Seasonal activity patterns of African savanna termites vary across a rainfall gradient

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Running title: Savanna termites and seasons

Abstract

Seasonal variations in temperature and moisture are strong drivers of biological activity and diversity. Termites are an important insect group previously shown to respond to seasonal variation, but results are mixed with unclear patterns across habitat types. We investigated seasonal variation in termite species density, activity levels and assemblage composition across three seasons (wet, transitional and dry) and four savanna types across a rainfall gradient (450 $mm.yr^{-1}$ – 900 $mm.yr^{-1}$) in South Africa using cellulose baits. Termites responded to seasonality in all savannas investigated, with lower species density and activity levels during the dry season compared to the wet and transitional seasons. In the more arid sites (≤ 550mm rainfall per year) activity levels were highest in the wet season, while at wetter sites (≥750mm rainfall per year) the highest activity was recorded in the transitional season. Assemblage composition did not differ much between seasons across all sites, but differences in both composition and activity levels across seasons were more pronounced in wetter sites compared to drier ones. Our results demonstrate that seasonal patterns in termite diversity vary with mean annual rainfall, with larger variation in wetter habitats where climatic variation between seasons is greater.

Keywords: cellulose baits, climatic variation, mean annual rainfall, moisture, soil organisms, temperature

Introduction

Seasonal variations in temperature and moisture are strong drivers of biological activity and diversity across the globe. Much recent literature focuses on effects on phenology, especially within the context of anthropogenic climate change (see Visser and Both, 2005; Donnelly et al., 2011; Rafferty and Ives, 2011), but seasonal variation is also evident in the abundance and activity of organisms, even enabling the co-existence of different species and so increasing diversity (Shimadzu et al., 2013). Insects are particularly susceptible to seasonality, with profound seasonal effects observed for several aspects of insect ecology including phenology, diapause behaviour and activity levels (Wolda, 1988; Pinheiro et al., 2002; Barrow and Parr, 2008).

Although seasonal differences may seemingly be more pronounced in cooler temperate climates, tropical areas, including savanna ecosystems, also exhibit seasonal variation, with differences more evident in rainfall and moisture variation, than temperature related changes. All savannas have a highly seasonal climate with a hot wet season and a warm to cool dry season (Scholes, 1997). In southern Africa, savannas have a single, hot rainy season followed by a warm dry season each year (Venter et al., 2003), with this seasonal pattern affecting many components of savanna biota, including plants (Scholes et al., 2003), ungulates (Owen-Smith and Ogutu, 2003) and insects (Braack and Kryger, 2003).

Termites (Blattodea: Termitoidae) are an important insect group in ecosystems across the tropics, including African savannas. They are considered ecosystem engineers, altering soil composition and hydrology (Jones et al., 1994; Mando et al., 1996) and are the dominant invertebrate decomposer in these environments (Collins, 1981; Holt, 1987; Schuurman, 2005), playing an important role in nutrient cycling (Holt and Coventry, 1990; Lepage et al., 1993; Konaté et al., 1999). They are also sensitive to moisture and temperature levels (Abensperg-Traun and De Boer, 1990; Smith and Rust, 1994; Korb and Linsenmair, 1998), and thus expected to respond to seasonal variation.

However, studies focussing on seasonality and termites display mixed results. While some studies record higher levels of termite abundance and activity during the wettest months of the year in savannas (Buxton, 1981; Pinheiro et al., 2002), others measured higher levels of termite activity in drought years and months of lower rainfall (Ohiagu, 1979; Braack, 1995) while still others recorded highest activity in the transitional season between wet and dry months (Dawes-Gromadzki and Spain, 2003, see also Abensperg-Traun 1991 for similar findings in Western Australia). Such contrasting responses in different savanna areas have resulted in unclear patterns with a need for more comprehensive studies. Studies conducted along environmental gradients are likely to be particularly useful in disentangling how termites respond to seasonality because they will examine responses in areas of differing degrees of seasonal variation, improving our understanding of termite ecology, and providing insight into their contribution to ecosystem functioning and how this may change across seasons. Furthermore, comprehensive data on seasonal patterns will contribute to developing better termite sampling protocols, which are still lacking for savanna ecosystems (see for e.g. Dawes-Gromadzki, 2003; Davies et al., 2013a).

In this study, we sampled termites across four savanna types and three seasons in order to determine i) how termite assemblage structure (species density and composition) and activity levels vary seasonally and ii) whether seasonal patterns are consistent across savanna types varying in the amount of mean annual rainfall received, and subsequent levels of net primary productivity. Due to their dependence on moisture (Abensperg-Traun and De Boer, 1990; Su and Puche, 2003), we expected greater levels of termite activity during the wet season and stronger responses to seasonality in high rainfall sites where variations between wet and dry seasons are more extreme.

Materials and methods

Study sites and termite sampling

The study was conducted in four savanna vegetation types across a rainfall gradient spanning some 700 km in two of South Africa's major reserves: Kruger National Park (KNP) and Hluhluwe-iMfolozi Park (HiP). Three savanna types were sampled in KNP: Mopane woodland (Mopani area, 450mm of rainfall per year), *Acacia* savanna (Satara area, 550mm of rainfall per year), and *Terminalia* woodland (Pretoriuskop area, 750mm of rainfall per year), as well as one savanna type in HiP representing mesic *Acacia* savanna (Hluhluwe area, 900mm of rainfall per year). Although different reserves, KNP and HiP both consist of savanna vegetation and contain

Table 1 : Termite species sampled with cellulose baits in three seasons across four savanna habitats. Numbers represent the number of sampling plots within which a specific species was sampled (maximum of 12 plots for each site except Hluhluwe where 11 plots were sampled). Sites are arranged in order of increasing mean annual precipitation. All species sampled belong to the family Termitidae.

Sub-family/Species	Mopani				Satara				Pretoriuskop				Hluhluwe		
		W	T	D		W	T	D		W	T	D		W	D
Macrotermitinae															
Allodontermes rhodesiensis	-	2	4		9	5	9		2	2	1		6	1	
Ancistrotermes latinotus	2	3	-		9	8	8		9	10	3		3	-	
Macrotermes michaelseni		7	1	6		8	6	7		-	-	-		-	-
Macrotermes natalensis	-	1	1		-	-	1		-	-	-		-	1	
Microtermes spp.		12	11	6		12	12	9		12	11	1		11	1
Odontotermes sp. 1	-	-	-		-	-	-		-	1	1		-	-	
Odontotermes sp. 2	-	-	-		-	-	-		1	-	-		3	2	
Odontotermes sp. 3	1	5	4		6	2	8		-	1	1		3	1	
Apicotermitinae															
Astalotermes spp		-	-	-		-	-	-		3	1	-		-	-
Termitinae															
Lepidotermes spp		-	-	-		-	-	1		-	-	-		-	-
Microcerotermes spp	4	2	-		8	2	-		-	5	-		2	-	
Promirotermes spp	-	-	-		-	-	-		-	-	-		1	-	
Nasutitermitinae															
Rhadinotermes coarctatus		-	-	-		-	-	-		1	-	-		-	-

Table 2: Analysis of similarity (ANOSIM) between termite assemblages across the four savanna habitats and three seasons. For the dry and transitional seasons, presence/absence data were used, whereas abundance data were available for 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. The Global R-statistic refers to overall differences between assemblages, whereas the paired comparisons refer to between site differences (Clark and Warwick 2001). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Wet season	Dry season	Transitional season
Global R	0.397***	0.271***	0.116**
Paired savanna comparisons			
Mopani vs. Satara	0.420***	0.185*	0.074
Mopani vs. Pretoriuskop	0.434***	0.393***	0.191**
Mopani vs. Hluhluwe	0.287**	0.203**	
Satara vs. Pretoriuskop	0.574***	0.326***	0.074
Satara vs. Hluhluwe	0.401***	0.389***	
Pretoriuskop vs. Hluhluwe	0.242*	0.262***	

similar termite fauna when variation in rainfall is controlled (the termite assemblages at HiP are similar to those at Pretoriuskop, see Tables 1 and 2 in Results) and can therefore be validly compared. This study forms part of a larger programme investigating aspects of savanna termite diversity (see Davies et al., 2012, 2013a) and sampling in KNP was subsequently carried out across a series of experimental burning plots (see Biggs et al., 2003; van Wilgen et al., 2007). Three sets of four sampling plots (12 plots per savanna type except for Hluhluwe where only 11 plots were available) spaced 10–20 km apart were selected from within each of the savanna types. The four in each set of plots form part of a burning experiment, but are representative of each savanna type and its fire regimes. Fire effects were not expected to influence sampling because both termite diversity (Davies et al., 2012) and mound distributions (Davies et al., 2014) display remarkable resistance to fire. Furthermore, the same four burning regimes were sampled in each habitat, thus controlling for any potential fire effects.

Termite sampling was conducted in three seasons during 2008 and early 2009: March to May 2008, representing a transitional season between the wet to dry seasons (the austral autumn), June to September 2008 representing the dry season (the austral winter), and November 2008 to February 2009 representing the wet season (the austral summer). Due to logistical constraints, sampling in Hluhluwe occurred in the wet and dry seasons only. However, we retained this site in order to extend the rainfall gradient and encompass the wettest savanna habitat available in South Africa. 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 experimental burn plot (see La Fage et al., 1973) , arranged in a grid of five by eight baits, spaced five metres apart. 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. These baits were wrapped around the middle with packaging tape to prevent unravelling and secured to the soil surface using a metal tent peg placed through the centre hole 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 time intervals of 7 (5 during the wet season), 14, 28 and 56 days. At each of these time intervals, five surface and five buried baits were removed without replacement, and a representative sample of any termites present collected. Baits were then visually assessed for intensity of termite attack (IA) and scored according 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 (following 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. This sampling design was repeated in each of the three seasons.

Termite Identifications

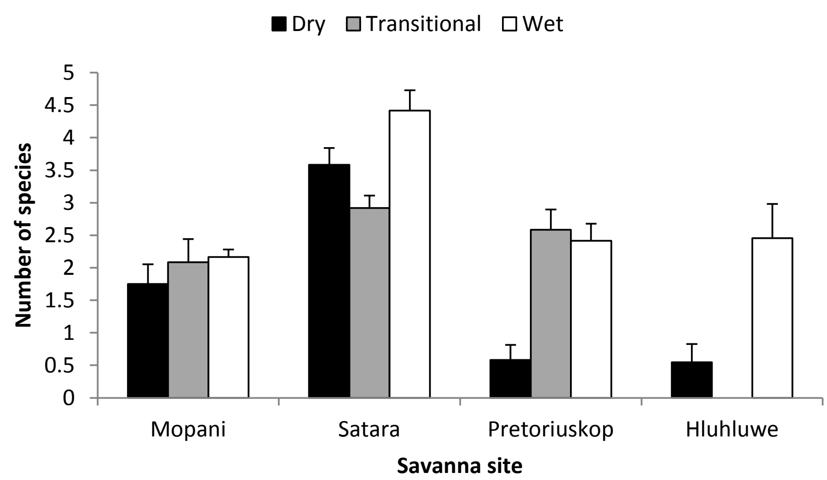
Termite specimens were identified to species where possible using soldier castes whenever available (when soldiers were not present, workers were used). Where this was not possible, genera were separated into morphospecies (e.g. for *Odontotermes*), and where even this was problematic (due to a lack of taxonomic revisions) the specimens were pooled to genera for that specific 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 at the University of Pretoria, South Africa.

Analyses

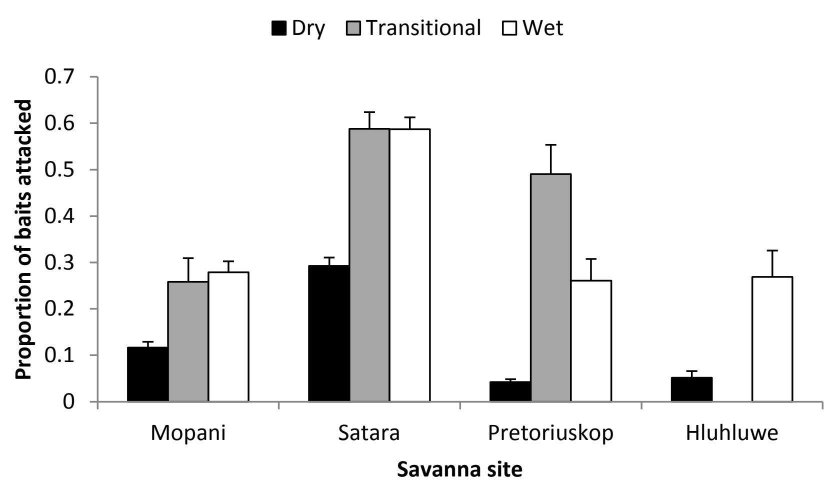
For all analyses, data were pooled to the plot level within each season to account for spatial and temporal autocorrelation. This included data from each sampling event (time interval) and bait position (surface or buried). Plots (12 per savanna site) were considered independent replicates as they were a minimum of several hundred meters apart and beyond the foraging distance of *Macrotermes* colonies, the largest and furthest ranging genus attracted to cellulose baits in African savannas (Darlington, 1982). Generalized linear models (GLM) with a Poisson (species density and intensity of termite attack) or Binomial (frequency of termite attack) error distribution and log-link function, corrected for overdispersion where deviance/d.f. was greater or less than *ca.* 1, were fitted to examine effects of savanna type and season on termite species density, intensity and frequency of attack at baits. For all these analyses, plots of standardised residuals *vs*. fitted values were used to assess model fit. These analyses were performed in R software, version 2.15 (R Development Core Team, 2012).

Seasonal patterns in termite assemblage composition were analysed using multivariate analyses in Primer v. 5.2 (Clarke and Gorley, 2001). Bray-Curtis similarity matrixes were constructed for each savanna site and across all sites, and a one-way analysis of similarity (ANOSIM) performed to test for significant differences in assemblage composition at each site. ANOSIM produces an R-statistic typically ranging from 0 to 1 as a measure of similarity between assemblages, the closer this value is to 1, the more dissimilar the assemblages are (negative values can be produced, indicating larger intra- than inter-site differences). An associated p-value indicates whether the R statistic is significant. Non-metric multidimensional scaling (NMDS) ordinations were then constructed to display seasonal patterns in assemblages. These were iterated several times from at least ten different starting values to ensure that a global optimum was achieved (Clarke and Gorley, 2001).

a)



b)



c)

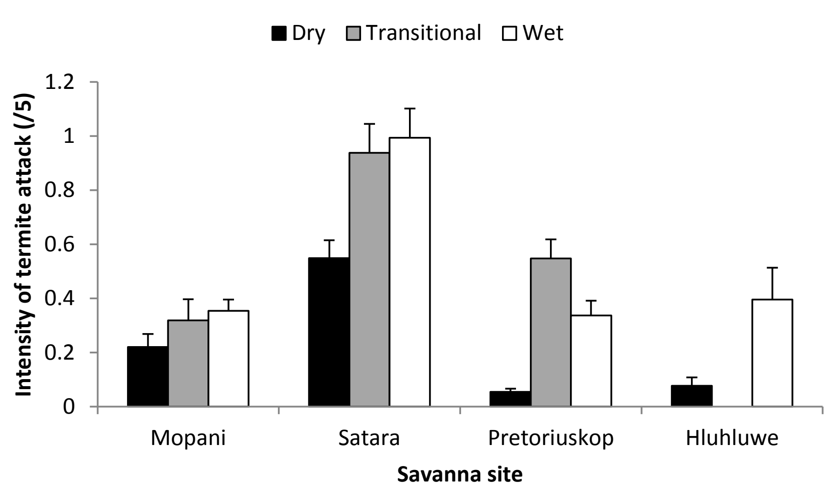


Figure 1: Termite activity levels across seasons and savanna sites recorded at cellulose baits: a) mean (±SE) termite species density per sampling plot, b) the mean (±SE) proportion of baits attacked by termites (frequency of attack), and c) mean intensity (±SE) of termite attack at baits.

Results

Termites from at least 13 species (11 genera and 4 subfamilies) were sampled during the study across the three seasons (Table 1). The termites sampled differed between the savanna types, with differences in assemblages strongest during the wet season (higher Global R statistic), followed by the dry season. Between sites, the wetter sites (Pretoriuskop and Hluhluwe) were generally the most similar to each other, and there were stronger differences between these sites and the drier ones (Mopani and Satara), although Mopani and Satara differed substantially during the wet season (Table 2).

Species density

Seasonality had a significant effect on species density, with fewer species recorded during the dry season than in the transitional and wet seasons ($F = 13.29$, $p < 0.001$, Fig. 1a). Savanna site also had a significant effect on species density per sampling plot ($F = 19.07$, $p < 0.001$, Fig. 1a), with significantly more species recorded at the second driest site, Satara (mean species $plot^{-1} \pm SE = 3.64 \pm 0.18$) than the other sites (Mopani: 2.00 ± 0.16, Pretoriuskop: 1.86 ± 0.22 and Hluhluwe: 1.50 ± 0.36). There was also a significant interaction between season and savanna habitat ($F = 7.24$, $p < 0.001$), with the wetter sites (Pretoriuskop and Hluhluwe) showing larger seasonal differences (Fig. 1a).

Frequency and intensity of attack

Generalized linear models revealed that season (FA: $F = 65.96$, $p < 0.001$; IA: $F = 25.67.45$, $p < 0.001$) and savanna site (FA: $F = 35.79$, $p < 0.001$; IA: $F = 33.91$, $p < 0.001$) as well as the interaction between the two variables (FA: $F = 5.54$, $p < 0.001$; IA: $F = 4.65$, $p < 0.001$) had a

Table 3: Analysis of similarity (ANOSIM) between termite assemblages across three seasons at each of the four savanna habitats. Presence/absence data were used for all comparisons. The R-statistic is a measure of similarity of assemblages, the closer this value is to 1, the more dissimilar assemblages are. The Global R-statistic refers to overall assemblage differences across seasons (across all sites and at each site separately), whereas the season comparisons refer to assemblage differences between those individual seasons (Clarke & Warwick 2001). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Seasonal comparison	Global R	Dry vs. Wet	Dry vs. Transitional	Wet vs. Transitional
Across all sites	0.121***	0.197***	0.092***	-0.01
Mopani	0.150**	0.147*	0.185**	0.131*
Satara	0.118**	0.124*	0.116*	0.129*
Pretoriuskop	0.235**	0.303***	0.202**	0.071
Hluhluwe		0.093*		

significant effect on termite frequency (FA) and intensity (IA) of attack at baits. Both frequency and intensity of attack were greatest at Satara compared to the other savanna habitats examined and higher during the transitional and wet seasons. FA and IA were highest during the wet season for both Mopani and Satara, but the highest levels at Pretoriuskop were recorded during the transitional season. Larger seasonal differences were recorded at the wetter sites (Pretoriuskop and Hluhluwe) than the drier ones (Mopani and Satara) (Fig.1b and c).

Assemblage composition

Analysis of similarity (ANOSIM) and non-metric multi-dimensional scaling (NMDS) revealed few differences between termite assemblages across seasons (Table 3, Fig. 2). Only at Pretoriuskop, the second wettest site, were seasonal differences fairly pronounced, particularly between the assemblages sampled in the dry and wet seasons. At all sites, any differences that did occur were more pronounced between the dry season and the other two, with the wet and transitional seasons showing very small differences. Differences were mostly related to species being sampled on fewer plots during the dry season (e.g. *Ancistrotermes latinotus* and *Microtermes* spp. at Pretoriuskop), although some species were entirely absent (e.g. *Astalotermes* spp. and *Microcerotermes* spp.) (Table 1).

When species which were relatively common across the entire rainfall gradient were considered, their relative abundances displayed stronger seasonal variation at the wetter sites (Pretoriuskop and Hluhluwe) compared to the drier sites (Mopani and Satara). This was true for *Allondontermes rhodesiensis*, *Ancistrotermes latinotus* and *Microtermes* spp. *Microcerotermes* spp. was an exception, being absent from all sites during the dry season (Table 1).

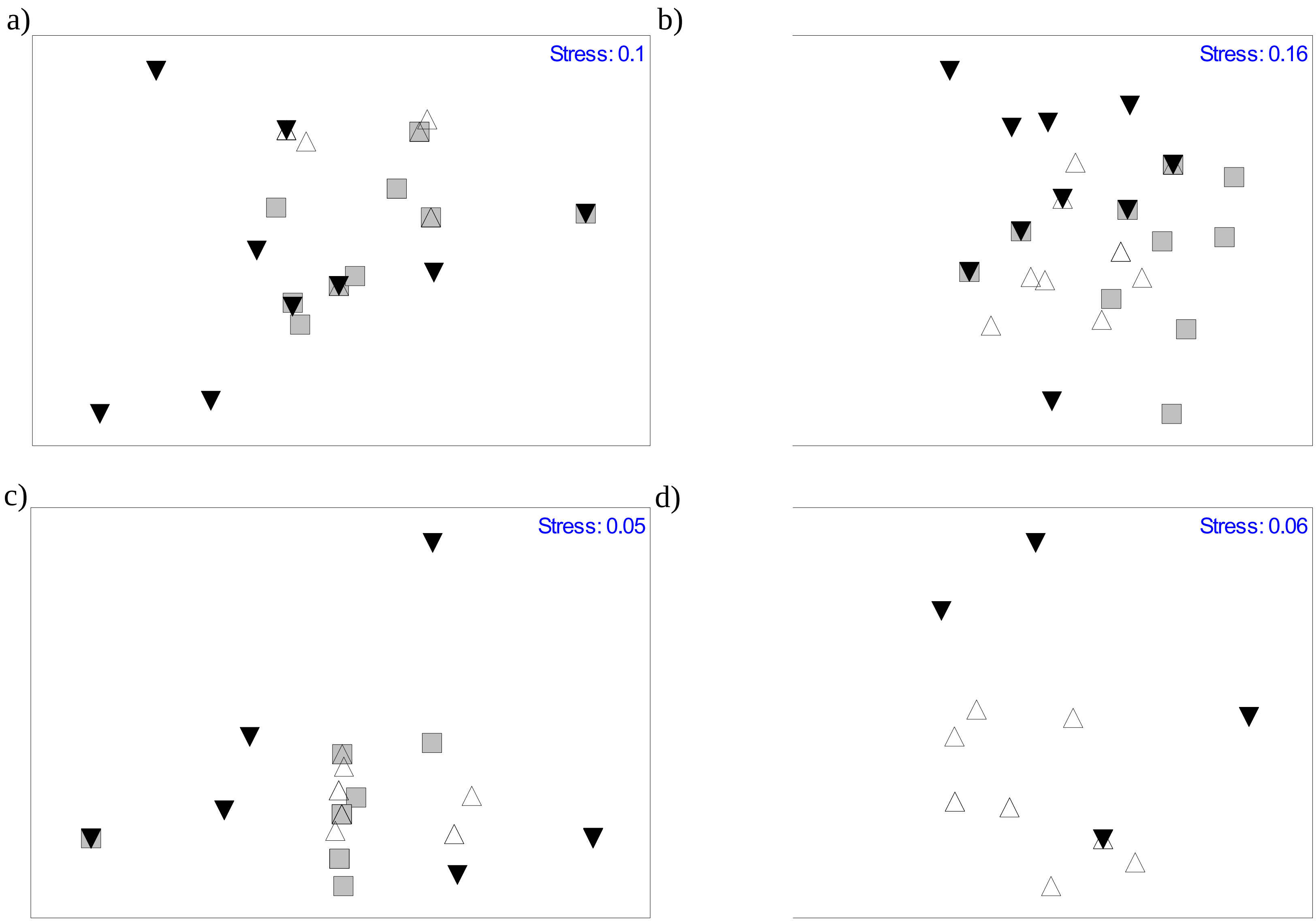


Figure 2: Non-metric multi-dimensional scaling ordination of termite assemblages sampled during three seasons at each savanna site a Mopani (450 mm MAP), b Satara (550 mm MAP), c Pretoriuskop (750 mm MAP), and d Hluhluwe (900 mm MAP). Inverted filled triangle dry season, open triangle wet season, open square transitional season

Discussion

Termite activity and species richness was highest during the wet and transitional seasons at all sites, following the general trend for insect activity (Wolda, 1988) and in agreement with similar findings for termites recorded elsewhere (e.g., east Africa: Buxton (1981), Western Australia: Abensperg-Traun (1991), northern Australia: Dawes-Gromadzki and Spain (2003)). This is likely to be a reflection of greater food and moisture availability during these seasons as well as warmer temperatures. These effects extend into the transitional season due to a lag effect on vegetation growth, but also because this season may be better suited to termite foraging than the wet season in certain habitats. In northern Australia, Dawes-Gromadzki and Spain (2003) recorded higher levels of termite activity during the transitional season and deduced that this was because of heavy monsoonal rainfall here during the wet season, causing soil to become waterlogged and unsuitable for termite foraging. Dibog et al. (1998), although failing to document any seasonal patterns in a seasonal tropical rain forest, 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 our study, the wetter 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. Being sensitive to temperature (Smith and Rust, 1994; Korb and Linsenmair, 1998) they will likely also avoid or be less active in cold conditions, which was the case in temperate Australia (Abensperg-Traun, 1991; Evans and Gleeson, 2001). Termites were most active during spring and autumn in Western Australia, avoiding the dry summers and cold, but wet, winters (Abensperg-Traun, 1991), while in eastern Australia termite foraging was reduced and localised around nests during winter (Evans and Gleeson, 2001).

The lowest levels of activity across all our study sites were recorded during the dry season. Being soft-bodied and susceptible to desiccation, termites are likely to move deeper into the soil during dry periods, becoming biologically inactive and less likely to be sampled. 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. In contrast to this, grass harvesting termites (such as *Hodotermes mossambicus* and *Trinervitermes geminatus*) have been observed to be more active during the dry season (Ohiagu 1979 for *T. geminatus* and Braack 1995 for *H. mossambicus*) because they prefer dead or senescing grass to live green grass (Ohiagu, 1979). These termites are not attracted to cellulose baits, feeding exclusively on grass (Uys, 2002), and so were not sampled during this study. However, Braack (1995) also recorded higher activity levels of *Allodontermes rhodesiensis* and *Microtermes* spp. (both species are attracted to cellulose baits and were sampled during this study) during drier months in South African savanna receiving approximately 550mm annual rainfall, concluding that these termites too favour dry conditions. This is in stark contrast to our findings and other studies looking at functionally similar termites (Buxton, 1981; Abensperg-Traun, 1991; Dawes-Gromadzki and Spain, 2003). Braack (1995) assessed termite activity by recording surface runways once a month. Giving the far higher incidence of rainfall days in wetter months and the type of rainfall received in southern African savannas (usually as heavy downpours) there is a high likelihood that such runways will be washed away more frequently in wetter months compared with dry ones, thereby resulting in higher levels of termite activity recorded in drier months. These results could thus be an artefact of weather conditions rather than actual patterns. Indeed, the author himself acknowledges that the data set was very small and that no correlation was found between monthly rainfall and termite activity, suggesting caution when interpreting his results.

The termite assemblages sampled did not display much variation between seasons, indicating that seasonality affects wood feeding termite species (those attracted to cellulose baits) fairly equally. Several different species of termites have been shown to be sensitive to soil moisture (see for e.g. Abensperg-Traun and De Boer, 1990; Su and Puche, 2003) and our results suggest similar findings: that all species respond in similar ways to low moisture in the dry season. Any assemblage compositional differences detected (which were mostly related to fewer occurrences on sampling plots) were more pronounced at Pretoriuskop, the second wettest site, indicating that seasonal differences were more pronounced in higher rainfall sites. Similarly, both this site and the wettest site (Hluhluwe) displayed larger seasonal differences in terms of activity and species density, and species that were present at all sites displayed the strongest seasonal differences here. Seasonal variation in rainfall is greater at these sites compared with the drier ones with concomitantly larger termite seasonal responses.

The stronger assemblage differences between savanna sites during the wet season reflect the higher activity levels overall during this season and also arise from several species being altogether absent during the dry season, predominantly at the wetter sites. During this season (wet), savanna site differences are most apparent. The drier sites differ further by having higher activity levels during the dry season than the wetter sites, with a peak in activity and species density at the intermediate rainfall site, Satara. This unimodal peak in diversity is unusual given the strong dependence of most termite groups on soil moisture and is attributed to factors related to the relatively high mammalian herbivore abundance here (see Davies et al., 2012) and fungus-growing termites (which are attracted to cellulose baits) being able to out compete fungi in semi-arid environments (see Aanen and Eggleton, 2005; Davies et al., 2013b)

Conclusion

Termites in South African savannas display high levels of seasonality in their activity levels, being largely inactive during the dry season, with these patterns more pronounced in wetter habitats. Ecosystem functions performed by termites have been suggested to complement similar functions performed by other taxa such as dung beetles. This because termites remain active during the dry season as well as in arid environments while dung beetles do not (Freymann et al., 2008; Jouquet et al., 2011). Although this may hold true at drier sites (≤ 550mm of rainfall per year, where seasonal variation is less pronounced and termites remain relatively active in the dry season), our results suggest that, especially at wet sites, termites too are largely inactive during the dry season. Their complementary roles, at least at wet sites, may therefore be restricted to wetter months.

These findings also have implications for termite sampling, for which standard protocols still need to be fully developed and implemented in savannas (see Dawes-Gromadzki, 2003; Davies et al., 2013a). We suggest that the optimum time to sample termites differs depending on the amount of mean annual rainfall received. At dry savanna sites (≤ 550mm of rainfall per year) sampling will be most effective at the peak of the wet season, whereas in wetter savannas, sampling should rather be conducted after the peak rains during the transitional season, unless comparable sampling is the goal.

Results here reflect only those termites attracted to cellulose baits (wood feeders). Other species, such as grass harvesters and soil feeders could respond differently to seasonal variation. Although soil feeders are likely to respond in similar ways because of their dependence on moisture and malleable soil (Bignell and Eggleton, 2000; Davies et al., 2012), grass harvesters may well be active in drier months as recorded in previous studies (Ohiagu, 1979; Braack, 1995), possibly substantiating claims that termites complement other taxa through the ecosystem functions they provide.

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