

# **The pyrodiversity-biodiversity hypothesis: a test with savanna termite assemblages**

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## **Summary**

1. Fire is an important disturbance in African savannas where it is generally assumed that high levels of pyrodiversity (variation in aspects of the fire regime) are necessary to maintain high levels of biodiversity. There is, however, little empirical evidence in support of this hypothesis

for animals. Furthermore, the relationship between pyrodiversity and biodiversity may vary with different savanna types, shaped by mean annual precipitation.

**2.** We made use of a long-term burning experiment to investigate the effect of interactions between precipitation and pyrodiversity on biodiversity. We sampled termites (major ecosystem engineers in savannas) within experimental plots involving a range of fire seasons and frequencies. Sampling was conducted in three distinct savanna types along a rainfall gradient in South Africa. We explored how termite diversity varied with mean annual precipitation and whether faunal responses to fire regimes varied with rainfall. Termites were sampled comprehensively during the wet season using cellulose baits and active searching in order to sample a variety of functional groups.

**3.** Assemblages differed significantly across savanna types with higher levels of diversity in the wetter site using the active searching method. Diversity was lowest at the most arid site but certain feeding groups peaked in the savanna with intermediate rainfall. Differences between these savannas are attributed to broad underlying changes in net primary productivity and temperature, with mammalian herbivores thought to generate a peak in diversity of some faunal groups at the intermediate savanna through their role in facilitating nutrient cycling.

**4.** Overall, termites were highly resistant to fire in all savanna types with little difference between fire regimes (season and frequency), but assemblage composition and some feeding groups were affected by burning. Differences between fire regimes were more pronounced with increasing rainfall. These differences are likely to be linked to changes in vegetation structure caused by fire, which are more significant in wet savannas.

**5. *Synthesis and applications.*** Our findings, along with those for other insect taxa, indicate limited support for the pyrodiversity-biodiversity hypothesis; this suggests that, at least for

invertebrates, management regimes can be flexible, although more caution is advisable in wetter savannas.

**Keywords:** burning, disturbance, fire, invertebrates, mean annual precipitation, patch mosaic burning

## **Introduction**

Fire is a frequent and widespread disturbance in many biomes across the globe, where it acts like a generalist herbivore modifying vegetation structure and composition (Bond & Keeley 2005).

With the increased focus in ecology on heterogeneity and variability (e.g. du Toit, Biggs & Rogers 2003), many fire management strategies in conservation areas now seek to increase fire variability in the landscape (Parr & Andersen 2006). A key assumption underlying this approach is that high variability in fire regimes and patterns promotes high levels of biotic diversity (Martin & Sapsis 1992; Parr & Andersen 2006), a process sometimes referred to as ‘pyrodiversity begets biodiversity’.

A common way to create high levels of pyrodiversity is by manipulating fire variables such as frequency and time of burn to create a mosaic of patches with different fire histories (patch mosaic burning), including areas which are left unburnt for long periods (Parr & Brockett 1999). This approach is especially well established in Australia and southern Africa, particularly in savanna regions (Parr & Brockett 1999; Parr & Andersen 2006). Patch mosaic burning is also often used for safety purposes as it is thought to prevent larger, uncontrolled fires later in the season (Laris 2002; Keeley & Fotheringham 2001).

There are, however, very few empirical tests of the pyrodiversity-biodiversity hypothesis and, as a result, information on the effects of variation in fire regimes on fauna, especially invertebrates, is lacking (Parr & Chown 2003; Davies, Parr & van Rensburg 2010). This is concerning since fire, often through patch mosaic burning, is used extensively as a management tool for both conservation goals in protected areas and livestock farming, especially in southern Africa and Australia (Biggs *et al.* 2003; van Wilgen *et al.* 2004; Andersen *et al.* 2005), but also increasingly elsewhere (e.g. in North America, Vermeire *et al.* 2004).

Habitat structure and complexity are known to strongly influence fauna (Tews *et al.* 2004). In wetter savannas where there is the potential for a large change in habitat structure due to fire (woody cover can vary from >60% in the absence of fire to <20% with repeated burning, Sankaran *et al.* 2005; Parr unpublished data), we would expect the faunal response to be large, and in such environments a higher level of pyrodiversity may be required to sustain biodiversity. Conversely, in arid savannas where there is less variation in woody cover across burning regimes, we would expect less impact on fauna, and hence these systems to require less pyrodiversity. Work on savanna ant assemblages by Parr *et al.* (2004) supports this notion by suggesting that faunal communities may be less resilient in wetter savannas than arid ones (there was greater variation in the assemblage structure of faunal communities when compared between different fire regimes in wetter than drier areas), and therefore to require greater pyrodiversity to maintain diversity there. In this study, we explore these ideas using termites, and investigate the response of termite assemblages to pyrodiversity across a range of savanna sites situated along a rainfall gradient in southern Africa.

Termites (Blattodea: Termitoidae) are an invertebrate group which has been largely neglected in savanna fire research (see Davies, Parr & van Rensburg 2010), even though, as

ecosystem engineers, they are crucial to ecosystem functioning (Jones, Lawton & Shachak 1994). Termites alter soil composition and hydrology (Jones, Lawton & Shachak 1994; Mando, Stroosnijder & Brussaard 1996), and are the dominant invertebrate decomposers in tropical forests and savannas (Collins 1981; Holt 1987; Schuurman 2005), playing an important role in nutrient cycling (Holt & Coventry 1990; Lepage, Abbadie & Mariotti 1993; Konaté *et al.* 1999).

To date, few studies examining savanna termite assemblage responses to rainfall variation exist at a regional scale (see Buxton 1981 for work in east Africa). Such comparative studies are, however, useful to ecologists for understanding challenges such as how different taxa might respond to global climate change. We thus first characterised the assemblages along the rainfall gradient before assessing how pyrodiversity affects them.

The aims of this study were to determine how termite assemblage structure (species density, abundance and composition) and termite activity: (i) vary between major savanna habitats situated along a gradient of increasing mean annual precipitation and (ii) will be influenced by different long-term burning regimes in each savanna habitat (i.e. respond to pyrodiversity), including how different feeding groups will be affected.

Several non-termite invertebrate taxa show high levels of resistance to savanna burning (Andersen, Cook & Williams 2003; Parr *et al.* 2004; Andersen *et al.* 2005; Parr & Andersen 2006) and we hypothesise that termites will follow a similar pattern, especially given that their subterranean habits will protect them from direct mortality from fire. However, we predict that (1) the response to burning will be greatest at the wettest sites (following Parr *et al.* 2004) and, (2) different termite feeding groups will respond differentially to fire, with wood and grass feeders being more sensitive to burning than soil feeders due to their nesting and feeding behaviour (Davies *et al.* 2010).

## Materials and methods

### *Study site and termite sampling*

The study was conducted in three savanna vegetation types along a rainfall gradient, spanning some 250 km in South Africa's Kruger National Park. The three savanna types sampled varied in mean annual precipitation (450, 550 and 750mm precipitation/year respectively) and consisted of Mopane woodland (Mopani area), *Acacia* savanna (Satara area) and *Terminalia* woodland (Pretoriuskop area). Within each savanna, termites were sampled on a series of long-term experimental burn plots varying in season, frequency and intensity of burning, as follows: annual dry season, triennial dry season, triennial wet season, and unburnt. The plots are ca. 7 ha in size, and the experiment has been running since 1954. Due to the duration of sampling and spatial extent of the study, the time since the last fire varied for each sampling event with a minimum of 4 months (annual dry season) to a maximum of 3 years (triennially burnt plots). Previous work (e.g. Parr *et al.* 2004) has shown that time-since-fire was only important in the first 4 months post-fire, following which vegetation (e.g. grass and shrubs) regrows and differences disappear. Accordingly, time-since-fire was not considered as important for this study as the burning regime (i.e. frequency and season of fire).

In order to sample and document the termite fauna comprehensively and hence feeding groups adequately, both cellulose baits and active searching were undertaken in each plot. Epigeal mound counts were not conducted due to very low mound densities (<1 mound/ha). Cellulose baits were also used to provide data on intensity of attack (ranging from 1 to 100%, Dawes-Gromadzki 2003) spanning four predetermined time intervals across a total of 56 days. A modified version of the standardised belt transect method described by Jones & Eggleton (2000) was used for the active searching, with each block (5 × 2 metres) being thoroughly searched for

ten person-minutes. Sampling was conducted during the wet season from November 2008 to February 2009 (the austral summer) when termites are known to be more active (Dawes-Gromadzki & Spain 2003; Davies unpublished data). Appendix S1 in Supporting Information provides more detailed site and termite sampling descriptions.

### *Termite Identifications*

Termite specimens were identified to species where 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 specimens were pooled to genus (this occurred, for example, with the genera *Microtermes*, *Microcerotemes* and *Astalotermes*). Although we 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 is lodged with the National Collection of Insects, Pretoria.

### *Analyses*

Termite assemblages (i.e. species composition, species density (number of species sampled per unit area [e.g. see Gotelli & Colwell 2001]) and abundance) and activity levels (intensity and frequency of attack) were compared between savanna types for each sampling method (baiting and active searching). In order to test termite response to fire along the rainfall gradient, comparisons across burning regimes were made for each savanna habitat separately. For bait data, Kruskal-Wallis tests were fitted to examine the effects of savanna type on termite species

density, intensity and frequency of attack at baits. Differences in species density across savanna types sampled *via* active searching were assessed using parametric ANOVA.

For termite abundance across savanna types (at baits and from active searching) ANOVAs were used to test for differences between savanna types. Due to the difficulties associated with collecting and counting all termites found at a given bait or in a block of a belt transect, the number of encounters for each method was used 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 defined as an occurrence of a population of termites of one species at one point (bait or block of transect) (Davies *et al.* 2003). Since animal disturbance resulted in a different number of baits being available for termite sampling, the number of encounters and density values obtained were corrected for the number of baits per site. This was achieved by taking the mean number of termites or species per bait at each site and multiplying this value by 40 to obtain the number of encounters or species per 40 baits.

Termites were classified into feeding groups based on the classification of Donovan, Eggleton & Bignell (2001), which places termites into four groups depending on the state of humification of the feeding substrate, which is a measure of the stage of decomposition of the feeding substrate and ranges from living plants and trees to recalcitrant organic material in the soil (Donovan, Eggleton & Bignell 2001). Group I comprises the non-termitids, all of which feed on dead wood or grass; while 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.

Termite species density and abundance across burning regimes in each savanna were assessed using ANOVAs when data were normally distributed and Kruskal Wallis tests when the data did not fit a normal distribution. The intensity and frequency of attack between burning regimes were also assessed using ANOVA or Kruskal Wallis tests. All these analyses were performed in R software, version 2.11.1 (R development core team 2010).

Differences in termite assemblage composition, based on the data collected from each sampling method, were analysed between savanna types, and separately between burning regimes using multivariate analyses in Primer v. 5.2 (Clarke & Gorley 2001). Data were square root transformed to weight common and rare species more equally (Clarke & Warwick 2001). Analysis of similarity (ANOSIM, Clarke & Warwick 2001) was used to test for significant differences in assemblage composition. For interpretation of the R-value produced with ANOSIM, the associated *P*-value should be considered somewhat as a function of the sampling effort as *P*-values may become less accurate (or less meaningful) when the sample size is low (Clarke & Warwick 2001). Similarity percentage analysis (SIMPER) from Primer was used to identify which species were contributing most to differences between these assemblages. Non-metric multidimensional scaling (nMDS) ordinations were constructed to display patterns in the data for cellulose baits and active searching separately. These were iterated several times from at least 10 different starting values to ensure that a global optimum was achieved (Clarke & Gorley 2001).

Finally, individual termite species characteristic of each burning regime in each savanna habitat were investigated using the Indicator Value method (IndVal) (Dufrêne & Legendre 1997; <http://old.biodiversite.wallonie.be/outils/indval/>). This was conducted for both the baiting and active searching data sets. This method uses a combination of site specificity (uniqueness to a

particular habitat) and fidelity (frequency of occurrence within that habitat) to assess the extent to which a species is indicative of that site. A high indicator value, expressed as a percentage, signifies that a species is characteristic of a specific site. Species that scored significant IndVal values greater than 60% were subjectively considered characteristic of that habitat (modified from McGeoch, van Rensburg & Botes 2002).

## Results

### Termite diversity along the savanna rainfall gradient

#### *Species density and abundance*

Termites from *ca.* 23 species (18 genera and 5 subfamilies) were collected during the study (see Table S2 Supporting Information for a species list). The genus *Anenteotermes* was recorded from South Africa for the first time. Since cellulose baits and active searching target different groups of termites, these results are treated separately. Baiting data, which targets mostly feeding group (FG) II, showed that savanna habitat type has a significant effect on species density per plot (Kruskal-Wallis test,  $H_{2,33} = 19.20$ ,  $P < 0.001$ , Fig. 1a), with a Multiple Steel test showing that significantly more species were recorded at Satara (mean species plot<sup>-1</sup> ± SE = 4.42 ± 0.31) than the other sites (Mopani: 2.17 ± 0.11 and Pretoriuskop: 2.42 ± 0.26). For active searching data, there was again a significant effect of savanna type on species density (ANOVA,  $H_{2,33} = 8.31$ ,  $P < 0.01$ ). Tukey Honest Significant Differences (Tukey HSD) tests revealed that these differences were between Mopani (the driest site) and the other sites, with Mopani having significantly lower species density than the other savannas (Fig. 1a).

Savanna type had a significant effect on termite abundance for both methods (ANOVA,  $F_{2,33} = 20.61$ ,  $P < 0.001$ ;  $F_{2,29} = 6.75$ ,  $P < 0.005$  for baits and active searching respectively).

Tukey HSD tests revealed that Satara (intermediate to low rainfall) had significantly more termites than the other sites for the bait data, and Mopani (the driest site) had significantly fewer termites than the other sites with active searching (Fig. 1b).

### *Assemblage composition*

ANOSIM revealed differences in termite assemblages among savannas that were fairly pronounced for bait data (Global  $R = 0.395$ ) (Table S3 Supporting Information). Pair-wise tests (as well as the nMDS) for the bait data showed that assemblage differences between Satara and Pretoriuskop contributed most to the overall assemblage differences followed by Satara vs. Mopani (Fig. 2a, Table S3). For the active searching data, overall differences were slightly more pronounced (Global  $R = 0.437$ ) (Table S3) and here the greatest contributor to the differences observed was the pair-wise test between Mopani and Pretoriuskop (Fig. 2b, Table S3). An examination of species feeding groups from both data sets indicates that termites at Mopani and Satara (drier sites) differ from those at Pretoriuskop (the wettest site): feeding group II dominates the assemblage at the drier sites, whereas the wetter site has a more even spread between feeding groups II and III, with feeding group IV also present (Fig. 3).

### *Frequency and intensity of attack*

Kruskal-Wallis tests revealed that savanna type (FA:  $H_{2,1261} = 40.92$ ,  $P < 0.001$ ; IA:  $H_{2,1261} = 113.89$ ,  $P < 0.001$ ) had a significant effect on termite frequency and intensity of attack. Both frequency and intensity of attack were greatest at Satara (Fig. 4).

## **Pyrodiversity: the response of termites to fire**

### *Species density and termite abundance*

Species density and occurrence of termites, within each savanna type, showed little variation across the different fire regimes (see Figs. 5 and 6 for density and occurrence respectively). In terms of species density, the only significant differences were recorded at the wettest site, Pretoriuskop, (ANOVA,  $F_{3,12} = 5.02$ ,  $P < 0.05$ , Fig. 5c) with active searching, although active searching data approached significance at Satara (intermediate rainfall) (ANOVA,  $F_{3,12} = 3.50$ ,  $P = 0.07$ , Fig. 5b). Tukey HSD tests showed that the differences at the wet site are between the dry triennial and dry annual plots, with the dry triennial plots recording more termite species. The dry triennial plot differed (though not significantly) from the other two burning regimes (unburnt and wet triennial), again with more species being recorded. At the intermediate rainfall site, the sites burnt during the dry season (high fire intensity and frequency) recorded lower species density than the triennially wet season burnt plot and the unburnt plot, although post-hoc tests did not record these as significant. Across all savannas, no significant differences were detected with baiting data (Fig. 5).

In terms of the effect of fire on termite abundance, the only significant difference was recorded at the driest site, Mopani, with active searching (ANOVA,  $F_{3,8} = 7.31$ ,  $P < 0.05$ ), Tukey HSD test revealed this difference to be between the wet triennial burning regime (where *Hodotermes mossambicus* was collected) and the others (Fig.6b).

### *Assemblage composition*

When examining differences in termite assemblages with burning regime, the results varied with sampling method, indicating that different suites of termites (i.e. FGs) sampled by the different

methods respond differently to fire. The ANOSIM revealed significant differences in assemblages with sampling method (active searching vs. baits) at the driest (Mopani) and wettest (Pretoriuskop) sites ( $R = 0.601$ ,  $P = 0.001$  and  $0.498$ ,  $P = 0.001$  for Mopani and Pretoriuskop respectively). The differences are less pronounced at the intermediate site, Satara ( $R = 0.247$ ,  $P = 0.001$ ). For the active searching data, assemblage differences between the burning regimes become less pronounced as sites become wetter: there are three pairs of burning regime that differ significantly at Mopani (unburnt vs. dry triennial, wet triennial vs. dry annual and dry triennial), two at Satara (unburnt vs. dry annual and dry triennial) and only one at Pretoriuskop (dry triennial vs. dry annual) (Table 1). In contrast, when bait data are considered, differences become more pronounced as sites become wetter: there are three pairs of burning regime differences at Pretoriuskop (unburnt vs. dry annual and wet triennial, wet triennial vs. dry annual), one at Satara (wet triennial vs. dry annual) and none at Mopani (Table 1).

SIMPER analysis showed that most differences were driven by FG II variation, indicating differences in abundances are more important than differences in species density; however, this varied with both savanna type and sampling method (Table S4 Supporting Information).

#### *Frequency and intensity of attack*

No significant differences in the percentage (frequency) of baits attacked by termites were recorded between burning regimes at any of the three savanna types. However, with intensity of attack, the response to burning regime becomes more pronounced as sites become wetter (Fig. 6c). There is no difference in termite attack between any of the burning regimes at Mopani, but

at both Satara and Pretoriuskop, we recorded a significant difference between the dry annual and unburnt plots (the two extreme burning regimes).

#### *Individual species response*

IndVal produced few species indicative of a given burning regime (Table 2). Three species were identified as characteristic of Pretoriuskop, the wettest site (*Anenteotermes* spp., *Allodontermes rhodesiensis*, both characteristic of the dry triennial burning regime and *Lepidotermes* spp., indicative of the unburnt plots), one from Satara (*Odontotermes* sp. 3, characteristic of the dry annual burn) and one from the driest site, Mopani (*Microtermes* spp., characteristic of the wet triennial regime).

## **Discussion**

#### *Termite responses to variation in rainfall*

Termite assemblages differed substantially among savanna types, which corresponds to extensive variation in rainfall, vegetation and soil type. In semi-arid areas such as South Africa, precipitation sets limits to net primary productivity, giving rise to a strong association between those two variables (see O'Brien 1998; O'Brien, Field & Whittaker 2000; van Rensburg, Chown & Gaston 2002). It is therefore reasonable to assume that changes in rainfall result in changes in primary productivity across the study sites, with corresponding impacts on termite diversity, as predicted by the species-energy theory (see Rosenzweig & Abramsky 1993; Wright, Currie & Maurer 1993). Indeed, Mopani (the most arid site and presumably with the lowest primary productivity) had significantly lower species density and abundance than the other sites, when active searching is considered (Fig. 1). This is in keeping with Eggleton, Williams & Gaston

(1994) who found a moderately strong relationship between primary productivity and termite generic richness within biogeographic regions.

A striking result, however, from our study was the significantly higher termite abundance and activity levels (from baiting, which targets wood-feeding termites of FG II) at Satara (representing intermediate rainfall) compared with the other sites examined, which is in contrast to species-energy relationships discussed above. One possibility is that higher mammalian herbivore densities at Satara drive higher termite abundances and activity levels through higher concentrations of dung and more intense grazing, which in turn may lead to higher nutrient concentrations in the soil as well as more food for termites (Freyman *et al.* 2008), and a positive feedback loop between ungulates and termites. FG II termites may be favoured here above other FGs because conditions are too dry for other termites (FG III and IV) to persist.

Indeed, changes in the composition of termite feeding groups along the rainfall gradient were most pronounced among the soil feeders (FG III and IV). This is likely to be because soil feeders are especially susceptible to habitat desiccation, and because they require malleable, carbon-rich soils (Bignell & Eggleton 2000) and so tend to be excluded from drier sites.

#### *Pyrodiversity: response of termites to fire*

Despite the temporal and spatial scale of the burning experiment examined here, our results in general indicated that there is little overall empirical support from termites for the hypothesis that high pyrodiversity leads to high biodiversity. Specifically, as predicted, termite assemblages showed high levels of resistance to fire, with little difference in response among fire regimes. This finding agrees with studies carried out on other savanna taxa (e.g. Andersen *et al.* 2005; Parr *et al.* 2004; Parr & Andersen 2006). The subterranean habits of termites offer protection

from the direct effects of fire, so the effects of repeated burning are likely to be primarily indirect, through changes to vegetation structure and resource (food) availability. While our findings contrast somewhat with studies on termites and fire from elsewhere (see Davies, Parr & van Rensburg 2010) this 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 & Lepage 2008). In addition to there being few mound-builders in our system, this study used long-term burning regimes, a broader range of fire treatments and a wider variety of sampling methods enabling us to assess effects of pyrodiversity on the entire termite assemblage.

Following our predictions, the response of termites to fire was, however, dependent on the suite of termites sampled. Our findings suggest different feeding groups (FGs) of termites respond differentially, and opposingly, to burning. Wood and grass feeders (FG II) for example were only significantly affected by fire at the wet savanna site (Pretoriuskop), with more of these termites present on burnt plots (especially annually burnt). Conversely, soil feeders (FGs III and IV) rarely occurred on burnt plots at Satara (intermediate rainfall) and annually burnt plots at Pretoriuskop and were altogether absent from Mopani (the driest site). Being susceptible to desiccation and temperature, these termites are excluded from more open burnt habitats, but as canopy cover increases with fire exclusion, they become dominant, possibly excluding fungus growing termites (FG II). Indeed, fungus growing termites have been found to be more prominent in savanna-like landscapes (Aanen & Eggleton 2005), and our data indicate a similar pattern, resulting from different burning regimes, and mirroring the global pattern of higher termite diversity in wet, hot environments (e.g. see Davies *et al.* 2003).

While generalisations are difficult to make because feeding group and hence sampling method influence responses, we recorded some variation in the overall termite response to

burning along the rainfall gradient, with a stronger response detected with increasing rainfall. IndVal results indicated three species indicative of two burning regimes at the wettest site (Pretoriuskop), while only one species were found to be present at both Satara and Mopani. This suggests that a greater range of fire regimes is necessary at Pretoriuskop, including longer-unburnt habitat, to ensure the persistence of these species and the important functional roles they perform. This is particularly relevant for soil feeders (FG III and IV) which were characteristic species here.

Furthermore, the baiting results recorded more significant differences in termite assemblage composition and activity levels in the wet savanna (Pretoriuskop), with these differences predominantly driven by the genus *Microtermes* which was present on all plots but most abundant on burnt (especially frequently burnt) plots. Our recorded patterns are in line with those recorded for ants (Parr *et al.* 2004) and suggest that termites are influenced by changes in vegetation structure caused by fire, these changes being most evident at wetter sites (Sankaran *et al.* 2005).

Although results from active searching show that assemblage composition differs between burning regimes at the arid sites, these differences are largely driven by, and are hence probably an artefact of, the occurrence of FG I termites (*Hodotermes mossambicus*) at Mopani. These grass harvesters tend to occur in a patchy, sporadic fashion and are highly influenced by local weather conditions (e.g., recent rain) (A.B. Davies, personal observation). Indeed, weather conditions when *H. mossambicus* were recorded were atypical compared with other days (overcast and cool instead of hot). Such conditions are ideal for *H. mossambicus* activity and possibly resulted in their sampling here, hence artificially biasing results.

Increased grazing is often recorded on burnt sites (Wilsey 1996; Archibald & Bond 2004; Parrini & Owen-Smith 2010), and may have led to the increased activity levels by FG II termites recorded on annually burnt plots. Increased herbivory may increase the availability of nutrients, resulting in a positive feedback loop (Freyman, de Visser & Olf 2010) similar to that suggested for the increased termite abundance at Satara (see above). However, it is possible that higher activity levels recorded here are more an artefact of increased detectability rather than abundance, due to a lack of food resources for termites on these annually burnt plots (the plots are often barren of vegetation).

#### *Synthesis and conservation implications*

Understanding the effect of savanna fires on termites is complicated by the range of feeding groups that occur and the different methods required to sample them adequately. Nevertheless, this is the first study that has explored the response of termites to long-term fire regimes at a range of savanna sites spanning a rainfall gradient. Our findings highlight the remarkably high resistance of some faunal groups to burning, and hence the limited importance of pyrodiversity for their conservation. We did record, however, some evidence for an increased response by termites to pyrodiversity with increasing rainfall, which suggests that a wider range of fire regimes, including longer-unburnt habitat may be required in these areas when applying prescribed burning. A similar pattern was observed for ants (Parr *et al.* 2004). Although further research on a range of other faunal groups is required before the generality of our findings is known, our data support the notion that for much of the savanna fauna, fire managers can generally afford to be flexible with their approach to burning. This is because much of the

savanna fauna (including termites) are little affected by the subtleties of pyrodiversity, and hence fire management.

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**Table 1:** Analysis of similarity (ANOSIM) of termite assemblages between four burning regimes at three savanna habitats during the wet season. The R-statistic is a measure of similarity of assemblages, the closer this value is to 1, the more dissimilar assemblages are. For all comparisons, *P* was not significant ( $>0.05$ ), which should be seen primarily as a function of the sampling effort as *P*-values may become less accurate (or meaningful) when the sample size is low (Clarke & Warwick 2001). Highlighted values are those above or equal to 0.250, which are considered markedly dissimilar. Sites are arranged in order of increasing rainfall.

Site	Active searching	Cellulose baits
	R	R
<b>Mopani</b>		
Global R	0.229	– 0.145
unburnt vs. dry annual	0.000	0.000
unburnt vs. dry triennial	<b>0.250</b>	0.074
unburnt vs. wet triennial	0.000	– 0.111
wet triennial vs. dry annual	<b>0.750</b>	– 0.296
wet triennial vs. dry triennial	<b>0.750</b>	– 0.259
dry triennial vs. dry annual	– 0.500	– 0.222
<b>Satara</b>		
Global R	0.137	0.031
unburnt vs. dry annual	<b>0.481</b>	0.000
unburnt vs. dry triennial	<b>0.259</b>	– 0.111
unburnt vs. wet triennial	0.148	– 0.148

wet triennial vs. dry annual	0.241	<b>0.333</b>
wet triennial vs. dry triennial	- 0.037	- 0.111
dry triennial vs. dry annual	- 0.444	0.074

### **Pretoriuskop**

Global R	0.074	0.170
unburnt vs. dry annual	0.000	<b>0.259</b>
unburnt vs. dry triennial	0.148	- 0.259
unburnt vs. wet triennial	- 0.185	<b>0.296</b>
wet triennial vs. dry annual	0.074	<b>0.630</b>
wet triennial vs. dry triennial	0.185	0.148
dry triennial vs. dry annual	<b>0.296</b>	0.074

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**Table 2:** Species identified as characteristic of specific burning regimes arranged along a climatic gradient from dry to wet. Shown are indicator values from the IndVal procedure (100% meaning a perfect indicator). All species shown were significant indicators at the  $P < 0.05$  level for at least one randomization test.

Savanna	Species and (feeding group)	IndVal %	Burning regime
Mopani	<i>Microtermes</i> spp. (II)	80	Wet triennial
Satara	<i>Odontotermes</i> sp. 3 (II)	60	Dry annual
Pretoriuskop	<i>Anenteotermes</i> spp. (III)	73	Dry triennial
Pretoriuskop	<i>Allodotermes rhodesiensis</i> (II)	67	Dry triennial
Pretoriuskop	<i>Lepidotermes</i> spp. (IV)	67	Unburnt

## Figure legends

**Figure 1:** Termite species density and abundance across savanna habitats: a) species density at cellulose baits and active searching, and b) number of termite encounters as a surrogate for abundance across savanna habitats for cellulose baits and active searching. Letters and numerals denote significant differences between savanna habitats for each method and error bars represent standard error.

**Figure 2:** Non-metric multi-dimensional scaling ordination of abundance of termite species for a) cellulose baits and b) active searching in three different savanna habitats. ▲ = Mopani, ○ = Satara, ■ = Pretoriuskop.

**Figure 3:** The relative contribution (measured as a percentage) each feeding group makes to the termite assemblage. See text for feeding group descriptions.

**Figure 4:** Frequency (a) and intensity (b) of termite attack across savanna habitats for cellulose bait data. An asterisk denotes significant differences between savanna habitats; error bars represent standard error.

**Figure 5:** Species density across fire regimes for a) Mopani, b) Satara and c) Pretoriuskop for cellulose baits and active searching. Letters denote significant differences at Pretoriuskop; error bars throughout represent standard error.

**Figure 6:** Termite abundance (measured as the number of encounters) and intensity of attack across burning regimes: a) abundance at cellulose baits, b) abundance recorded with active searching and c) intensity of attack at cellulose baits in each savanna habitat. Letters denote significant differences within savanna habitats and error bars represent standard error.

## **Supporting Information**

**Appendix S1:** Detailed site and sampling descriptions.

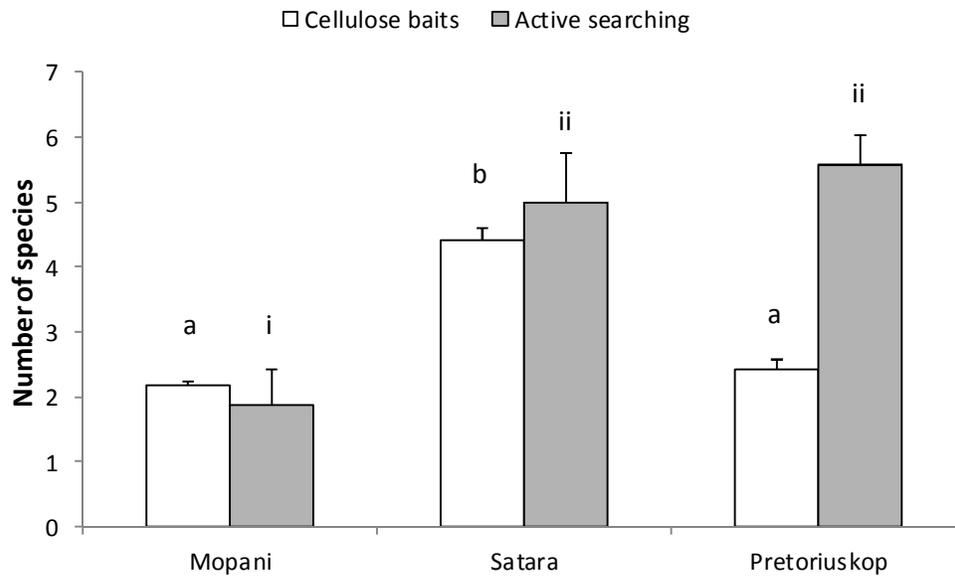
**Table S2:** Table consisting of the termite species sampled during the study, as well as which savanna site each species was sampled in and to which feeding group the species belongs to.

**Table S3:** Analysis of similarity (ANOSIM) for termite assemblages between three savanna habitats.

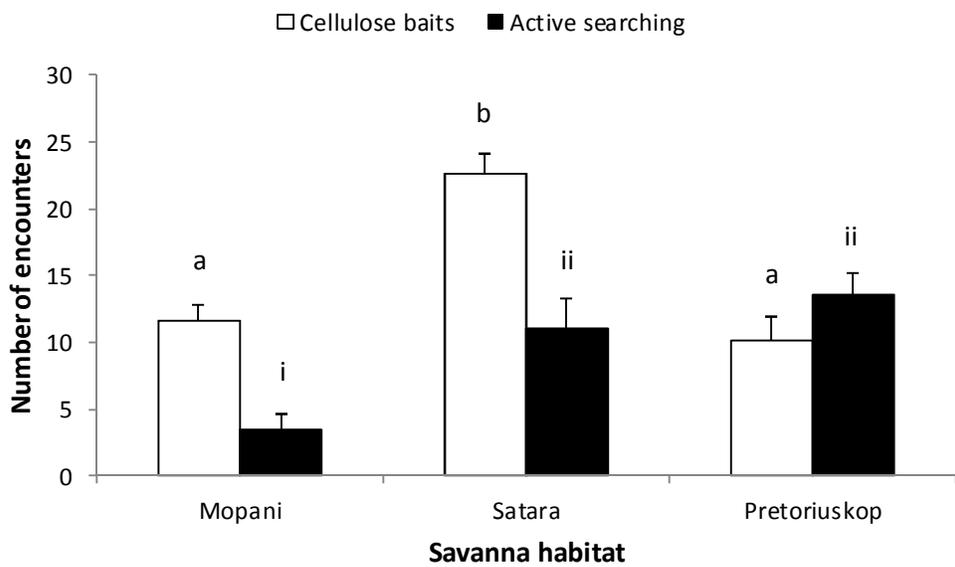
**Table S4:** Similarity percentage analysis (SIMPER) for termite abundance per burning regime in each savanna type.

**Figure 1**

a)

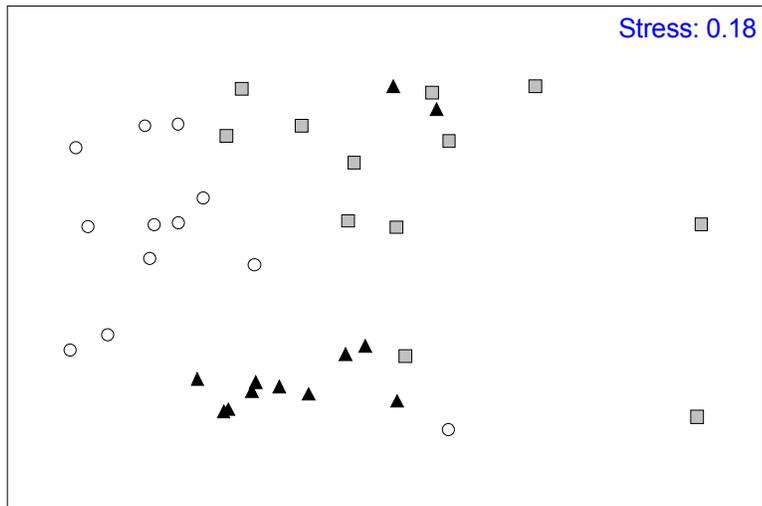


b)

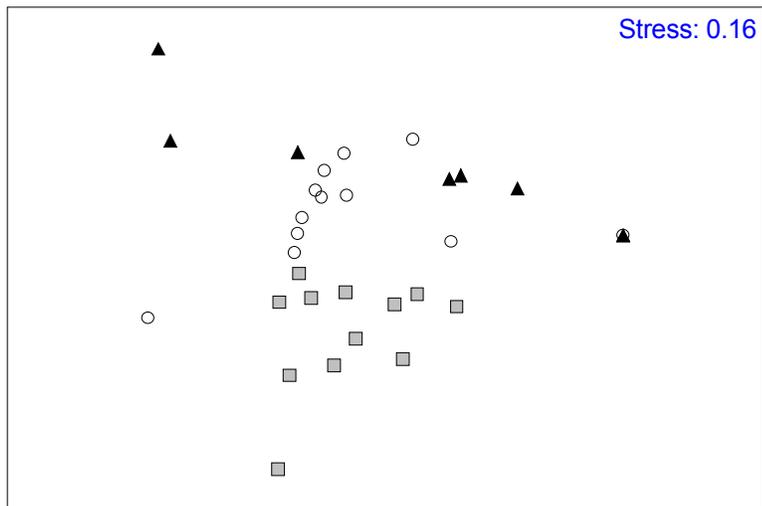


**Figure 2**

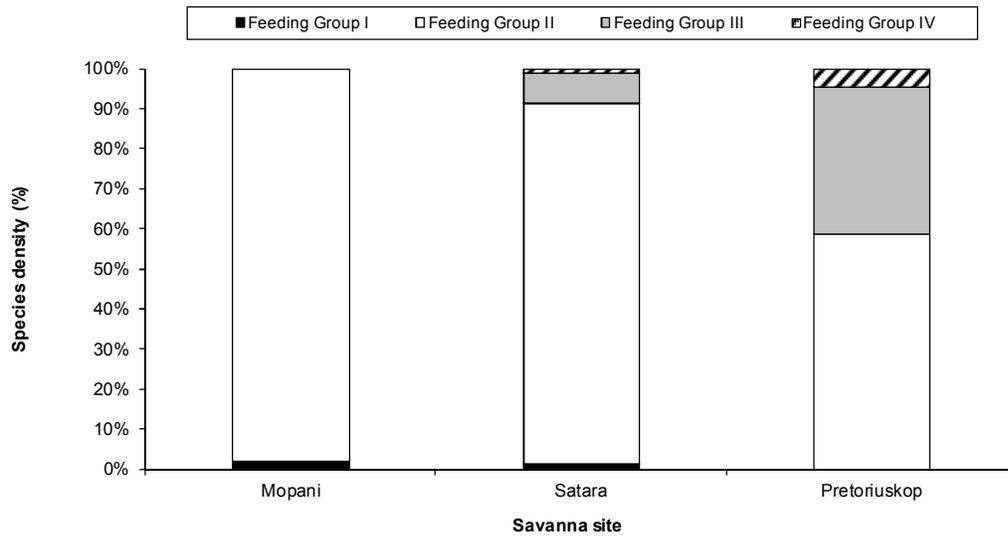
a)



b)

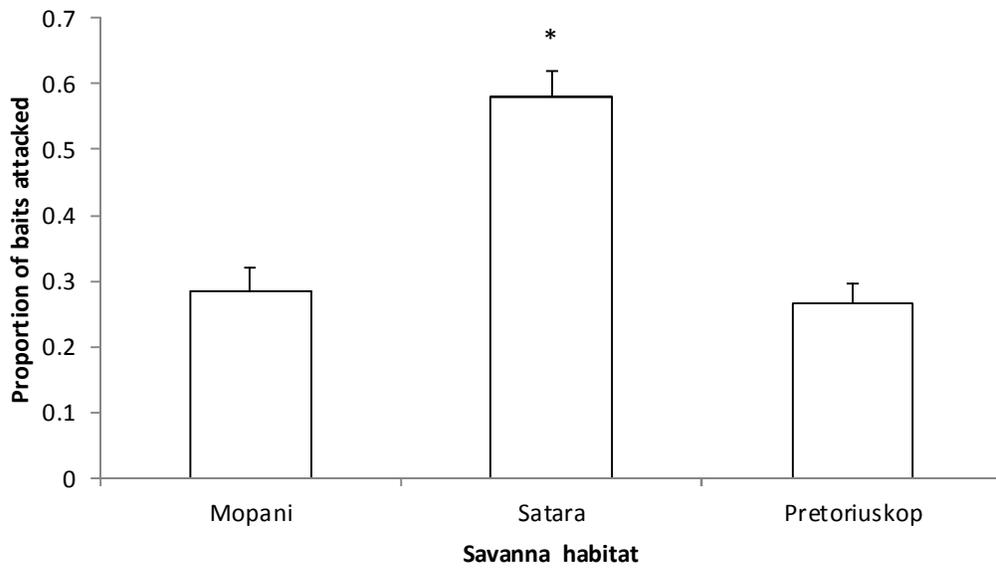


**Figure 3**

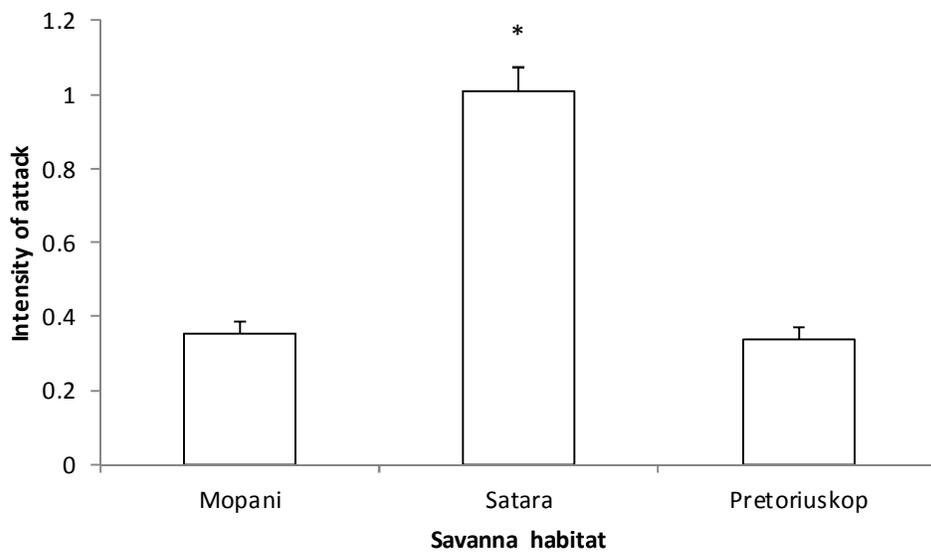


**Figure 4**

a)

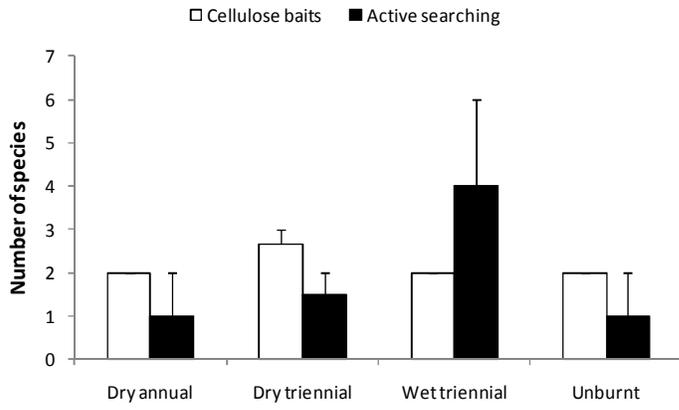


b)

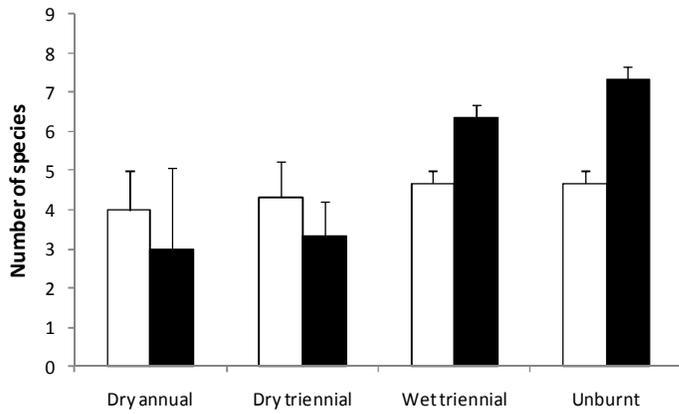


**Figure 5:**

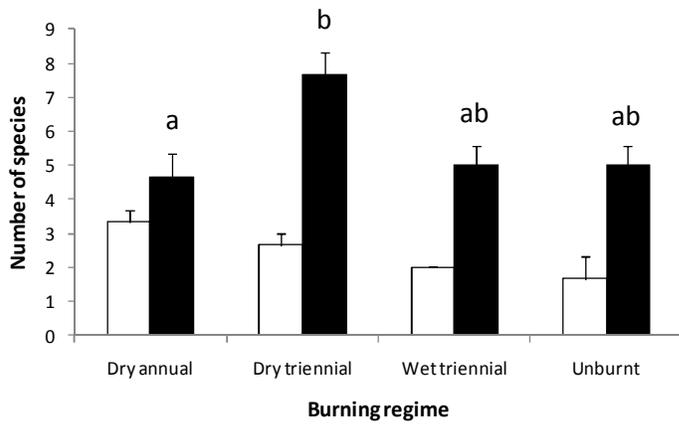
a)



b)

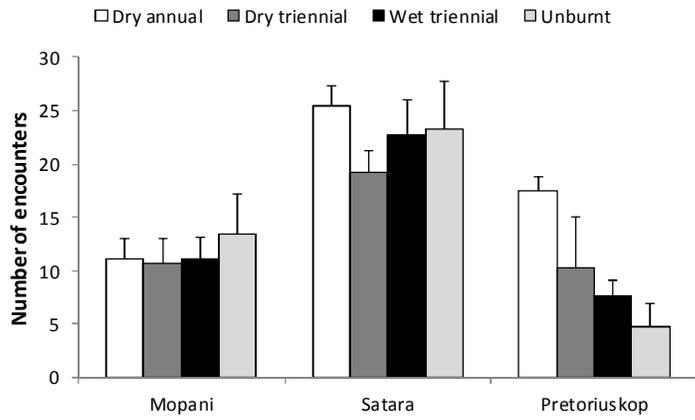


c)

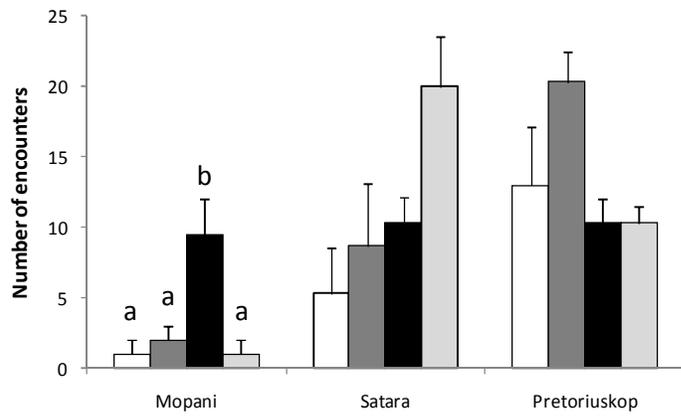


**Figure 6:**

a)



b)



c)

