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

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Running title: Fire and African termites

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 we use examples of studies conducted in savannas across the globe to highlight what we see as a critical research gap: the lack of published information on the interactions between termites specifically (Blattaria: Termitidae) and fire. Furthermore, we 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 we 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. We 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 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 we 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 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 (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 (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), we 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 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, we 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. We 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.* 2000), 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.

We 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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