried and on the surface) across four burning regimes and three seasons at a) Mopani, b) Satara, and c) Pretoriuskop. Arrows distinguish sites which differ significantly, with differences being considered significant at the α-level of 0.05.

Appendix A

Termite species sampled in the four savanna habitats with their respective feeding groups. Codes in parenthesis indicate the season/s in which a particular species was sampled; w = wet, t = transitional, and d = dry season. Feeding group I comprises the lower termites which feed on dead wood and grass; group II is made up of Termitidae with a range of feeding habits which include dead wood, grass, leaf litter and micro-epiphytes; group III feed in the organic rich upper soil layers and are also Termitidae; and group IV contains the true soil-feeders which ingest mineral soil, again all Termitidae.

Species	Mopani	Satara	Pretoriuskop	Hluhluwe	Feeding group
Hodotermitidae					
Hodotermes mossambicus	X(w)	X(d)			I
Termitidae					
Macrotermitinae					
Allodontermes rhodesiensis	X(w,t,d)	X(w,t,d)	X(w,t,d)	X(w,d)	II
Ancistrotermes latinotus	X(w,t)	X(w,t,d)	X(w,t,d)	X(w)	II
Macrotermes falciger	X(d)		X(d)		II
Macrotermes michaelseni	X(w,t,d)	X(w,t,d)	X(t)	X(w)	II
Macrotermes natalensis	X(t,d)	X(w,d)	X(w,d)		II
Microtermes spp.	X(w,t,d)	X(w,t,d)	X(w,t,d)	X(w,d)	II
Odontotermes sp. 1			X(w,t,d)	X(w)	II
Odontotermes sp. 2		X(w)	X(w)	X(w,d)	II
Odontotermes sp. 3	X(w,t,d)	X(w,t,d)	X(t,d)	X(w,d)	II
Apicotermitinae					
Adaiphrotermes spp			X(w)	X(w)	III
Alyscotermes spp			X(w)	X(w)	III
Anenteotermes spp			X(w)		III

Astalotermes spp.		X(w)	X(w,t)	X(w)	III
Termitinae					
Amitermes hastatus		X(w)	X(d)		II
Amitermes messinae		X(w)	X(d)		II
Angulitermes spp.		X(w)			III
Cubitermes spp.			X(w)		IV
Lepidotermes spp.		X(d)	X(w)	X(w)	IV
Microcerotermes spp.	X(w,t,d)	X(w,t)	X(w,t,d)	X(w,d)	II
Promirotermes spp.		X(w)	X(w)	X(w)	III
Nasutitermitinae					
Trinervitermes trinervoides		X(w)	X(w)	X(w,d)	II
Rhadinotermes coarctatus			X(w)		II

Supplementary Material

S1: *Study site*

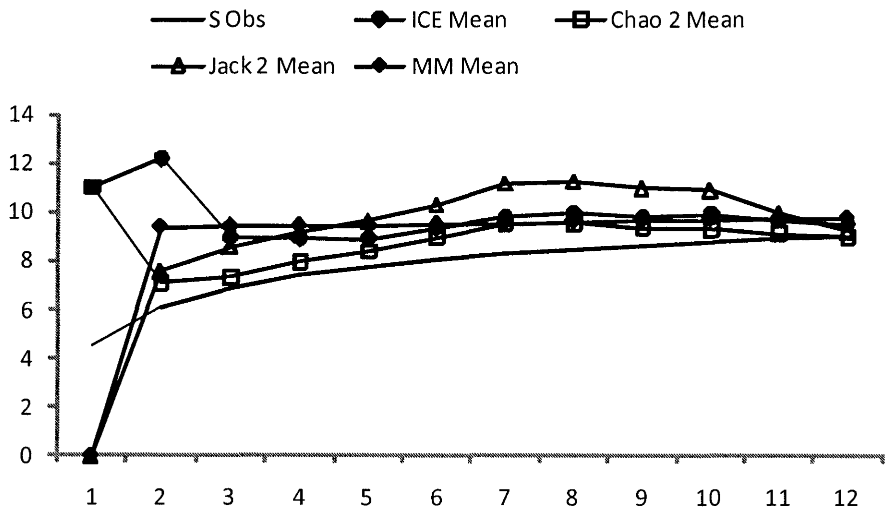
The three replicates used in the Mopani section of KNP were Tsendse (23°41′S 31°31′E), Mooiplaas (23°34′S 31°27′E) and Dzombo (23°26′S 31°22′E); the replicates used in the Satara region were N'wanetsi (24°26′S 31°51′E), Marheya (24°32′S 31°46′E) and Satara (24°24′S 31°45′E); and the replicates in the Pretoriuskop area were Kambeni (25°15′S 31°26′E), Numbi (25°13′S 31°20′E) and Shabeni (25°12′S 31°23′E). In HiP, all sites were located in the northen Hluhluwe section of the reserve.

The Mopani plots were situated in the Mopani shrubveld, which is a mopani (*Colophospermum mopane* J. Kirk ex J. Léonard) dominated habitat with few other woody species present (Low & Rebelo 1996). The mean annual rainfall is 450 to 500 mm and the area ranges in altitude from 300 to 340 m a.s.l. (Gertenbach 1983). In the Satara region, the plots were situated in a mixed knobthorn *Acacia nigrescens* Oliv. and marula *Sclerocarya birrea* (A. Rich. Hochst.) savanna in the sweet lowveld bushveld (Low & Rebelo 1996). The area ranges in altitude from 240 to 320 m a.s.l. and has a mean annual rainfall of 550 mm (Gertenbach 1983). The Pretoriuskop region is sour lowveld bushveld, consisting of open tree savanna dominated by silver clusterleaf (*Terminalia sericea* Burch. ex DC), but bushwillow (*Combretum collinum* Fresen.) is also common (Low & Rebelo 1996). The region has a mean annual rainfall of 700 mm and the altitude varies from 560 to 640 m a.s.l. (Gertenbach 1983). The sites situated in HiP were located within Natal lowveld bushveld, dominated by various acacia species, notably *A. tortilils* and *A. karoo*., but with several other species also being common (Low & Rebelo 1996). The mean annual rainfall here is 800 to 900 mm and the altitude ranges from 500 to 750 m a.s.l. (Archibald et al. 2005). Both the Mopani and Satara regions have basalt-derived clay soils while the Pretoriuskop region has granite-derived sandy soils (Gertenbach 1983). At Hluhluwe the underlying geology is predominantly sandstone and shale resulting in sandy soils (Archibald et al. 2005).

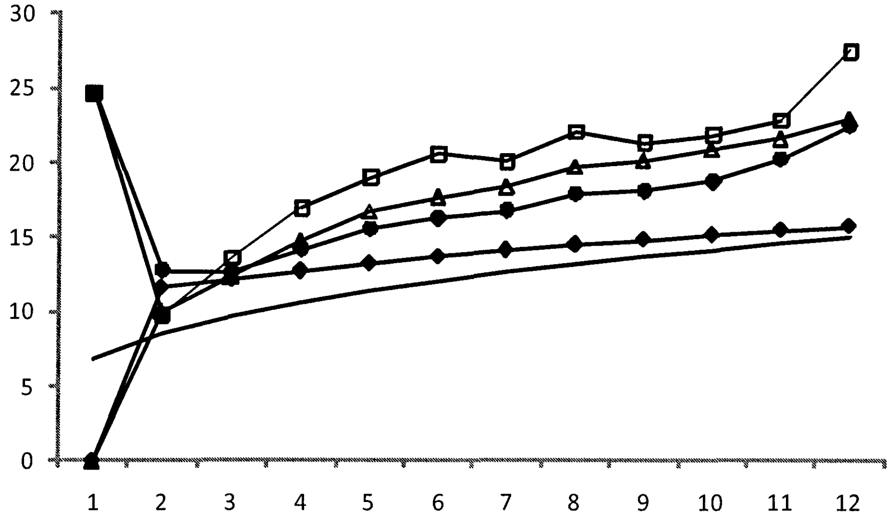
S2: *Modification of standardised transect method*

The active searching transect method was modified from that of Jones & Eggleton in that less time was spent searching in each block (ten minutes in my study compared to the standard sixty minutes), this was primarily because the Jones & Eggleton method was designed for tropical forests which have a much higher termite diversity and density than semi-arid savannas and are also much easier to sample given the softer soils and more variable microhabitiats. Additional logistical constraints prevented more time been spent searching each block. In this study, the transect was also divided into two 50 metre transects because of the small size of the burn plots and in order to limit any edge effects.

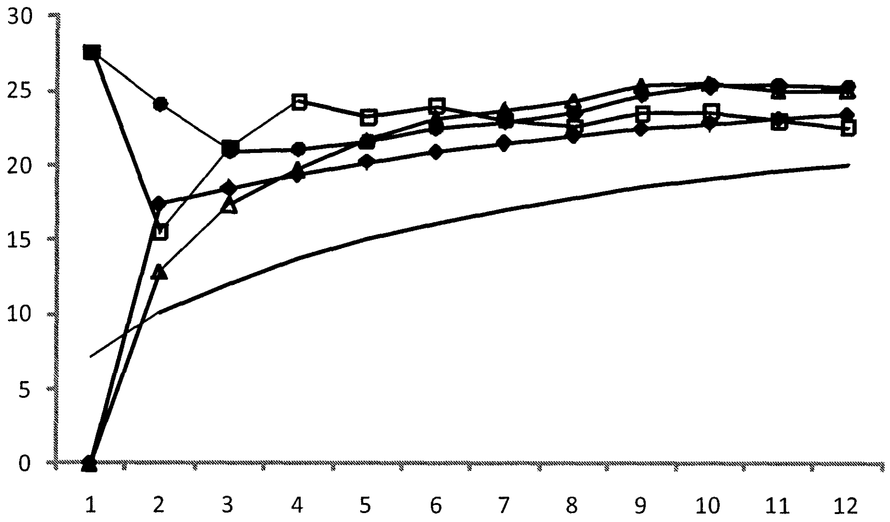
a)


S Obs
ICE Mean
Chao 2 Mean
Jack 2 Mean
MM Mean
14
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10
11
12

b)


30
25
20
15
10
5
0
1
2
3
4
5
6
7
8
9
10
11
12

c)



d)

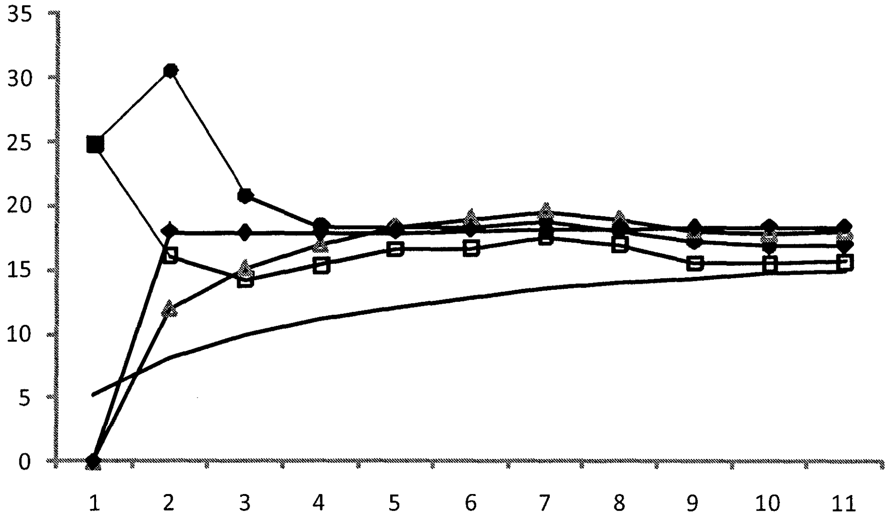


Figure S3: Species accumulation curves for all seasons data pooled, for a) Mopani, b) Satara, c) Pretoriuskop and d) Hluhluwe using estimators (ICE, Chao 2, Jack 2, Michaelis-Menten) from EstimateS (Colwell 2005).

Table S4: SIMPER analysis for termite abundance per burning regime in each savanna type. Only those pair-wise tests which were significantly different in assemblage composition are included. Av. abund. = average abundance, Av. diss. = average dissimilarity, Cum. % = cumulative percentage of similarity.

Burning regimes	Species	Av. abund.		Av. Diss.	Cum. %
Mopani					
Unburnt vs. August 3 (AS)					
	Microtermes spp.	0.00	1.00	42.15	44.74
	Microcerotermes spp.	0.05	1.00	24.07	70.29
	Macrotermes michaelseni	0.50	0.00	14.00	85.14
	Allodontermes rhodesiensis	0.50	0.00	14.00	100.00
December 3 vs. August 1 (AS)					
	Microcerotermes spp.	0.55	3.50	22.81	30.41
	Macrotermes michaelseni	0.00	1.50	18.81	55.48
	Microtermes spp.	0.50	2.00	12.87	72.64
	Odontotermes sp3	0.00	1.00	7.58	82.74
	Hodotermes mossambicus	0.00	1.00	7.58	92.85
December 3 vs. August 3 (AS)					
	Microcerotermes spp.	1.00	3.50	21.85	29.88
	Macrotermes michaelseni	0.00	1.50	17.02	53.15
	Microtermes spp.	1.00	2.00	14.93	73.57
	Odontotermes sp 3	0.00	1.00	7.14	83.33
	Hodotermes mossambicus	0.00	1.00	7.14	93.10
Satara					
Unburnt vs. August 1 (AS)					
	Ancistrotermes latinotus	4.00	0.67	10.75	15.79
	Microtermes spp.	5.33	1.67	9.35	29.52
	Microcerotermes spp.	3.33	0.37	9.04	42.81
	Allodontermes rhodesiensis	2.67	0.67	8.60	55.44

Promirotermes spp.	1.33	0.00	6.69	65.27
Astalotermes spp.	1.33	0.00	5.92	73.97
Odontotermes sp 3	0.67	1.33	4.92	81.20
Amitermes hastatus	0.33	0.00	2.55	84.95
Amitermes messinae	0.33	0.00	2.55	88.70
Trinervitermes trinervoides	0.33	0.00	2.18	91.90
Unburnt vs. August 3 (AS)				
Microcerotermes spp.	3.33	1.00	8.65	14.21
Allodontermes rhodesiensis	2.67	1.00	7.95	27.28
Ancistrotermes latinotus	4.00	0.67	7.89	140.25
Microtermes spp.	5.33	2.33	7.49	52.57
Odontotermes sp 3	0.67	3.00	7.13	64.29
Promirotermes spp.	1.33	0.00	6.09	74.30
Astalotermes spp.	1.33	0.33	4.86	82.28
Amitermes hastatus	0.33	0.00	2.30	86.06
Amitermes messinae	0.33	0.00	2.30	89.85
Odontotermes sp 2	0.00	0.33	2.19	93.45
December 3 vs. August 1 (baits)				
Odontotermes 3 sp	32.00	0.00	9.06	21.33
Ancistrotermes latinotus	1.00	3.33	8.79	42.04
Macrotermes michaelseni	4.33	2.67	8.14	61.20
Microtermes spp.	7.67	10.67	5.91	75.12
Microcerotermes spp.	0.33	1.33	5.40	87.83
Allodontermes rhodesiensis	0.67	2.00	5.17	100.00
Pretoriuskop				
August 3 vs. August 1 (AS)				
Astalotermes spp.	5.00	1.00	7.57	14.89
Aneneotermes spp.	2.67	0.33	6.78	28.23
Microcerotermes spp.	1.67	1.67	5.72	39.48
Allodontermes rhodesiensis	1.00	0.00	4.38	48.09
Ancistrotermes latinotus	1.00	2.33	4.08	56.13
Alyscotermes spp.	0.67	0.67	3.77	63.54
Adaphriotermes spp.	1.00	0.33	3.69	70.79
Promirotermes spp.	0.67	0.00	3.63	77.93

	Microtermes spp.	5.67	6.33	2.44	82.72
	Rhadinotermes coarctatus	0.00	0.33	1.83	86.32
	Odontotermes sp 1	0.33	0.00	1.81	89.89
	Trinervitermes trinervoides	0.33	0.00	1.81	93.46
Unburnt vs. August 1 (baits)					
	Microtermes spp.	3.33	10.67	18.12	35.10
	Ancistrotermes latinotus	0.33	3.00	15.60	65.33
	Allodontermes rhodesiensis	0.00	1.67	7.73	80.31
	Astalotermes spp.	0.33	0.67	6.49	92.89
Unburnt vs. December 3 (baits)					
	Ancistrotermes latinotus	0.33	2.67	22.82	54.59
	Microtermes spp.	3.33	4.67	14.28	88.76
	Astalotermes spp.	0.33	0.00	4.70	100.00
December 3 vs. August 1 (baits)					
	Microtermes spp.	10.67	4.67	11.35	34.75
	Allodontermes rhodesiensis	1.67	0.00	6.72	55.33
	Astalotermes spp.	0.67	0.00	6.55	75.36
	Ancistrotermes latinotus	3.00	2.67	4.88	90.31

Chapter 4

Assessing the efficiency of termite sampling methods in southern African savannas

For submission to *Journal of Insect Conservation* as: Andrew B. Davies, Berndt J. van Rensburg, Paul Eggleton & Catherine L. Parr

Abstract

Although termites are of great importance in tropical and sub-tropical ecosystems across the globe, termite ecology is often constrained by sampling difficulties and a lack of sampling protocols in savannas. A comparison of two often used sampling methods, cellulose baits and active searching, was conducted across four savanna types situated along a rainfall gradient in South Africa during the wet season. The efficiency of sampling method varied with annual rainfall and a single method was not the best for all savanna types. In mesic savannas, active searching (an often neglected sampling method in savannas) was most effective at sampling termite diversity while baiting was more effective in arid savannas, although this method samples mostly wood feeding termites from feeding group II. Baiting also provides a better measure of termite activity than active searching. The type of study and feeding group needing to be targeted will determine which method is most appropriate, as well as the savanna site were sampling is to be conducted.

Keywords: active searching, baiting, feeding groups, invertebrate sampling, sampling protocols

Introduction

Termites (Blattodea: Termitidoidae) are considered key ecosystem engineers in tropical and sub-tropical systems. They are responsible for the redistribution of soil particles and alter the mineral and organic composition of soils, their hydrology, drainage (Jones et al., 1994; Konaté et al., 1999) and infiltration rates (Mando et al., 1996). Termites are also considered to be the dominant arthropod decomposer in tropical systems (Collins, 1981; Holt, 1987; Schuurman, 2005) and hence influence nutrient cycling and distribution (Holt & Coventry, 1990; Lepage et al., 1993). Their vast biomass alone makes them an important consideration in tropical and sub-tropical ecology (Josens, 1983); in African savannas they have been shown to have a comparable biomass to ungulates and mega-herbivores (Dangerfield et al., 1998). Termites are also a diverse and varied group comprising of several feeding groups, including wood feeders, grass harvesters and soil feeders which exert different ecological effects on ecosystems (Donovan et al., 2002; Josens, 1983).

However, despite their importance in tropical and subtropical systems, detailed knowledge on termites and their function in ecosystems is scarce, with even basic natural information lacking for many species (Dangerfield & Schuurman, 2000; Dawes-Gromadzki, 2003). This can largely be attributed to taxonomic and sampling difficulties. Although termites are often considered to be 'taxonomically tractable' (Brown, 1991), there are still major gaps in their taxonomy, particularly for southern hemisphere regions (Eggleton et al., 1996; Eggleton et al., 1995) and many genera are in need of revision (Eggleton, 1999; Uys, 2002). In order for taxonomists and ecologists to address these challenges, termites need to be sampled and herein lie more difficulties. Most termite species are cryptic in nature, being subterranean with a patchy distribution, resulting in many conventional insect sampling methods, such as pitfall trapping or sweep netting, being ineffective. A lack of standardised sampling protocols also causes difficulties, making comparisons between studies and ecosystems problematic (Dawes-Gromadzki, 2003), this is particularly true for savanna systems. Jones & Eggleton (2000) have designed a sampling protocol for tropical forests which is widely used (e.g. Donovan et al., 2002; Eggleton et al., 2002; Gathorne-Hardy et al., 2001), but its suitability for other systems, particularly more arid ones such as savannas which have drier, harder soils, which make searching and digging difficult, is questionable.

Several studies have investigated termite sampling methods in savanna environments in an attempt to develop a standardised sampling protocol (e.g., (Dawes-Gromadzki, 2003; Zeidler et al., 2004), but as yet none are widely used. Baiting, especially with toilet paper rolls, is a commonly used and seemingly effective method (Le Fage et al., 1973), but is useful for a limited suite of termites only (mostly those which feed on wood) and also does not easily provide true abundance data because not all termites present can be sampled. Added to this is uncertainty regarding an optimal baiting system, such as the length of time baits should be in the field before checking, and whether they should be buried or simply placed on the substrate surface. Savannas are also highly variable environments when considering vegetation and abiotic variables (House et al., 2003) and sampling methods in one savanna system could well be inappropriate for another, given this variation. Prior to this study, however, the efficiency of sampling techniques focusing specifically on termites has not been compared between savanna types.

The aims of this study were to compare (i) the efficiency of different forms of baiting techniques, namely the position of cellulose baits, and time available for termite attack, and (ii) two commonly used termite sampling techniques: cellulose baits and active searching. Comparisons were made by assessing how well the techniques sampled termite diversity (richness, relative abundance and assemblage composition) and activity levels (frequency and intensity of attack). I evaluated these two techniques in savannas situated along a rainfall gradient of approximately 600 kilometers in South Africa, and thus were able to compare the efficiency of different methods in markedly different savanna systems. This is the first study on savanna termite sampling methods to be conducted on such a large spatial scale.

Methods

Study site

The study was conducted in four distinct savanna vegetation types situated along a rainfall gradient in two of South Africa's major reserves: Kruger National Park (KNP, situated between 22° 25' and 25° 32' latitude south and 30° 50' and 32° 02' longitude east) and Hluhluwe-iMfolozi Park (HiP, situated between 28° 01' and 28° 25' latitude south and 32° 15' and 32° 26' longitude east). These parks are located in the eastern part of the country and have a sub-tropical climate with a distinct summer rainfall pattern.

The four savanna types consisted of Mopani woodland (Mopani area of the northern KNP), *Acacia* savanna (Satara area of the central KNP), *Terminalia* woodland (Pretoriuskop area of the southern KNP) and mesic *Acacia* savanna (Hluhluwe section of HiP). This study forms part of a larger study investigating the effects of long-term burning regimes on termites and accordingly sampling in KNP was carried out on a series of experimental burning plots (for more information on this burning trial see Biggs et al. 2003 and van Wilgen et al. 2007). Twelve replicated sampling plots (except for Hluhluwe where 11 plots were used) spaced 10 – 20 km apart were selected from within each of the four savanna habitats. These plots do, however, differ in their fire histories since they form part of a burning experiment, but together are considered representative of the habitat in question and a variety of its fire regimes. The total rainfall gradient represented by the four savanna types ranged from 450 mm (Mopani woodland in KNP) to 900 mm (mesic *Acacia* savanna in HiP) (see Appendix S1 of Chapter 3 for more information on the replicated sites in each of the four habitat types).

Termite sampling

Termites were sampled using two commonly used methods: cellulose baits and active searching. Sampling was conducted during the austral summer (wet season) from November 2008 to February 2009, which represents a time of peak termite activity (Dawes-Gromadzki & Spain, 2003). These methods were selected because, although commonly used, are often used in different systems (but see Zeidler et al. (2004) for a comparison): active searching in tropical forests (see e.g. Davies, 1997; Eggleton et al., 2002; Jones & Eggleton, 2000) and baiting in savannas (see e.g. Dawes-Gromadzki, 2003; Ferrar, 1982). Their relative efficiency in different savanna types has, so far, not been investigated.

Forty cellulose baits in the form of toilet paper rolls (500-sheet single-ply, unscented, unbleached - hereafter referred to as baits) were placed on each plot (see Le

Fage 1973), in a grid formation of five by eight baits, spaced five metres apart. In order to test differences in bait placement (position relative to the substrate and amount of time left in the field), half (twenty) of the baits were placed directly on the soil surface, any litter present was brushed aside to ensure direct contact was made with the soil and the base of the bait (Dawes-Gromadzki, 2003). These baits were wrapped around the middle with packaging tape to prevent unravelling and secured to the soil surface using an aluminium tent peg placed through the centre hole of each toilet roll. The other half of the baits (20) were buried below the soil surface to a depth of approximately 2 cm which ensured they were adequately covered with soil. Each line of eight baits consisted of four buried and four surface baits with the position of the baits alternated. Baits were checked for the presence of termites and assessed for termite attack after predetermined intervals of 5, 14, 28 and 56 days. At each of these time intervals, five surface and five buried baits were removed, and any termites present were sampled (at least ten of each caste where sampled when present to ensure a representative sample, Uys, 2002). The baits were then scored according to the intensity of attack (IA) using visual estimation. This involved giving each bait a score of one of six ratings as to how much of the bait had been consumed. Baits which were completely intact with no evidence of termite activity were assigned a value of 0, subsequent to this baits were scored according to the following scale: 1 = 1 – 25% consumed, 2 = 26 – 50% consumed, 3 = 51 – 75% consumed, 4 = 76 – 99% consumed and 5 = 99 – 100% consumed (Dawes-Gromadzki, 2003). Baits which had been disturbed by vertebrates or other factors (e.g. no longer in direct contact with the soil surface or completely destroyed) were excluded from analysis.

For the active searching, a modified version of the standardised belt transect method described by Jones & Eggleton (2000) was used. Two 50 by 2 metre transects were laid out on each plot, with each sub-divided into ten 5 by 2 metre blocks and each block searched for ten person minutes. During this time period the entire block was searched for termites; this included excavating soil and searching dead wood, termite nests and other microhabitats. Vegetation up to a height of one metre was searched, this included termite runways up treetrunks. This method was modified from that of Jones & Eggleton in that less time was spent searching in each block (ten minutes in my study compared to the standard sixty minutes), this was primarily because the Jones & Eggleton method was designed for tropical forests which have a much higher termite diversity and density than semi-arid savannas and are also much easier to sample given the softer soils and more variable microhabitiats. Additional logistical constraints prevented more time been spent searching each block. The transect was also divided into two 50 metre transects in order to limit any edge effects due to the small sizes of the plots sampled.

Termite Identifications

Termite samples were identified at the Natural History Museum, London, U.K., the University of Pretoria and the National Collection of Insects, Pretoria, South Africa. Specimens were identified to species were possible using soldier castes whenever available (when soldiers were not present, workers were used). Where this was not possible, morphospecies were used (e.g. for the genus *Odontotermes*), and where even this was problematic the specimens were treated as an aggregate for that specific genus (e.g. this occurred for the genera *Microtermes, Microcerotemes, Astalotermes* and others). With many termite genera in need of revision (Uys, 2002), it was considered a more conservative approach to treat many genera as an aggregate instead of risking the possibility of finding differences in community assemblages when species thought to be different were actually the same. Voucher specimens are lodged at the National Collection of Insects, Pretoria, South Africa.

Analyses

The efficiency of different forms of baiting were compared as well as how baiting performed compared to active searching seeing that termite ecologists are usually faced with this question when designing a sampling protocol. For comparisons of baiting techniques, a general linear model (GLM) was fitted to examine the effects of time (number of days in the field), bait position (surface or buried) and site (savanna habitat) on the frequency of termite attack and a separate GLM was fitted to test these effects on the number of species sampled (species richness). A generalised linear model with a Poisson distribution and log-link function was fitted to examine the effects of time (number of days in the field), bait position (surface or buried) and site (savanna habitat) on the intensity of termite attack. Data were first tested for overdispersion, but a correction was not necessary. For all these analyses, plots of standardised residuals vs. fitted values were used to assess homogeneity of variance.

The efficiency of baiting compared with active searching was assessed by (i) how many species each method sampled in each savanna type (species richness), (ii) how the assemblages sampled differed and broadly, (iii) how each method compared in terms of the feeding groups sampled. For these comparisons, data from both surface and buried baits were combined because comparisons between these two methods have been performed above and the assemblages sampled (in terms of FG) are very similar, differences lie more in termite activity and abundance.

For species richness comparisons, student's t-tests were used to compare total number of species sampled by each method in each savanna. This was the total species richness for all bait checks combined. Assemblages sampled were compared using analysis of similarity (ANOSIM, Clarke & Warwick, 2001) in Primer v. 5.2 (Clarke & Gorley, 2001). Bray-Curtis similarity matrices of the data were constructed in order to asses overall compositional changes. The data were square root transformed before analysis (to weight common and rare species equally)(Clarke & Warwick, 2001). ANOSIM was used to test if there were significant differences in termite assemblage composition with sampling method. ANOSIM is a non-parametric permutation procedure applied to rank similarity matrices which underlie sample ordinations (Clarke & Warwick, 2001; Parr et al., 2004), in which a significant global R-statistic of close to one indicates distinct differences between the assemblages compared, this R-statistic can take on any value between -1 and 1.

The R-value itself is not unduly affected by the number of replicates in a sample, however, the significance level of this R-statistic is. This can result in a situation where the R-value is, for example, very low, which indicates that assemblages are barely separable, but this value may be significantly different from zero, perhaps leading to an interpretation that the assemblages in question are indeed different. However, this significance level is more a reflection of a high number of replicates or samples, and the R-value is of greater importance for interpretation (Clarke & Warwick, 2001; Parr et al., 2004). The opposite may also be true with an R-value being close to one.

The composition of the feeding groups sampled were compared descriptively in graphical form. Termites were classified into feeding groups based on the classification described by Donovan et al. (2001), which designates termites into four groups based on the humification of the feeding substrate. Group I comprises the lower termites which feed on dead wood and grass; group II is made up of Termitidae with a range of feeding habits which include dead wood, grass, leaf litter and micro-epiphytes; group III feed in the organic rich upper soil layers and are also Termitidae; and group IV contains the true soil-feeders which ingest mineral soil, again all Termitidae. Different termite feeding groups are considered to play different ecological roles and so an understanding of how different sampling methods affect the suite of termites collected is of importance.

Results

Termites from 18 genera and 5 subfamilies were collected during the study. Half of the species were from Feeding Group II, one third from Feeding Group III, 11 % from Feeding Group IV and 6 % from Feeding Group I (Table 3).

Cellulose baits

Mean number of species recorded at baits (species richness) varied significantly over time, with higher incidences of attack as time progressed at the more arid sites, species richness dropped off at the last bait check for both mesic sites ($F_{1, 376} = 74.72$, $P < 0.0001$; Fig. 1a). Across all sites, bait position had a significant effect on species richness ($F_{1, 376} = 17.30$, $P < 0.0001$). For days 1 – 28, species richness was greater at buried baits, but at the last bait check (56 days) species richness was similar for buried and surface baits (Fig. 1b). The effect of site on number of species sampled was also significant ($F_{3, 376} = 26.90$, $P < 0.0001$), which interacted significantly with position ($F_{3, 376} = 3.60$, $P < 0.05$). The highest species richness recorded was at Satara for all bait checks and the lowest was at Mopani for all bait checks except the last one, where Mopani had greater richness than both mesic sites (Fig. 1a).

Mean frequency of attack (FA) varied significantly over time, with higher incidences of attack as time progressed at all sites except Hluhluwe ($F_{1, 376} = 194.99$, $P < 0.0001$; Fig. 1c). The drier sites (Mopani and Satara) showed markedly steeper increases from 28 to 56 days (Fig. 1c). Across all sites, FA was also significantly greater at buried (43.27 ± SE 2.75 %) than surface (27.96 ± SE 2.50 %) baits ($F_{1,376} = 28.80$, $P < 0.0001$). The effect of site on FA was also significant ($F_{3,376} = 31.12$, $P < 0.0001$), but this interacted significantly with position ($F_{3,376} = 7.17$, $P < 0.001$). The highest incidences of attack were at Satara for all bait checks (Fig. 1c).

There was a positive correlation between mean intensity of attack (IA) and time, which was significant (Table 1, Fig. 1d). At Mopani and Satara, there was a marked increase between days 28 and 56. Bait position also had a significant effect on IA (Table 1), with higher attack recorded at buried (0.69 ± SE 0.02) than surface (0.35 ± SE 0.01) baits. Site also had a significant effect on IA (Table 1, Fig. 1d), with higher attack levels at Satara than the other sites, which interacted significantly with position (Table 1).

Baits and active searching comparison

In contrast to the more arid sites where no significant differences in species richness sampled between methods were found, active searching compared to baits clearly sampled more species in Hluhluwe ($T_{20,12} = 2.07$, $P = 0.0517$, Fig. 2) and significantly more in Pretoriuskop ($T_{22,12} = 5.70$, $P < 0.0001$, Fig. 2).

Analysis of similarity (ANOSIM) revealed that the different sampling methods sampled different components of the overall termite assemblage as composition varied significantly being most pronounced at Mopani, followed by Pretoriuskop. They were somewhat distinct at Satara and fairly similar at Hluhluwe (Table 2).

A comparison of feeding groups (FG) sampled with each method in each savanna type separately shows that at the more arid sites (Mopani and Satara) FG composition does not differ much with sampling method (Fig. 3). However, at the mesic sites (Pretoriuskop and Hluhluwe), the FG sampled and relative contributions differ with sampling method; AS resulted in a wider range of feeding groups being sampled. At all sites, the baits sampled almost entirely FG II, although at the mesic sites some samples contained FG III. This is particularly pronounced at Pretoriuskop where FG III becomes more common and FG IV is recorded with AS only (Fig. 3).

Discussion

It is often assumed for termites that one particular sampling method is better suited to a specific habitat type or it is only tested within one form of this habitat. Generally active searching transects are thought appropriate for sampling in tropical forested areas (Jones & Eggleton, 2000) and baiting methods for drier areas such as deserts (Taylor et al., 1998) and savannas (Dawes-Gromadzki, 2003). However, my results show that the efficiency of each method and baiting technique in sampling the termite fauna differed significantly between savanna types; one method was not the most appropriate or effective for all habitats.

Baiting techniques

In terms of the baiting technique, there were profound differences in termite diversity and activity levels recorded between the arid and mesic savanna sites. Although overall species richness increased significantly over time at all sites, the difference between the 3rd and 4th censuses is of consequence (Fig. 1a). My results suggest that the temporal scale of a baiting protocol is of importance and should be modified according to the savanna type being sampled and not only the presentation or type of bait used (for bait type comparisons see Dawes-Gromadzki (2003) and Taylor et al. (1998)). At the arid sites, the number of species sampled, intensity of attack and frequency of attack, increased substantially between the 3rd and 4th censuses, which contrasts to that of the mesic sites which show a decrease or levelling off between these censuses. In northern Australia over this same time scale (8 weeks), Dawes-Gromadzki (2003) also found a decrease in species richness sampled (although attack levels increased), but these changes may have been more related to seasonality, in contrast to my study which was conducted within one season (wet) only. At the mesic sites in my study (particularly Hluhluwe), fungus was found growing on many baits at the last census which may repel termites (Abensperg-Traun, 1993; Dawes-Gromadzki, 2003) and could explain why activity and richness recorded decreased. This would imply that in more mesic savannas, there is no benefit to leaving baits in the field for extensive periods of time (at least not as long as 56 days). In contrast, in arid environments a longer time period may be necessary to adequately sample the termite assemblages. Although not reflected in the analysis, however, at the 4th census period baits were occasionally completely consumed with no termites present. This can occur where termite activity levels are very high (e.g. in Satara in the present study), and is an important consideration when selecting the optimal temporal scale for baiting.

My results indicate that bait position also plays an important role in baiting protocols. In contrast to studies in desert regions (e.g., (Ettershank et al., 1980; Taylor et al., 1998), but in agreement with savanna studies (e.g., (Dawes-Gromadzki, 2003), buried baits were more attractive to termites during the first three censuses. Dawes-Gromadzki (2003) suggested that savanna termites contrast to desert populations in that they do not use thermal shadows to locate surface baits (as suggested by Ettershank et al. (1980) for desert termites) due to higher levels of canopy cover (or grass biomass). My results support this idea, although the attractiveness of surface and buried baits did not differ at the last census (56 days) which is much earlier than in northern Australia (Dawes-Gromadzki, 2003). I suggest this could be due to lower levels of canopy cover, different feeding habits of African termites or higher levels of activity. It also implies that if there are no time constraints for a study, surface baits may be better to use as they are less labour intensive to establish, although they are more susceptible than buried baits to disturbances such as removal by people and animals.

Active searching in savannas

In the most arid savanna, termite diversity did not vary with sampling method (baiting or active searching). This suggests that if a termite species inventory is required it would make little difference which approach was used in arid savannas. This compares well with a previous study conducted in an arid Namibian environment, where species richness was similar with each sampling method, active searching and cellulose baits (Zeidler et al., 2004). However, if a measure of termite activity or relative abundance is necessary then baiting would be more appropriate as higher relative abundances of termites were sampled this way and signs of activity detected by active searching (e.g. tunnelling, sheeting) may only be evident immediately after termites have been active, which is likely to be soon after rainfall events. For savannas of intermediate rainfall, such as Satara, the assemblages seem very similar from the ANOSIM results, and it may seem from these that either method would adequately sample the termite fauna present, however, 36 % of species sampled were only collected with active searching while only 1 species (7 %) was sampled with baiting alone. This would suggest that active searching should be considered when designing sampling protocols for even intermediate rainfall savannas.

For the mesic savannas, the success rate of each method was notably different, with active searching sampling a higher number of species and wider range of feeding groups. Previously, studies of savanna termites have not generally employed active searching (see e.g. Dawes-Gromadzki & Spain, 2003; Ferrar, 1982; Schuurman, 2005), citing sampling difficulties associated with harder soils and lower termite diversity (Dawes-Gromadzki, 2003). However we found that using active searching in these more mesic savannas can make a valuable contribution; if only baiting had been used a large proportion of the termite species present would not have been sampled. Indeed, none of the soil feeding termites would be represented and a new genus record for South Africa (*Aneneotermes*) would not have been recorded; this shows that although often neglected, active searching can play an important role in understanding termite communities of mesic savannas.

Synthesis and recommendations

My results show that sampling methods for termites need to be adjusted according to the characteristics of the study site (particularly rainfall), this being the case even within broad vegetation types. If a termite sampling protocol for savannas is to be established similar to that of Jones & Eggleton (2000) for tropical forests, this needs consideration. More method comparisons across a variety of savanna habitats would be welcomed in achieving this aim.

An optimal sampling design employed for savanna termites will also depend on which termite feeding groups are being targeted and whether diversity or only activity levels need to be assessed. If a study is aimed at diversity then the sampling methods need to target all feeding groups and a method, or composite methods, which sample as many species as possible should be implemented. However, if the study is related to other aspects of termite ecology, such as pest species which are mostly wood feeding termites

(Uys, 2002), a complete array of termite diversity need not be sampled. Here, baiting may well be more efficient as it samples this group more efficiently and gives an indication of termite activity, which would be beneficial for pest management strategies.

Other sampling methods such as mound density counts (e.g. Benzie, 1986; Traoré & Lepage, 2008; Trapnell et al., 1976), litter bags (e.g. Bocock, 1964; Ohiagu & Wood, 1979; Yamashita & Hiroshi, 1998) and other forms of baiting (e.g. Abensperg-Traun, 1993; Dawes-Gromadzki, 2003; Taylor et al., 1998) could also contribute to a sampling protocol. Although not assessed here, these can be valuable methods depending on the objectives of the study. While mound counts are often criticised for their limited scope and underestimation of diversity (Eggleton & Bignell, 1995), they can provide a quick and easy estimation of colony density, particularly if one specific species which builds charismatic mounds is the focus of a study. In addition mounds can be used in conjunction with remote sensing and related techniques to provide large scale estimates of termite distributions and densities. Litter bags also give an indication of termite activity levels and are focused on grass feeding termites, in contrast to the wood feeders targeted by cellulose baits. They can be useful in studies relating to decomposition and grass harvesting termites which are missed with baiting alone. Other forms of baiting such as wooden stakes (Abensperg-Traun, 1993; Dawes-Gromadzki, 2003) and dung (Taylor et al., 1998) have also been shown to be effective, although a disadvantage to using dung is that it is also consumed by other taxa which could possibly confound results.

These findings argue for more within-biome comparisons of termite sampling methods if a commonly used protocol is to be established. This is certainly the case for savannas and is likely to also hold true for other systems which show similar levels of variation. Advancement toward such protocols will enhance our presently limited understanding of termite ecology.

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Table 1: Results from a factorial generalized linear model (Poisson distribution, log-link function) comparing intensity of termite attack among time (number of days), position of bait (surface or buried) and savanna site. Scaled deviance for the model was 0.82. N = number of baits sampled, > significantly larger, < significantly smaller. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	N	df	X^2	Wald statistic	Effect
Time (days)	1641	1	509.79***	482.49	5<14<28<56
Position	1641	1	63.75***	61.23	buried>surface
Site	1641	3	153.49***	167.11	Satara>others
Position*Site	1641	3	8.53*	8.54	

Table 2: Analysis of similarity between two sampling methods used to sample termite assemblages (active searching and cellulose baits) for each savanna type. The R-statistic is a measure of similarity of assemblages, the closer this value is to 1, the more dissimilar assemblages are (Clarke & Warwick 2001). *P* is considered significant at the α-level of 0.05.

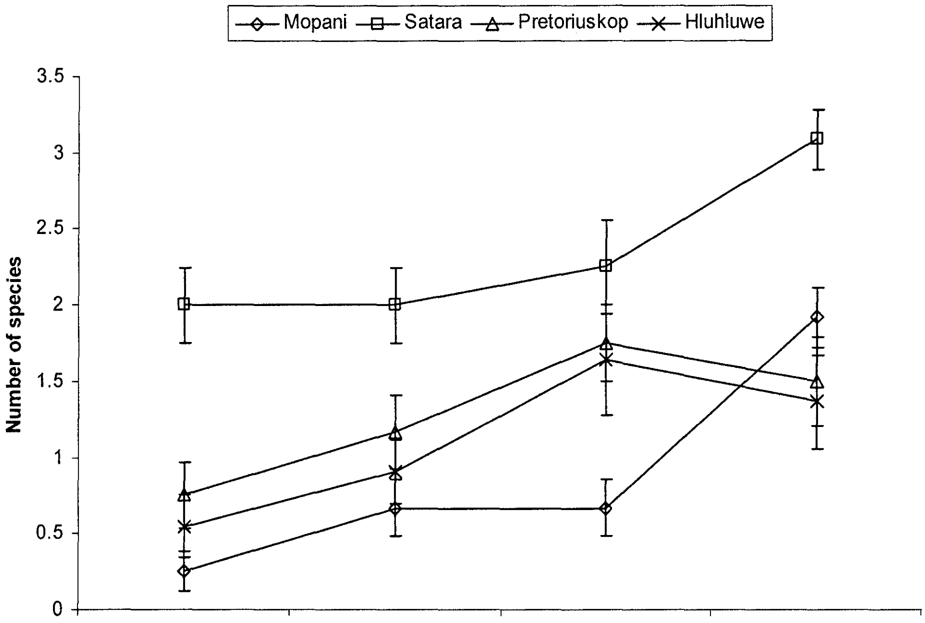
	R	P
Mopani	0.601	0.001
Satara	0.247	0.001
Pretoriuskop	0.498	0.001
Hluhluwe	0.201	0.008

Table 3: Occurrence of termite species for each method at all 12 sites at each savanna habitat. For bait data, occurrence values are for all time checks. The Feeding Group for each species is also indicated. AS = active searching, SB = surface baits, BB = buried baits and FG = Feeding Group.

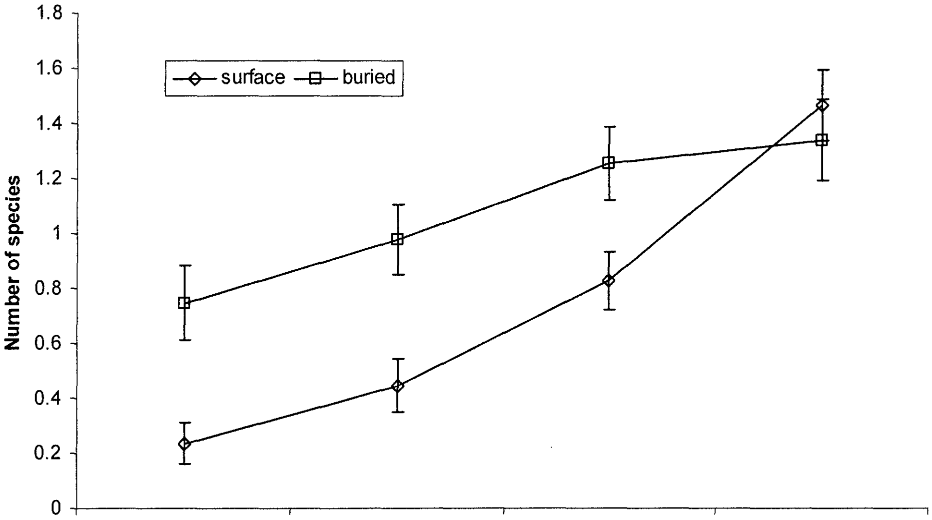
Termite species	Mopani			Satara			Pretoriuskop			Hluhluwe			FG
	AS	SB	BB	AS	SB	BB	AS	SB	BB	AS	SB	BB	
Hodotermitidae													
Hodotermes mossambicus	2	-	-	-	-	-	-	-	-	-	-	-	I
Termitidae													
Macrotermitinae													
Allodontermes rhodesiensis	2	-	-	16	7	9	3	6	4	20	8	4	II
Ancistrotermes latinotus	-	3	1	22	9	19	17	3	17	18	3	4	II
Macrotermes michaelseni	4	1	11	3	9	16	-	-	-	1	-	-	II
Macrotermes natalensis	-	-	-	1	-	1	-	-	-	7	-	1	II
Microtermes spp.	7	36	66	34	44	86	46	39	38	31	27	28	II
Odontotermes sp. 1	-	-	-	-	-	1	3	-	-	3	-	-	II
Odontotermes sp. 2	-	-	-	3	-	1	1	1	-	17	5	5	II
Odontotermes sp. 3	2	-	1	18	4	7	-	-	-	1	2	2	II
Apicotermitinae													
Adaiphrotermes spp.	-	-	-	-	-	-	7	-	-	10	-	-	III

Alyscotermes spp.	-	-	-	-	-	-	7	-	-	1	-	-	III
Anenteotermes spp.	-	-	-	-	-	-	6	-	-	-	-	-	III
Astalotermes spp.	-	-	-	6	-	-	38	2	2	8	1	1	III
Termitinae													
Amitermes hastatus	-	-	-	1	-	-	-	-	-	-	-	-	II
Amitermes messinae	-	-	-	1	-	-	-	-	-	-	-	-	II
Angulitermes spp.	-	-	-	1	-	-	-	-	-	-	-	-	III
Cubitermes spp.	-	-	-	-	-	-	2	-	-	-	-	-	IV
Lepidotermes spp.	-	-	-	-	-	-	2	-	-	2	-	-	IV
Microcerotermes spp.	10	3	3	21	6	4	15	-	-	25	1	1	II
Promirotermes spp.	-	-	-	5	-	-	4	-	-	-	-	1	III
Nasutitermitinae													
Trinervitermes trinervoides	-	-	-	1	-	-	1	-	-	4	-	-	II
Rhadinotermes coarctatus	-	-	-	-	-	-	1	-	-	-	-	-	II

(a)


Mopani
Satara
Pretoriuskop
Hluhluwe
Number of species
3.5
3
2.5
2
1.5
1
0.5
0

(b)


surface
buried
Number of species
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0

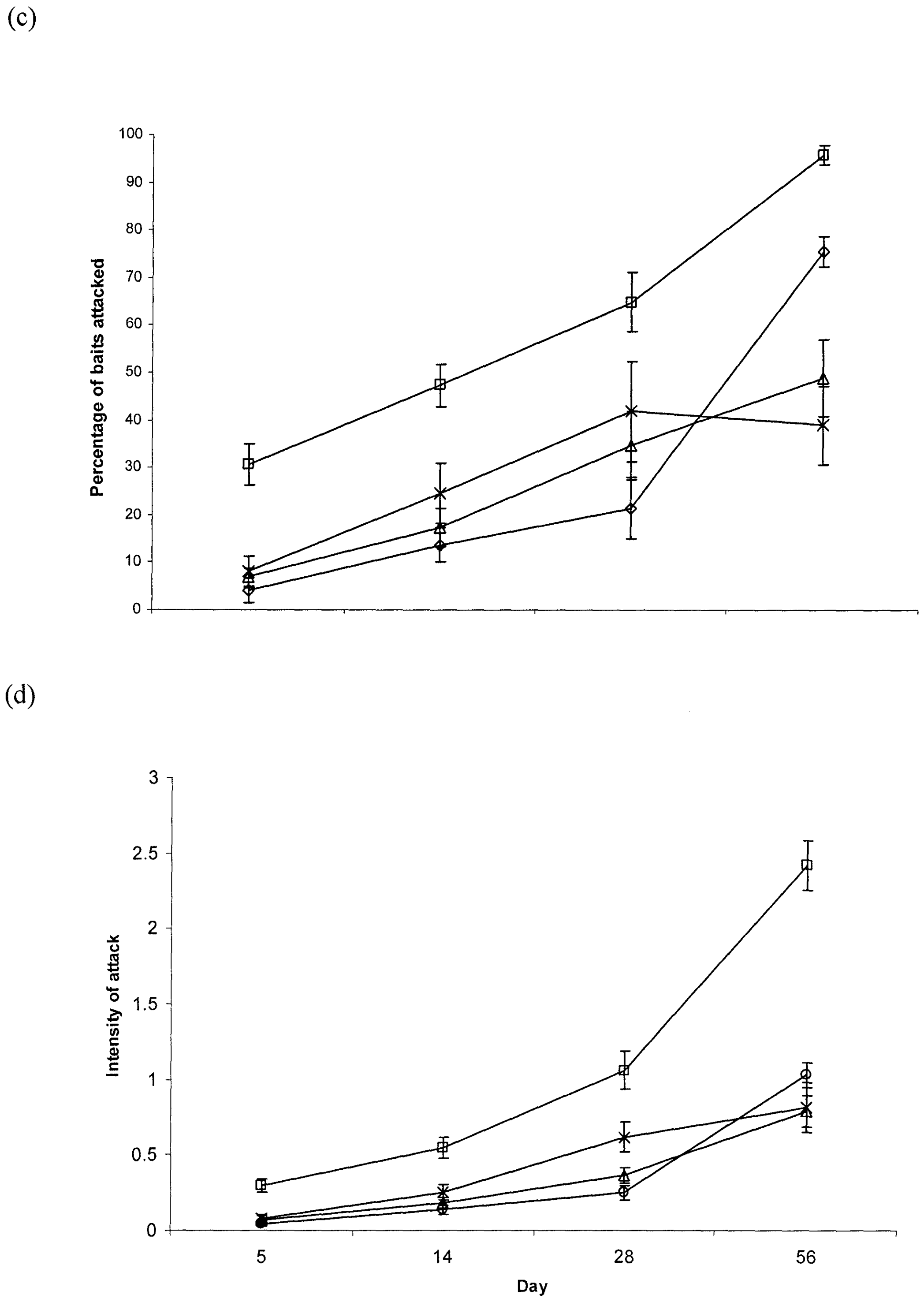


Fig. 1 Mean (± SE) (a) number of species recorded at baits, (b) number of species recorded at surface and buried baits, (c) intensity of attack on baits, and (d) percentage of baits attacked by termites at four censuses across four savanna sites

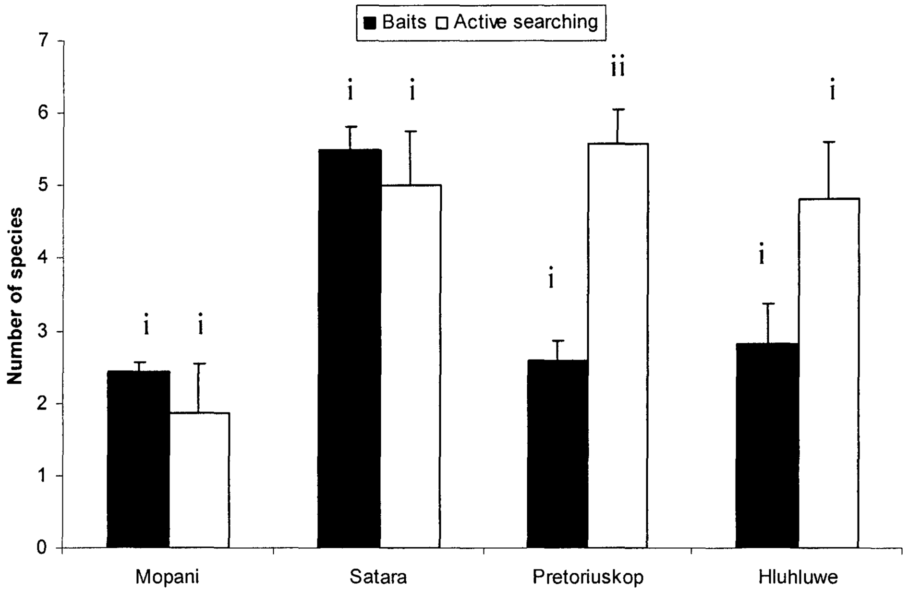


Figure 2: Overall mean (± SE) number of species recorded at baits and during active searching across four savanna types. Numerals denote significant differences within each savanna type.

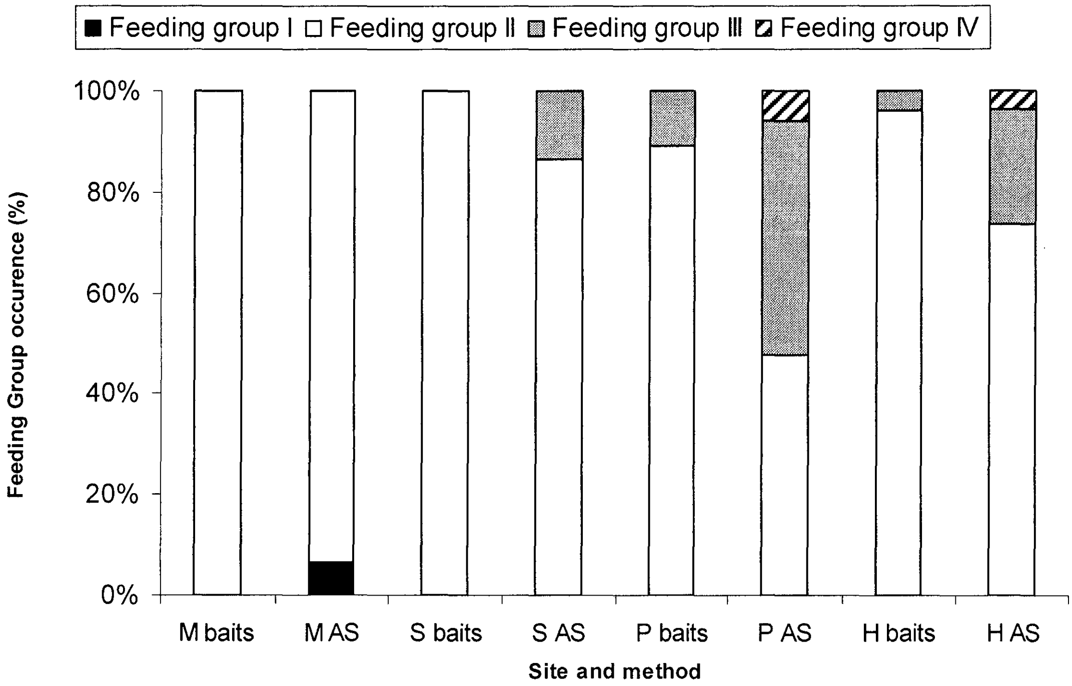


Figure 3: Feeding group composition of the termite assemblages sampled at each savanna site using baits and active searching. Feeding group I comprises the lower termites which feed on dead wood and grass; group II is made up of Termitidae with a range of feeding habits which include dead wood, grass, leaf litter and micro-epiphytes; group III feed in the organic rich upper soil layers and are also Termitidae; and group IV contains the true soil-feeders which ingest mineral soil, again all Termitidae. M = Mopani; S = Satara, P = Pretoriuskop, H = Hluhluwe, baits = cellulose baits, AS = active searching.

Chapter 5: Conclusions and recommendations

This thesis has addressed aspects of savanna termite ecology, a field of ecology which has been largely neglected relative to other taxa. In doing so, extensive termite sampling employing various methods has been undertaken, which is among the most comprehensive savanna termite sampling carried out to date for savannas across the globe. In addition to gathering information on effects of ecological patterns and processes on termites, a new genus record for South Africa, *Aneneotermes*, was recorded. Although comprehensive termite sampling has occurred elsewhere in the world (e.g. Eggleton *et al.* 1995, 1996), this is the first quantitative, systematic, repeatable and relatively complete sampling to be undertaken in multiple savanna habitats across several seasons.

As comprehensive as this sampling was, there are still other savanna habitats, even within Kruger National Park and Hluhluwe-iMfolozi Park, which have not been adequately sampled, for example the granite plains in the north of KNP where *Macrotermes* spp. mounds appear to occur at very high densities. In addition, the taxonomic constraints faced by termitologists, no doubt place further strain on our understanding of termite ecology, and if termite taxonomy were better resolved, surely higher levels of diversity would be recorded and an improved understanding of the underlying mechanisms responsible for spatial and temporal patterns of this diversity would be attained. The roles termites play in ecosystem functioning would also be better appreciated. Responses to burning regimes could well also be different if a finer scale analysis was possible highlighting the importance of multi-scale analyses in order to draw general conclusions from.

In terms of fire ecology and termites, much is still lacking in terms of empirical studies and broad conclusions cannot yet be drawn. In light of the results of this thesis, this becomes even clearer as termite communities along a rainfall gradient responded differently to fire. Findings prior to this thesis should therefore only be interpreted within the relevant savanna habitats sampled, and indeed within the termite suites sampled, as these are also shown here to respond differently to fire.

However, since fire is such a prevalent and important component of savanna ecosystems around the globe (Bond & Keeley 2005; Bond *et al.* 2005), studies investigating its effects on diversity should be a priority. This is especially true in light of the current biodiversity crises (Abell 2002; Gilbert 2009; Olson *et al.* 2002) and the acknowledgement that the future survival of one species may be dependent on the survival of others; if species critical to ecosystem functioning become extinct or endangered, the implications for other taxa may be considerable (Koh *et al.* 2004; Pimm & Raven 2000). Potential mismanagement of fire in protected and non-protected areas could well lead to situations where diversity is threatened as a result of being susceptible to fire. Yet, in savanna systems of Africa and beyond, fire is used extensively as a management tool, often with a poor understanding of these potential repercussions.

Although effects of fire on vegetation are relatively well understood, this is not the case for fauna, especially invertebrates, which perpetuates the situation. This thesis aimed at addressing this shortfall to some extent, but runs the risk of standing alone if only a few other studies employing comprehensive sampling and carried out on long-term burning regimes are conducted. This highlights a current problem with fire ecology studies in that many of them are incomparable (see Parr & Chown 2003). If ecologists and conservation organisations are to better understand and manage savanna biodiversity, more comparable studies are necessary. This thesis suggests that this needs to take the form of studies focused on long-term burning regimes as indirect effects of fire are often more pronounced than direct effects. This is because many animals, particularly subterranean taxa such as termites, are often able to escape direct fire effects.

Using long-term burning regimes, this thesis found savanna termites overall to be highly resistant to fire. However, this level of resistance varied between markedly different savanna habitats, as did the termite communities present. This implies that studies which do investigate faunal responses to fire should be conducted in more than one habitat form, even within one dominant vegetation type or biome; conclusions from one form of habitat do not necessarily hold true for other areas. This has implications for more than just faunal studies, but also for more general ecology and indeed macroecological approaches.

Similar to the results related to variation in termite resistance, the efficiency of methods to sample termites showed significant differences when compared across savanna types. Consequently, studies (and especially sampling methods) need to be comprehensive enough to encompass if not all, as many aspects of diversity as possible, particularly with regards to termites. Sampling method may also need to be adjusted according to the study site, one method which works well in one habitat may well be inappropriate for another.

Conservation implications

The maintenance of biodiversity in all its forms is one of the major goals of conservation bodies. Although in the past this goal has focused more on large, charismatic species, especially in southern Africa, the focus needs to shift to other taxa if the goal is to be met, including invertebrates (Parr & Chown 2003). In terms of conservation planning, vertebrates have also been favoured in the past as bioindicators to identify important areas for conservation and for tracking ecological change, with invertebrates often been ignored. However, it is important that invertebrates are included in this process, although this is often quite difficult to do because of insufficient knowledge of what is present and the distribution ranges of species. Invertebrates are proving, however, to be more reliable as bioindicators when data on distributions are available (McGeoch 1998; McGeoch & Chown 1998). Since fire is used as a management tool in southern African savanna reserves and elsewhere, it is important to have an understanding of the implications of different management forms for both the management of conservation areas and for future conservation planning. In lieu of this, several recommendations can be made from the findings of this thesis.

Firstly, termite communities showed large differences across savanna types, implying that ecologically, these systems function differently. Management approaches, whether fire policies or other issues, should therefore be modified according to different savanna habitats. One blanket approach to management in a large savanna park will not be appropriate for all areas; flexibility is necessary.

Second, because termite communities showed high levels of resistance to burning, mangers can afford to focus attention on other taxa. Although not investigated fully, this seems to be the case for several other invertebrate groups. Ants for example have also shown high levels of both resistance and resilience in southern Africa (Parr *et al.* 2004), as have invertebrate groups in savanna systems elsewhere, such as springtails, flies, mites, crickets, wasps, heteroptera, spiders, ants and grasshoppers in northern Australia (Andersen *et al.* 2005). This thesis does, however, provide support for the 'stable', 'unstable' approach to savanna systems suggested by Sankaran *et al.* (2005) with the implication that termites, and possibly other invertebrate groups, show more response to burning in mesic savannas; Parr *et al.* (2004) also found this to be true for ants. There is thus reason to suggest that in arid savannas, fire policies need not pay much attention to termites, but where burning occurs in mesic savannas, more care is necessary.

Finally, this thesis demonstrates that termite sampling should be adjusted according to savanna type. This is of relevance because efficient sampling of taxa is necessary in order to formulate species inventories and to understand ecological processes for better conservation efforts. This is particularly pertinent for termites, which are highly important taxa for ecosystem functioning and notoriously difficult to sample in savannas, with no widely applied sampling protocols yet developed. The findings of this thesis suggest a composite sampling protocol where possible, but where logistical constraints limit this, the savanna type being sampled needs to be considered when selecting for a specific sampling protocol.

Suggested future research directions

In order to further enhance understanding of both fire and termite ecology and improve efforts aimed at the conservation of biodiversity, the following are suggested future research directions:

- More comparable studies focused on fire ecology in Africa and around the globe are necessary. These should be focused on long-term burning regimes and, for termites, focus on the entire range of diversity.

- Studies comparing termite sampling methods in savanna systems would also be welcomed, especially studies comparing sampling efficiency across natural gradients such as vegetation changes.

- Turning it around, studies investigating the influence of termites on savanna ecology (e.g. decomposition processes and nutrient cycling) will also be beneficial and help place this thesis in better context, as the implications of fire on termites will be better appreciated.

- Termites could also play a role in promoting or inhibiting fires and fire spread because of their foraging activities which remove dead grass and wood. Investigation of this would indeed contribute to fire and savanna ecology.
- Termite herbivore interactions were used in this thesis to explain some of the findings, yet they have been little tested. How termites, by concentrating nutrients, may effect herbivore distributions and how herbivores, by producing dung, may influence termite distribution and activity is also a research field worth exploring. (Eggleton *et al.* 1996)

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