

The effects of long-term burning regimes on savanna spider assemblages

by

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In memory of Ryan

I, Bradley Neil Reynolds, 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.

SIGNATURE:

A handwritten signature in black ink, appearing to be 'BRADLEY NEIL REYNOLDS', written in a cursive style.

DATE: 8 July 2014

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Abstract

Fire is an important disturbance in many biomes throughout the world and plays a major role in savannas, where it affects the composition and structure of vegetation, which in turn structures faunal assemblages. Higher intensity and more frequent fires tend to simplify habitat structure, leading to a decrease in faunal abundance and diversity. Fire is often used as a tool in conservation areas, but the effects of fire, in particular long-term burning regimes, on fauna is largely unknown, especially in the case of invertebrates. This is problematic given the pivotal roles that invertebrates play in ecosystem functioning. The study aimed to address this paucity of studies on the effect of long-term burning regimes on invertebrates by making use of the long-term fire experiment in Kruger National Park, South Africa, initiated in 1954 and using spiders, which are important predators that play critical roles in ecosystem functioning and are a highly diverse group, known to be sensitive to changes in vegetation structure. Specifically, the study aimed to investigate whether spider taxonomic diversity, composition and functional traits were affected by four burning regimes and how this response varied across three different savanna types along a rainfall gradient. This was explored in the context of changes in vegetation structure. It was hypothesised that spider assemblages would be influenced more by high intensity, frequent fires and that the response to the burning regimes would be greatest at the wettest savanna site, where burning has a greater effect on vegetation structure. The burning

regimes used were annual and triennial, high intensity winter burns, respectively, and triennial, low intensity summer burns, which were all compared to unburnt plots, enabling comparisons of the effects of fire intensity, frequency and the presence of fire versus its absence. Burning regimes were replicated three times in three savanna types and spider sampling took place in autumn, spring and summer using a variety of sampling techniques in order to encompass seasonal variation in spider assemblages and to sample spiders in all components of the savanna systems. Spiders were found to be highly resistant and resilient to changes in habitat structure related to the burning regimes examined, with no major differences in abundance, species richness, assemblage composition and distribution of spiders in the various functional trait groupings investigated across burning regimes. However, there was a response by spiders between annual, high intensity burns and unburnt plots at the wettest savanna site in terms of abundance suggesting the possibility of a greater response by spiders to burning in wetter savannas as hypothesised. Spider abundance and species richness decreased along the rainfall gradient and assemblages were shown to change across the study areas as predicted. This study is one of the most comprehensive studies on savanna spiders (and the effects of long-term burning regimes on them) in terms of spatial and temporal extent and sampling intensity but more studies are required to further investigate the questions asked in light of the enormous turn-over in species that is encountered when sampling spiders.

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Preface

The format of this thesis does not follow the traditional layout and has instead been amalgamated into one single chapter. During the course of the study it became apparent that presenting the work in two separate chapters would result in much redundancy and that the two initial research aims were inextricably linked with each other as many aspects of ecology are. It thus made sense to present both aspects of the study in one chapter to allow for ease of reading and understanding of the complex processes investigated in this study and the way that they work together in unison.

Introduction

Fire is a widespread and common disturbance in many biomes throughout the world, and plays a major role in savanna systems (Tainton & Mentis 1984; Keely 1986; Walker 1987; Johnson 1992; Scholes & Walker 1993; van Langevelde *et al.* 2003) where it is also used extensively as a management tool for livestock farming, and often to achieve conservation goals in protected areas (Trollope 1982; Mentis & Bailey 1990; van Wilgen *et al.* 1998; Biggs & Potgieter 1999; Brockett *et al.* 2001). The role of fire has been described by Bond & Keeley (2005) as a large-scale, generalist herbivore that plays a critical role in shaping the structure and assemblage composition of vegetation in fire-prone ecosystems. This change in habitat structure and complexity in turn plays an important role in the structuring of faunal assemblages (Andersen 1991; Tews *et al.* 2004; Warui *et al.* 2005; Jiménez-Valverde & Lobo 2007). In general, more structurally complex habitats have a higher abundance and diversity of fauna and the removal of vegetation by fire leads to lower structural complexity and a resultant decrease in faunal abundance and diversity (Tews *et al.* 2004; Spencer & Baxter 2006; Jiménez-Valverde & Lobo 2007).

Globally, the frequency and intensity of fires is expected to increase in many areas due to large scale changes in climatic conditions attributed to anthropogenically driven climate change events (e.g. Pinõl *et al.* 1998; Dale *et al.* 2001; Cary 2002; Mouillot *et al.* 2002) with obvious implications for ecosystems prone to fires. Some examples of proposed mechanisms for this include increased biomass production due to increased CO₂ levels, which would lead to higher intensity fires in dry spells (Dale *et al.* 2001), increased aridity, which could result in an increase in fire frequency (Pinõl *et al.* 1998), and an increase in the stress on post-fire communities due to a lack of water and higher temperatures, making them more prone to fires, thus causing a knock-on effect of increasing fire frequency (Mouillot *et al.* 2002).

Andersen *et al.* (1998) note that since fire driven biomes (such as savannas) are extensively used for the production of livestock, the focus of fire research globally has largely been on the effects that fire has on grass composition, biomass and productivity or the underlying ecosystem processes instead of the system as a whole. Elsewhere, many studies have focussed on the effects of fire on vegetation structure and composition purely from a botanical and conservation point of view (e.g. Enslin *et al.* 2000; Shackleton & Scholes 2000; Kennedy & Potgieter 2003; Higgins *et al.* 2007; Smit *et al.* 2010). In recent years however, studies on the

effects of fire on vertebrates have become more common but there is still a distinct paucity of studies on its effects on invertebrates (Parr & Chown 2003) and the results are extremely varied (see review by Swengel 2001; Davies *et al.* 2010). This is problematic as fire-driven biomes possess an enormous number and diversity of invertebrates, all of which have pivotal roles to play in ecosystem functioning (e.g. Scholtz & Chown 1993; McGeoch 2002). Many, if not all, existing studies (up until the date of a review by Parr & Chown 2003) have numerous limitations and complications, such as inadequate replication, focussing on single fires or short burning periods (i.e. not a true long-term burning regime), not reporting sample sizes and poor experimental design, to name but a few. These authors highlight that the lack of knowledge on the effects of fire on biodiversity as a whole is problematic because many decisions in protected areas with regard to fire management are made without a proper understanding of the impacts that these decisions could have, possibly to the detriment of the conservation of biodiversity in these areas.

Furthermore, many studies are short-term (often merely the immediate effects of single fires as noted in Swengel 2001) and small scale, which often bears little resemblance to the long-term, large scale fire policies that are in place in some protected areas where they are often employed as management tools (Andersen *et al.* 1998; Parr & Chown 2003 and references therein; Parr *et al.* 2004 and references therein). Examining the effects of long-term burning regimes (outlined by Gill (1975) as being a combination of the intensity of the fire, its frequency and the season in which it occurs) may be very different from studies on a single fire event or a series of burning events spanning only a few years (Andersen *et al.* 1998; Parr & Chown 2003 and references therein). Studies on the effects of single fires or short burning histories may yield results that are not purely indicative of the effects of fire, and may be due to other ecological factors that happen to coincide with the short duration of the burning period (Andersen *et al.* 1998; Parr & Chown 2003 and references therein). It cannot be assumed that the effects of an isolated fire are indicative of the long-term effects of a series of fires of that type (Andersen *et al.* 1998). Therefore, studies should focus on long-term burning regimes in order to detect a true ecological response (Andersen *et al.* 1998; Parr & Chown 2003 and references therein).

The problems mentioned above are concerning as often one of the main aims of conservation agencies is to retain as much of a region's biodiversity as possible (Scholtz & Chown 1993; Driver *et al.* 2005), including functional diversity, an aspect of biodiversity that is

becoming more predominant in recent studies as it relates species diversity with the functions that they provide in ecosystems (Díaz & Cabido 2001). Conserving biodiversity is critical as it has been shown to relate to the stability of ecosystems with higher biodiversity relating to higher ecosystem stability (e.g. see Tilman 1996). It is therefore clear from the above that further studies on the effects of long-term burning regimes on ecosystems and biodiversity as a whole (but especially from an invertebrate perspective) are necessary in order to effectively conserve and manage this biodiversity.

In light of this, it is promising to see that there has been an increased interest in investigating the effects that fire has on invertebrate assemblages, especially in Australian savannas, as part of the Kapalga long-term fire experiment (e.g. Andersen 1991; Andersen & Müller 2000; Orgeas & Andersen 2001; Andersen *et al.* 2005) and in South African savannas, making use of the long-term experimental burn plot (EBP) trial in Kruger National Park (KNP) (Parr *et al.* 2004; Davies *et al.* 2012).

The fire experiment in KNP was initiated in 1954 in response to the general lack of information on the role of fire in preserving fauna and flora (Biggs *et al.* 2003). This experiment was initially established to test the effects of burning regimes (season and frequency combinations) on vegetation (Brynard 1964) and therefore, to date this study has mainly focussed on the response of vegetation to long-term burning regimes with minimal work conducted on animals (Biggs *et al.* 2003). Furthermore, the experiment is situated along a rainfall gradient and it has been shown that vegetation (habitat) structure and the effects of fire on this structure are influenced by rainfall in savanna systems (Parr *et al.* 2004) due to differences in fire intensities, which are higher in wetter areas (because of a larger build-up of dead biomass) and lower in drier areas (because of a lower build-up of dead biomass) (Govender *et al.* (2006). Higher intensity fires in higher rainfall areas correspond with greater changes in vegetation structure (and consequently, greater effects on faunal assemblages, see above) and these effects tend to decrease as areas become drier, with a high degree of resistance and resilience (Pimm 1984) to the effects of fire shown in ant (Parr *et al.* 2004) and termite (Davies *et al.* 2012) assemblages in drier areas.

Given the varied effects that fire appears to have on fauna and the severe lack of studies on the effects of long-term burning regimes on this fauna (rather than single-fire events), the aim of this study was therefore to complement existing invertebrate datasets by examining the effects

of long-term burning regimes on spider assemblages along a rainfall gradient making use of the EBPs in KNP.

Spiders were used because they are important predators in ecosystems and are a very diverse group, known to be sensitive to changes in habitat structure (e.g. Pearce *et al.* 2004; Tews *et al.* 2004; Jiménez-Valverde & Lobo 2007; Foord *et al.* 2008; Hore & Uniyal 2008; Pinto-Leite *et al.* 2008). Furthermore, they are highly mobile and play critical roles in ecosystem functioning (Wise 1995) and predators are hypothesised to be strongly affected by ecological change (Cardoso *et al.* 2011). These characteristics make spiders ideal for such a study because their responses are potentially indicative of many changes that may occur due to the direct effects of fire on habitat structure or the indirect effects of burning on prey species. Although spiders are often difficult to deal with from a taxonomic point of view, the South African National Survey of Arachnida (Dippenaar-Schoeman & Haddad 2006) has made great advances in the taxonomy of South African spiders through the extensive arachnid atlas that is currently being compiled for the region. This atlas project and the knowledge gleaned from it made the use of spiders ideal to address the aims of the current study.

Specifically, the study aimed to examine how spider assemblages differ across different savanna types along a rainfall gradient and furthermore to examine (i) how different burning regimes affect spider taxonomic diversity and composition, (ii) the influence of fire regimes on spider functional traits, and (iii) how the response of spider communities to fire varies across the different savanna types along the rainfall gradient. Furthermore, the results will be explored in the context of changes in vegetation structure.

It was hypothesised that spider diversity and abundance would be lower where fire regimes consist of high intensity and frequent fires, and that this would link to less complex habitat structure. In terms of functional traits, it was expected that frequently burnt areas, subjected to high intensity fires, would be dominated by spiders better able to survive the more open habitat that results from these burning regimes (for example, free-living species able to deal with hotter, drier habitats). Conversely, in areas subjected to less frequent, less intense fires (or no fires at all), the spiders making up the assemblages would be better suited to inhabit the more dense and complex habitat that results from these burning regimes (for example, a greater proportion of species that build webs between trees and shrubs).

Responses by spider assemblages to the burning regimes investigated were expected to be greatest at the study area subjected to the highest rainfall where greater change exists in vegetation structure among burning regimes and vice versa for the lowest rainfall study area (discussed below).

Methods

Study Area

Three different study areas representing three savanna habitats along a rainfall gradient were sampled in Kruger National Park (KNP), South Africa, where a long-term burning experiment has been in place since 1954 (Biggs *et al.* 2003). The savanna habitats were situated in the Pretoriuskop area in the south of the reserve (mean annual precipitation, MAP, of 750 mm), the Satara area towards the centre of the reserve (MAP 550 mm) and the Mopani area towards the north of the reserve (MAP 450 mm).

The vegetation in the Pretoriuskop area is classified as sour lowveld bushveld (Low & Rebelo 1996) on sandy and granite- or gneiss-derived soils (Gertenbach 1983). This is an open tree savanna dominated by *Terminalia sericea* and *Dichrostachys cinerea* subsp. *nyassana* (Gertenbach 1983). The altitude varies between 550 m and 650 m above sea level (a.s.l.) (Gertenbach 1983). The Satara area is in sweet lowveld bushveld, which is a mixed *Acacia nigrescens* and *Sclerocarya birrea* savanna (Low & Rebelo 1996) on basalt-derived clay soils (Gertenbach 1983). This area varies in altitude between 240 m and 320 m a.s.l. (Gertenbach 1983). Lastly, the Mopani area is a Mopani shrubveld dominated by *Colophospermum mopane* with few other woody species (Low & Rebelo 1996) and on basalt-derived clay soils (Gertenbach 1983). The altitude varies between 300 m and 340 m a.s.l. (Gertenbach 1983).

Sampling was undertaken on experimental burn plots (EBPs), approximately 380 x 180 m (ca. 7 ha) in size and representing different burning regimes (i.e. season and frequency combinations). The experimental burn plots are separated by firebreak roads (approximately 6 m wide). The fire regimes have remained virtually constant since the long-term burning experiment's inception in 1954 (Biggs *et al.* 2003). Four different fire regimes were sampled: (i) August annual (August 1), (ii) August triennial (August 3), (iii) December triennial (December 3) and (iv) an unburnt plot that has remained virtually unburnt since 1954. August fires tend to be relatively "hot" and intense due to a large fuel load following winter, whereas the December fires tend to be "cool" and less intense than the winter fires because the vegetation is greener and there is a relatively low fuel load compared to winter (Govender *et al.* 2006). There were three replicates of the fire regimes, spaced 10 to 20 km apart, in each of the three study areas (Biggs *et al.* 2003). The study consisted of a total of 36 sampling sites (three study areas x three replicates

per savanna type x four burning regimes per replicate). Coordinates for the study areas and experimental burning plots are summarised in Table 1.

Table 1. Summary of the study areas (with mean annual precipitation, MAP), replicates, fire regimes and their corresponding GPS coordinates used in this study.

Area (MAP)	Replicate	Fire regime	Coordinates
Pretoriuskop (750 mm)	Kambeni	August annual	25.154°S 31.271°E
		August triennial	25.153°S 31.264°E
		December triennial	25.153°S 31.261°E
		Unburnt	25.153°S 31.253°E
	Shabeni	August annual	25.123°S 31.237°E
		August triennial	25.107°S 31.232°E
		December triennial	25.112°S 31.234°E
		Unburnt	25.134°S 31.233°E
	Numbi	August annual	25.140°S 31.208°E
		August triennial	25.135°S 31.207°E
		December triennial	25.123°S 31.208°E
		Unburnt	25.143°S 31.206°E
Satara (550 mm)	Satara	August annual	24.402°S 31.745°E
		August triennial	24.399°S 31.736°E
		December triennial	24.401°S 31.741°E
		Unburnt	24.405°S 31.766°E
	N'wanetsi	August annual	24.445°S 31.889°E
		August triennial	24.449°S 31.851°E
		December triennial	24.449°S 31.854°E
		Unburnt	24.448°S 31.865°E
	Marheya	August annual	24.544°S 31.777°E
		August triennial	24.520°S 31.773°E
		December triennial	24.526°S 31.774°E
		Unburnt	24.530°S 31.774°E
Mopani	Dzombo	August annual	23.437°S 31.377°E

(450 mm)	August triennial	23.452°S 31.384°E
	December triennial	23.445°S 31.381°E
	Unburnt	23.425°S 31.372°E
Mooiplaas	August annual	23.562°S 31.457°E
	August triennial	23.595°S 31.461°E
	December triennial	23.593°S 31.462°E
	Unburnt	23.582°S 31.464°E
Tsendze	August annual	23.691°S 31.518°E
	August triennial	23.685°S 31.518°E
	December triennial	23.688°S 31.518°E
	Unburnt	23.705°S 31.515°E

Sampling

Spiders

Within each experimental burn plot, three different techniques were used to sample spiders, namely active searching, sweep netting and leaf litter sifting. Tree beating and pitfall trapping were conducted for autumn and spring. However, due to logistical problems and excessive rain in the summer sampling period there were large gaps in these datasets. In addition, tree beating yielded very low numbers of spiders. Consequently these results are not presented. The three different sampling techniques were used in order to sample all spider functional groups or guilds from all habitat strata present. Spiders were sampled at least 50 m from the edge of each respective plot in order to reduce edge effects and trapping of individuals from adjacent plots. Sampling took place once in the austral autumn, spring and summer, respectively, (from March 2008 to February 2009) in order to include seasonal variation in spider assemblage composition. Winter sampling was excluded because mostly immature spiders are collected in winter (A. S. Dippenaar-Schoeman, pers. comm.) and these were not the primary focus of this study.

Active searching was conducted along a belt transect near the centre of each plot. The transect consisted of ten 3 x 3 m quadrats and searching took place in 10 person-minute bouts within each of these quadrats. Searching covered all vegetation strata from ground level to the upper vegetation storey and took place before 10:00 and after 14:30 in order to avoid the heat of

the day, as spiders are not very active during this time (A. S. Dippenaar-Schoeman, pers. comm.). Spiders were caught by hand or using an aspirator.

On each plot, sweep netting consisted of 30 sweeps along three transects, each 50 m long and spaced at least 20 m apart, using a net with a diameter of 55 cm. These transects were positioned near the centre of each plot and at least 50 m away from the areas where active searching and the collection of leaf litter took place. This technique effectively sampled spiders dwelling on grass and low bushes. Spiders were removed from the net by hand or using an aspirator.

Leaf litter sifting was used to sample litter-dwelling spiders that may have been missed by the other sampling techniques. The leaf litter was collected from square metre quadrats in a 5 x 4 grid design (each quadrat spaced 10 m apart) and was sifted using a sieve with 5 x 5 mm mesh. Spiders were collected on a white sheet and caught using an aspirator.

Specimens collected at each sampling event were pooled for the relevant plot where they were collected for the purpose of analysis. Spiders were preserved in 70% ethanol and were first identified to Family level and parataxonomic units (Oliver & Beattie 1993; Krell 2004) using a stereomicroscope. The specimens were then identified to species level by A. S. Dippenaar-Schoeman (Agricultural Research Council – Plant Protection Research Institute, Pretoria, South Africa), C. R. Haddad (Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa) and W. Wesolowska (Institute of Zoology, Wrocław University, Sienkiewicza, Wrocław, Poland). A reference collection is lodged at the National Collection of Arachnida, Agricultural Research Council – Plant Protection Research Institute, Pretoria, South Africa.

Data analysis

In this study, two main datasets were used in the analyses. The original intent of the study was to focus on adult spiders and eliminate immatures because it was assumed that they would be difficult to identify. However, the large majority of spiders sampled were immatures and identification of these immatures was possible to species (or at least genus) level in most cases. It was thus decided to include these immature spiders to fully utilise the specimens sampled.

The first dataset comprised only adult spider data (i.e. the species sampled and the number of individuals of each of these species sampled at the respective EBPs at each study

area). The second dataset comprised only presence/absence data and included information on all immature spiders sampled as well as the adult spiders sampled. This latter dataset was transformed into a presence/absence dataset in order to capture the full suite of spider species sampled while avoiding any artificially inflated numbers of individuals for certain species where, for example, a whole nest of spiderlings were sampled, most of which would die because of a range of factors, such as predation, desiccation and being trampled by larger animals.

During the summer sampling period, there was heavy rain and flooding at the Pretoriuskop study area resulting in gaps in the active searching data. For this reason, the data had to be discarded for the purpose of analysis. Therefore, when conducting any analyses across the study areas (rainfall gradient), the summer active searching data were excluded from all three study areas to allow for an equal sampling effort across these areas. However, when conducting analyses among burning regimes within a given study area (where each study area was considered separately), the summer active searching data were only excluded from the Pretoriuskop dataset.

In the following analyses where means were compared, data were first tested for normality and then homoscedasticity (using a Levene's test). One-way ANOVAs and subsequent Tukey HSD post-hoc tests were used when the data were normally distributed (as was the case throughout). However, when the variances were shown not to be homogenous, a Kruskal-Wallis test and a subsequent Pairwise Wilcoxon Rank Sum post-hoc test were used.

Comparisons across the rainfall gradient

Overall abundance, species density and Family richness were first calculated for the entire study and were then compared across the study areas. Mean abundance and standard error were calculated using the adult-only dataset and were then compared across the study areas using a Kruskal-Wallis test and a subsequent Pairwise Wilcoxon Rank Sum post-hoc test to show where any differences existed. The same was done for mean species density, but in this case, the adult-only and presence/absence datasets were used. However, only the results generated using the presence/absence dataset are presented because this dataset increased the number of species that could be used in the comparisons, thus improving the quality of the data used.

The adequacy of the sampling effort was investigated using the adult-only dataset and the software programme EstimateS v7.5 (Colwell 2005). Species rarefaction curves were produced

and used to compare the observed number of species at each study area to corresponding estimated species richness values using a variety of estimators (Gotelli & Colwell 2001). The estimators used were the Incidence-based Coverage Estimator (ICE; Chazdon *et al.* 1998), Chao 2, Jack 2 and Michaelis-Menten (Colwell & Coddington 1994). Convergence of the rarefaction curves with the observed species density curve (S Obs) indicates that the number of species sampled accurately represents the species richness likely to be found in the relevant area where the sampling was conducted (Longino *et al.* 2002; Magurran 2004).

The rarefaction curves indicated that sampling under-represented species richness when compared to the estimators used. This was likely due to the high rate of species turnover (number of species per number of individuals) encountered and we therefore used estimated species richness, estimated by the mean of the incidence-based coverage estimator (ICE Mean), to compare species richness across the study areas. This estimator was used because it has been shown to be reliable and quick to stabilise and is independent of sample size (Chazdon *et al.* 1998; Longino *et al.* 2002). These results were compared with a one-way ANOVA and Tukey HSD post-hoc test.

An analysis of similarity (ANOSIM) and non-metric multi-dimensional scaling (MDS) were used to compare assemblages across the study areas using the adult-only and presence/absence datasets, but only the results of the latter are presented (for the same reasons as previously discussed) using the PRIMER software package v5 (Clarke & Warwick 2001). Adult data were first fourth root transformed in order to give equal weighting to both common and rare species and a Bray-Curtis similarity measure was used to create a similarity matrix (Clarke & Warwick 2001). ANOSIM is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordination (Clarke 1993) in which a significant Global *R* statistic of close to one indicates more distinct differences between the assemblages or sites being compared and an *R* value closer to zero indicates the opposite. An MDS plot was produced to visually depict the results of the ANOSIM.

A similarity percentage (SIMPER) analysis was conducted using the adult-only dataset and the PRIMER software programme to investigate whether there were any species that contributed to the bulk of the similarity between pairs of study areas indicated as similar in the ANOSIM. The SIMPER analysis determines the contribution of each species to the average

Bray-Curtis similarity in each group of combinations (i.e. between pairs of study areas) (Clarke & Warwick 1994).

The Indicator Value (IndVal) method (Dufrene & Legendre 1997) was used to investigate whether any indicator species existed for any of the study areas using the adult-only dataset. This method uses the criteria of specificity (uniqueness to a particular area) and fidelity (frequency of occurrence within the area) and assesses the degree (expressed as a percentage) to which a particular species fulfils these criteria. Species are considered to be representative of an area when their associated IndVal (indicator value) is high, indicating a high degree of specificity and fidelity to the area in question. Significance was tested following Dufrene & Legendre (1997), where study areas were randomly reallocated among the study area group to test the significance of the associated IndVal for each species analysed. Indicator species of a particular area are generally regarded as those species with significant IndVals that are greater than a subjective threshold of 0.70 (van Rensburg *et al.* 1999; McGeoch *et al.* 2002). In this study, a threshold of 0.70 was initially used and then this threshold was reduced to 0.60 to investigate whether any further indicator species emerged (because of the high species turnover (number of species per number of individuals) encountered).

Comparisons among burning regimes

The analyses used to compare the burning regimes within each respective study area (each area was considered separately) were similar to those used to compare ant communities across the different burning regimes in the same study areas. Mean abundance and standard error (using the adult-only dataset) and mean species density and standard error (using the adult-only and presence/absence datasets, but only presenting the results of the latter for the same reasons as discussed in the previous section) were calculated for each burning regime at each study area. One-way ANOVAs and Tukey HSD post-hoc tests were then used to compare the mean abundance and mean species density values across burning regimes at each study area.

Mean estimated species richness was calculated for each respective burning regime at each study area using the adult-only dataset and the ICE and these results were compared across burning regimes within each study area using one-way ANOVAs and Tukey HSD post-hoc tests.

An ANOSIM was conducted using the adult-only and presence/absence datasets (only the results of the latter are presented, according to previous reasoning) to compare spider

assemblages across burning regimes at each respective study area. Subsequently, an MDS was produced for each respective study area to visually depict the similarities in assemblage composition across burning regimes shown in the results of the ANOSIM.

A SIMPER analysis was conducted for each study area using the adult-only dataset to investigate whether any species stood out as driving the similarity across burning regimes at each respective area.

Potential indicator species for burning regimes at each separate study area were investigated using the IndVal method and the adult-only dataset. The possibility of indicator species for each respective burning regime not considering the three study areas separately (i.e. pooling all data for each burning regime, respectively, across the three study areas and not taking study area into account) was also investigated using the IndVal method and the adult-only dataset.

Spider assemblages were also compared across burning regimes for each respective study area in terms of functional traits. This analysis was not conducted across the rainfall gradient in its entirety because the aim was to examine whether the burning regimes influenced the distribution of spiders across the functional traits and whether the responses (if any) differed among the study areas along the rainfall gradient.

Six different functional traits were chosen: i) vertical position/habitat (i.e. at what level of the vertical structure a spider prefers to live), ii) hunting strategy, iii) lifestyle (i.e. how sedentary or free-living a spider is), iv) sclerotisation of the carapace, v) abdominal scutes/sclerotisation, and vi) diet specialisation (specifically ants). The rationale that lead to the selection of these functional traits is as follows.

The level of the vertical structure at which a spider prefers to live was chosen because it relates to the habitat structure of the sampled area. Previous studies have shown that fire influences habitat structure (e.g. Jacobs & Biggs 2001; Bond *et al.* 2005; Spencer & Baxter 2006; Higgins *et al.* 2007; Smit *et al.* 2010) and that in turn this influences the composition of the assemblages of the resident fauna, especially spiders (e.g. Andersen 1991; Tews *et al.* 2004; Warui *et al.* 2005; Jiménez-Valverde & Lobo 2007; Foord *et al.* 2008; Pinto-Leite *et al.* 2008, Blaum *et al.* 2009). Furthermore, studies conducted on vegetation and habitat structure on the EBPs in KNP have shown marked differences in this structure across burning regimes (discussed below). Following this logic, areas with different habitat structure (e.g. open grassy areas with

small shrubs versus heavily wooded areas) could be expected to have different patterns in the distribution of spiders that use different vertical levels of the habitat. This component of the functional traits analysis addressed this and investigated whether different patterns existed across burning regimes.

Hunting strategy was chosen following a similar rationale to that for vertical structure/habitat. Differences in habitat structure would potentially influence the assemblage composition of prey species, which could in turn influence which spiders would occur in respective areas determined by whether their hunting strategy allows for the capture of the prey species present. These differences in habitat structure may also influence the niches that are available for spiders using various hunting strategies. For example, open, grassy areas would be unlikely to provide suitable habitat for spiders that rely solely on orb-webs placed between trees to catch flying prey, whereas more wooded areas would.

The lifestyle functional trait describes the general way of life of a spider species that govern factors such as where it may be found (e.g. web-bound vs. burrow-bound) and how sedentary it may tend to be (e.g. free-living vs. web-bound). This trait is related to hunting strategy in many ways (e.g. web-bound spiders (lifestyle) utilise webs to catch their prey (hunting strategy)) but it also links to how well a spider may be able to survive the effects of fire. An example of the latter is as follows: a burrow-bound spider is probably more likely to survive a fire because it is able to retreat relatively far underground whereas a grass-dwelling orb-weaver may be more likely to perish in a fast-spreading fire. The lifestyle of a spider could also influence the spider's ability to recolonise an area after a fire event and one would expect that more mobile, free-living species would be better at recolonising areas than highly sedentary species.

In a study by Langlands *et al.* (2011), it was hypothesised that more heavily sclerotised spiders would be most abundant in open areas subjected to frequent fires than in densely wooded areas. They proposed that this would be because sclerotised spiders can avoid desiccation in frequently burnt areas that are more exposed and experience higher temperatures. In this vein, sclerotisation of the carapace and abdomen was investigated in the spiders sampled in this study to investigate whether similar results were found compared to the aforementioned study.

Furthermore, diet specialisation (specifically spiders that specialise on preying on ants) was investigated to determine whether there was a relationship with the patterns found in ant

assemblages in response to burning regime in a previous study done on ants by Parr *et al.* (2004) on the KNP EBPs.

Within each of the abovementioned groups of functional traits, different categories were used to group spider species for analysis. As far as information on life history permitted, information on functional traits was collected at the species level. When species-level information was not available, information was collected at genus level, Sub-family level or Family level. Based on the findings by Cardoso *et al.* (2011), this was considered sufficient for the analyses performed in this study. These authors investigated whether information on functional traits of spiders at the Family level was a suitable surrogate when species-level information was lacking. When comparing assemblages using Family-level functional trait information versus species-level information, they found that only 11% of spiders were incorrectly allocated to a guild or functional group when using the former information. To conclude, they suggested that Family-level information could indeed be used as a suitable surrogate when other information is lacking.

Information used to group the spiders in this study was obtained from Dippenaar-Schoeman & Jocqué (1997), Dippenaar-Schoeman & van den Berg (2010) and A. S. Dippenaar-Schoeman (pers. comm.). The categories that spiders were divided into for the vertical position/habitat, hunting strategy and lifestyle functional traits is summarised in Table 2.

Table 2. The categories that spiders were divided into for the vertical position/habitat, hunting strategy and lifestyle functional traits.

Functional trait	Category
Vertical position/habitat	<ul style="list-style-type: none"> i) Ground dwellers ii) Spiders found on both the ground and in the grass/shrub layer iii) Spiders only found in the grass/shrub layer iv) Spiders found in grass/shrubs and in trees v) Spiders dwelling predominantly on the ground but also under the bark of trees close to the ground vi) Tree specialists vii) Spiders utilising any or all sections of the vertical habitat structure

Hunting strategy	<ul style="list-style-type: none"> i) Spiders that solely use webs to capture prey ii) Spiders that utilise a combination of webs and an ambush strategy iii) Spiders that utilise webs and are also semi-active hunters iv) Spiders that use webs, ambush strategies and sometimes hunt actively v) Active hunters vi) Spiders that use a combination of ambushing prey or hunting it actively vii) Spiders that purely ambush prey viii) Spiders that utilise a sit-and-wait strategy
Lifestyle	<ul style="list-style-type: none"> i) Web-bound ii) Semi web-bound iii) Semi web-bound or free-living iv) Burrow-bound v) Semi-burrow-bound vi) Free-living

Sclerotisation of the carapace was separated into four categories, namely i) yes, ii) no, iii) partially, and iv) sometimes. The abdominal scutes/sclerotisation functional trait was analysed using five categories, namely i) yes, ii) no, iii) partially (i.e. always partly sclerotised), iv) sometimes (i.e. sclerotisation exists sometimes, e.g. in males or in some species within a genus where species-level information was lacking), and v) sometimes/partially (i.e. partial sclerotisation sometimes occurs (following the reasoning for the previous trait)).

When investigating patterns in spiders that specialise on ants as prey, three categories were used: i) yes, ii) sometimes/mostly, and iii) no.

For each of the categories in each of the functional trait groupings, mean abundance and standard error was calculated for each burning regime at each study area using the adult-only dataset and mean species density and standard error was calculated using the adult-only and presence/absence datasets (only the results of the latter are presented, according to previous reasoning). These results were compared for each functional trait separately, and mean

abundance and mean species density was compared across burning regimes for each category within each functional trait at each study area using one-way ANOVAs and Tukey post-hoc tests.

Results

Comparison across the rainfall gradient

Species density and abundance

In total, 1025 adult spiders from 334 species and 40 families were collected (see Appendix 1 for the species list). When excluding summer active searching data (as explained in the Methods section), the 919 individual adult spiders were dispersed along the rainfall gradient in descending order from the wetter Pretoriuskop study area (415), to the intermediate Satara study area (349) to the drier Mopani study area (155). Overall species density followed the same pattern with 97 species from Pretoriuskop, 71 from Satara and 54 from Mopani. When considering the presence/absence dataset, which included both adult and immature spiders (also with summer active searching data excluded), the 310 species represented in this dataset followed a similar trend as above with 233 collected at the Pretoriuskop study area, 154 at Satara and 146 at Mopani.

Mean abundance (adult-only dataset) and mean species density (presence/absence dataset) mirrored these results (Fig. 1) and significant differences in mean abundance were found between Pretoriuskop and Mopani and between Satara and Mopani respectively using a Kruskal-Wallis test ($H_{2,33} = 21.925, p < 0.001$) and a subsequent Pairwise Wilcoxon Rank Sum post-hoc test. When considering the presence/absence dataset, mean species density followed a slightly different pattern and an ANOVA and subsequent Tukey HSD post-hoc test indicated significant differences in mean species density between Pretoriuskop and Satara and between Pretoriuskop and Mopani respectively ($F_{2,33} = 25.520, p < 0.001$).

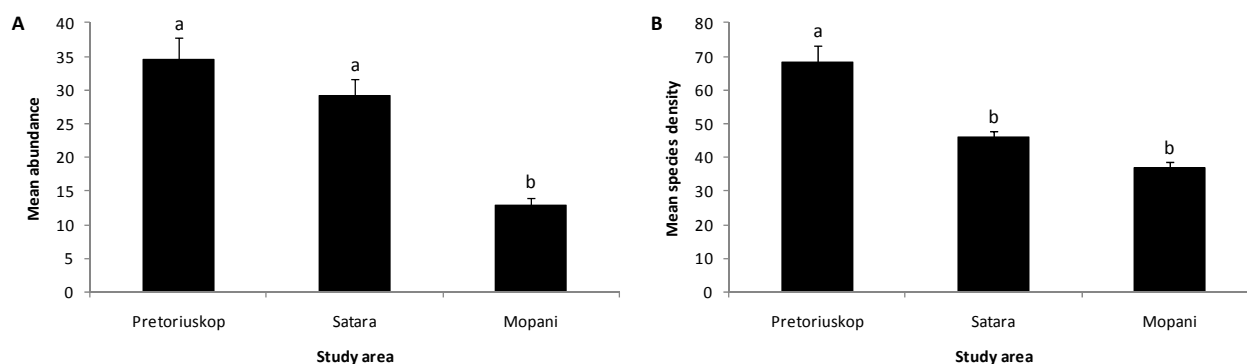


Figure 1. Mean abundance of adult spiders (A) and mean species density based on the presence/absence dataset (including both adult and immature spiders) (B) for the three study areas, Pretoriuskop, Satara and Mopani (positioned along a rainfall gradient with the wettest area at Pretoriuskop and the driest area at Mopani). Error bars indicate standard error. Lowercase letters refer to where significant differences occur in either mean abundance or mean species density. These results were obtained using a Kruskal-Wallis test and a subsequent Pairwise Wilcoxon Rank Sum post-hoc test for (A) and a one-way ANOVA and subsequent Tukey HSD post-hoc test for (B).

Estimated species richness

An investigation of sampling adequacy, using EstimateS and the adult-only dataset, indicated that sampling under-represented species richness when compared to the estimators used (Fig. 2). Observed species richness (S Obs) at each study area was lower than all of the corresponding estimated richness values (Fig. 2) and in the case of Pretoriuskop, species richness was underestimated by approximately 50 species compared to the lowest richness estimate (MM Mean). This was likely due to the high rate of species turnover encountered in this study and the data were therefore analysed using estimated species richness, estimated by the mean of the incidence-based coverage estimator (ICE Mean) to compare species richness across the study areas (Fig. 3). The trend in estimated species richness corresponded closely to that found in the observed species density, but with elevated numbers of species. Significant differences existed between estimated species richness at Pretoriuskop and Satara and at Pretoriuskop and Mopani respectively ($F_{2,33} = 19.970, p < 0.001$).

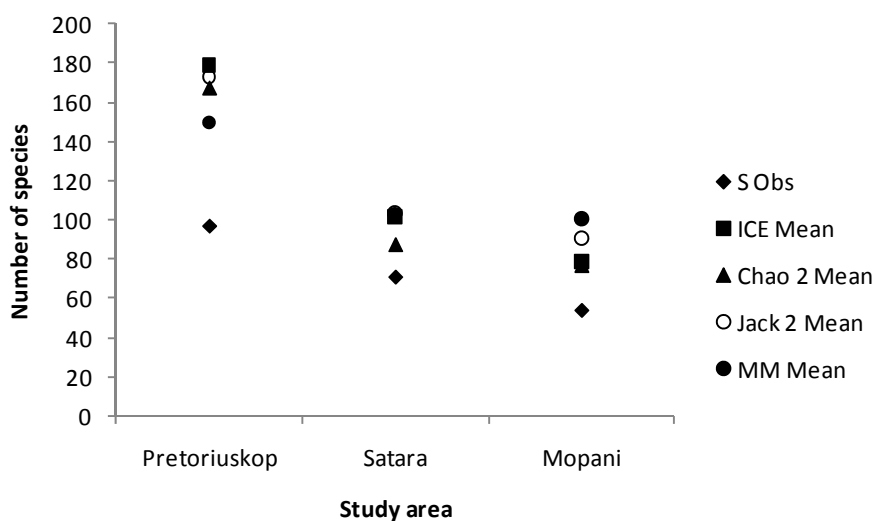


Figure 2. Estimated species richness values at each study area for the observed number of species (S Obs), incidence-based coverage estimator mean (ICE Mean), Chao 2 Mean, Jack 2 Mean and Michaelis-Menten Mean (MM Mean), based on the adult-only dataset.

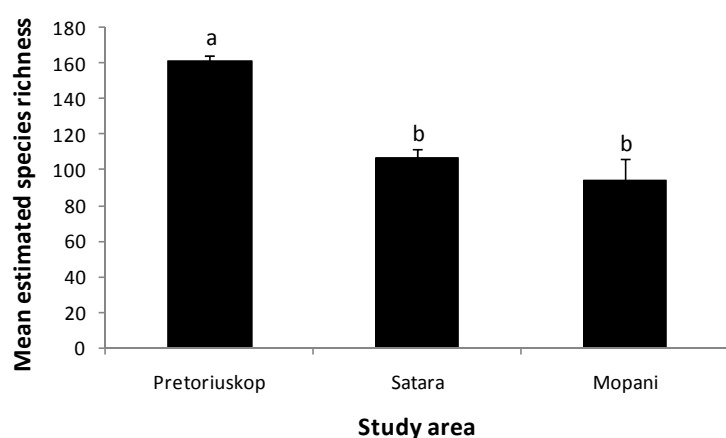


Figure 3. Mean estimated species richness of adult spiders across the three study areas (estimated using the incidence-based coverage estimator (ICE Mean) in the software program EstimateS). Error bars indicate standard error. Lowercase letters refer to where significant differences occur in mean estimated species density. These results were obtained using a one-way ANOVA and subsequent Tukey HSD post-hoc test.

Assemblages

An analysis of similarity (ANOSIM) conducted on the presence/absence dataset showed large differences across study areas (Global $R = 0.576$, $p = 0.001$). The largest separation between spider assemblages was found between Pretoriuskop and Satara ($R = 0.829$, $p = 0.001$), followed by Pretoriuskop vs. Mopani ($R = 0.656$, $p = 0.001$). Assemblages at Satara and Mopani showed moderate levels of separation ($R = 0.379$, $p = 0.001$). The MDS plot (Fig. 4) illustrates the degrees of similarity across the study areas and it is evident that Pretoriuskop is clearly separated from Satara and Mopani.

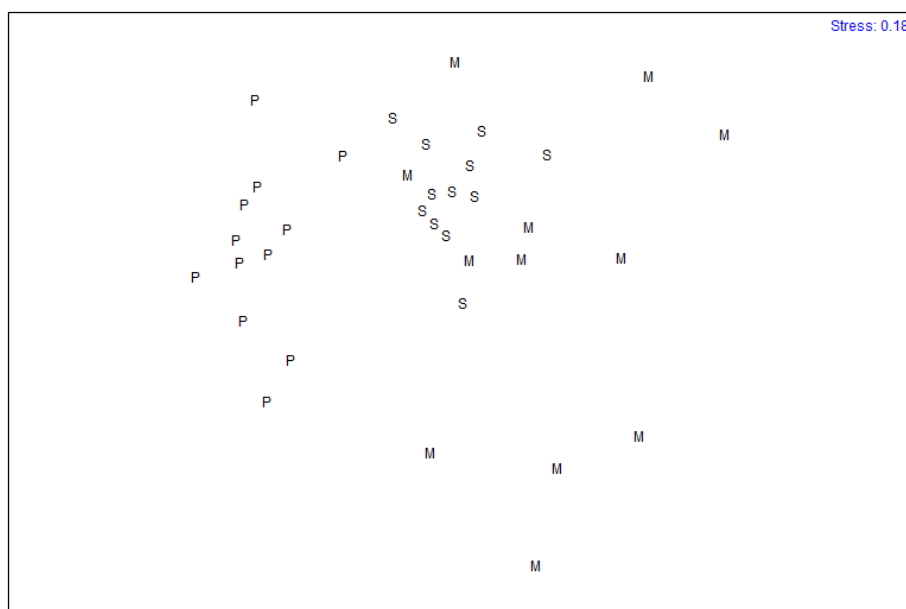


Figure 4. Multi-dimensional scaling plot comparing spider assemblages (with immature spiders included) across the three study areas. Label abbreviations are as follows: P = Pretoriuskop, S = Satara and M = Mopani.

A SIMPER analysis was used to investigate which species were the main drivers of the dissimilarity between pairs of study areas (e.g. Pretoriuskop vs. Satara) using both the adult-only dataset and the presence/absence dataset. However, no species were found to contribute to the bulk of the similarity, which is most likely due to the high degree of species turnover found in this study.

Indicator species

The IndVal analysis conducted on the adult-only dataset showed that one species, *Festucula festuculaeformis* (Salticidae), showed high levels of specificity and fidelity to the Pretoriuskop study area (IndVal = 0.833, $p = 0.001$) when using an IndVal threshold of 0.70 (refer to van Rensburg *et al.* 1999). No additional indicator species emerged when this threshold was reduced to 0.60.

Effects of burning regime

Species density and abundance

Within each of the study areas examined, there was no significant difference in mean adult spider abundance (Pretoriuskop: $F_{3,8} = 2.100$, $p = 0.179$; Satara: $F_{3,8} = 0.089$, $p = 0.964$; Mopani: $F_{3,8} = 2.534$, $p = 0.130$) across the burning regimes (Fig. 5). However, based on the presence/absence dataset, significant differences were found in mean species density between plots burnt annually in August and the unburnt control plots only at the wettest study area, Pretoriuskop (Pretoriuskop: $F_{3,8} = 4.579$, $p = 0.038$; Satara: $F_{3,8} = 0.496$, $p = 0.695$; Mopani: $F_{3,8} = 0.438$, $p = 0.732$) (Fig. 5).

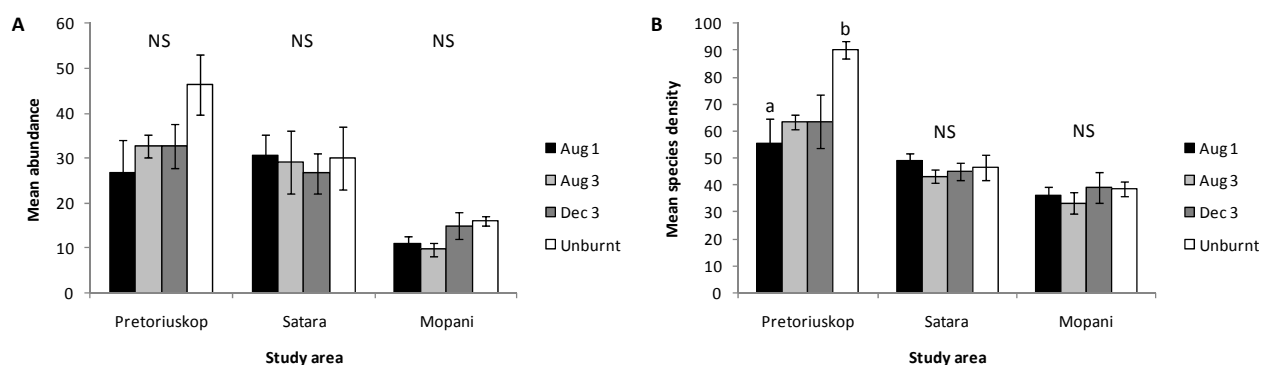


Figure 5. Mean abundance of adult spiders (A) and mean species density based on the presence/absence dataset (including both adult and immature spiders) (B) across burning regimes for the three study areas, Pretoriuskop, Satara and Mopani. Error bars indicate standard error. NS denotes no significant differences across burning regimes and lowercase letters refer to where significant differences occur. These results were obtained using a one-way ANOVA and subsequent Tukey HSD post-hoc test. Burning regime abbreviations are as

follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

Estimated species richness

Once again, ICE Mean values generated in EstimateS were used to compare estimated species richness values across burning regimes at the respective study sites because sampling appeared to have been underestimated (Fig. 6). These estimated values, apart from being greater than the species density values, showed no significant differences across burning regimes at each of the study areas (Pretoriuskop: $F_{3,8} = 2.997$, $p = 0.095$; Satara: $F_{3,8} = 2.160$, $p = 0.171$; Mopani: $F_{3,8} = 0.233$, $p = 0.871$). However, different patterns in species richness emerged at the respective study areas when compared to species density although none of these were statistically significant.

At Pretoriuskop, mean species density was shown to be significantly different between August 1 plots and the unburnt plots (Fig. 5b), but this pattern was not as evident in the estimated species richness values (Fig. 6) where mean estimated species richness at the August 1 plots was not significantly different to that at the unburnt plots. Mean estimated species richness was almost equal between the August 1 and December 3 plots and these richness estimates were less than those of the August 3 and unburnt plots, respectively.

Patterns in mean estimated species richness at Satara (Fig. 6) were similar to mean species density (Fig. 5b) except that the estimated richness across the burnt plots were each much less than the unburnt plots.

The patterns in mean estimated species richness at Mopani (Fig. 6) were quite different to those in mean species density (Fig. 5b), but there was much more variation in the former for each burning regime respectively. Species density values were similar across burning regimes, whereas estimated richness values were highest at the August 1 plots and decreased across the burning regimes with values at the unburnt plots the lowest.

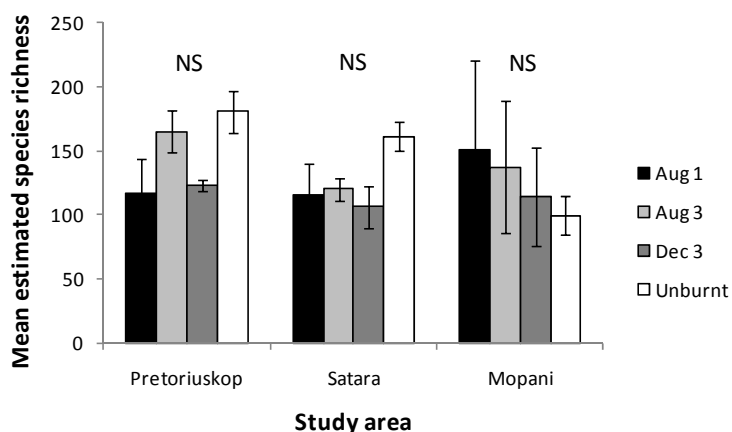


Figure 6. Mean estimated species richness of adult spiders across burning regimes for the three study areas, Pretoriuskop, Satara and Mopani. Error bars indicate standard error. NS denotes no significant differences across burning regimes. These results were obtained using a one-way ANOVA and subsequent Tukey HSD post-hoc test. Burning regime abbreviations are as follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

Assemblages

Regarding the ANOSIM results that follow, many of the results are shown not to be significant, most likely due to the small sample size in this study. However, these results are still presented because as discussed in Clarke & Gorley (2001), the R -values in studies where sample size is small are of greater importance than the significance of the result and more emphasis should therefore be placed on the R -value in such cases.

When the presence/absence dataset was used to perform an ANOSIM for Pretoriuskop (Table 3; Fig. 7), the Global R of 0.343 ($p = 0.014$) indicated some separation between all possible combinations of burning regimes with the greatest separation (i.e. values closer to 1) between assemblages found at August 1 and December 3 ($R = 0.556$, $p = 0.100$), and August 1 and the unburnt plots ($R = 0.556$, $p = 0.100$), respectively.

Considering all possible combinations of burning regimes, both Satara (Global $R = 0.130$, $p = 0.140$; Table 3; Fig. 8) and Mopani (Global $R = 0.099$, $p = 0.261$; Table 3; Fig. 9) showed little separation between spider assemblages using presence/absence data. Similarly, and as expected based on the Global R results, the highest level of assemblage separation between any

two specific fire regimes remained low for Satara (August 1 vs. August 3; $R = 0.296$, $p = 0.200$) and moderate for Mopani (August 3 vs. December 3; $R = 0.315$, $p = 0.200$).

Table 3. Analysis of similarity results for the presence/absence dataset (including both adults and immatures) for all three study areas, Pretoriuskop, Satara and Mopani.

Comparison	R statistic	p -value
Pretoriuskop	Global $R = 0.343$	0.014
Aug 1 vs. Aug 3	0.519	0.100
Aug 1 vs. Dec 3	0.556	0.100
Aug 1 vs. Unburnt	0.556	0.100
Aug 3 vs. Dec 3	0.111	0.500
Aug 3 vs. Unburnt	0.296	0.200
Dec 3 vs. Unburnt	0.296	0.100
Satara	Global $R = 0.130$	0.140
Aug 1 vs. Aug 3	0.296	0.200
Aug 1 vs. Dec 3	0.222	0.300
Aug 1 vs. Unburnt	0.222	0.300
Aug 3 vs. Dec 3	0.000	0.600
Aug 3 vs. Unburnt	0.148	0.400
Dec 3 vs. Unburnt	-0.037	0.800
Mopani	Global $R = 0.099$	0.261
Aug 1 vs. Aug 3	-0.111	0.700
Aug 1 vs. Dec 3	0.111	0.300
Aug 1 vs. Unburnt	0.074	0.500
Aug 3 vs. Dec 3	0.315	0.200
Aug 3 vs. Unburnt	0.259	0.100
Dec 3 vs. Unburnt	0.185	0.400

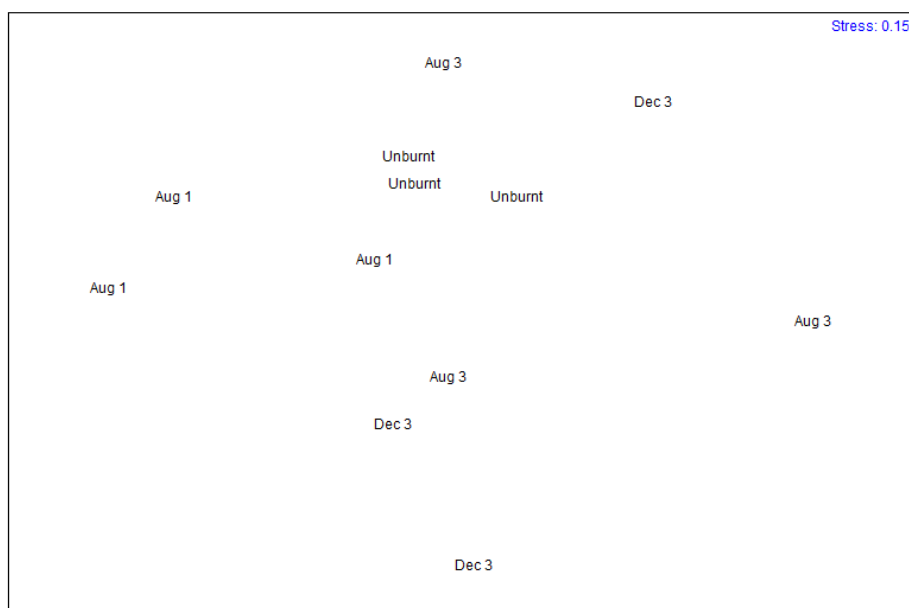


Figure 7. Multi-dimensional scaling plot comparing spider assemblages (with immature spiders included) across burning regimes at Pretoriuskop. Label abbreviations are as follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

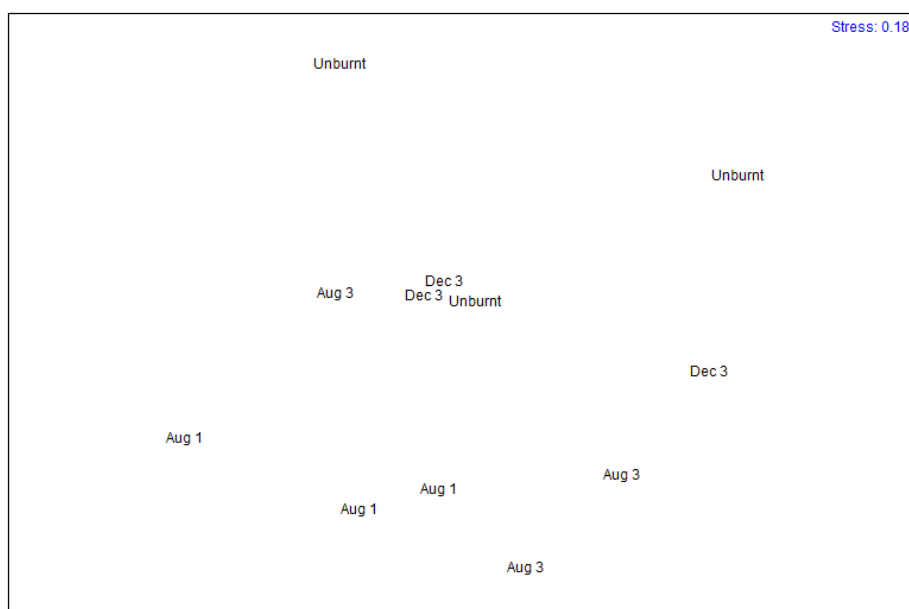


Figure 8. Multi-dimensional scaling plot comparing spider assemblages (with immature spiders included) across burning regimes at Satara. Label abbreviations are as follows: Aug 1

= annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

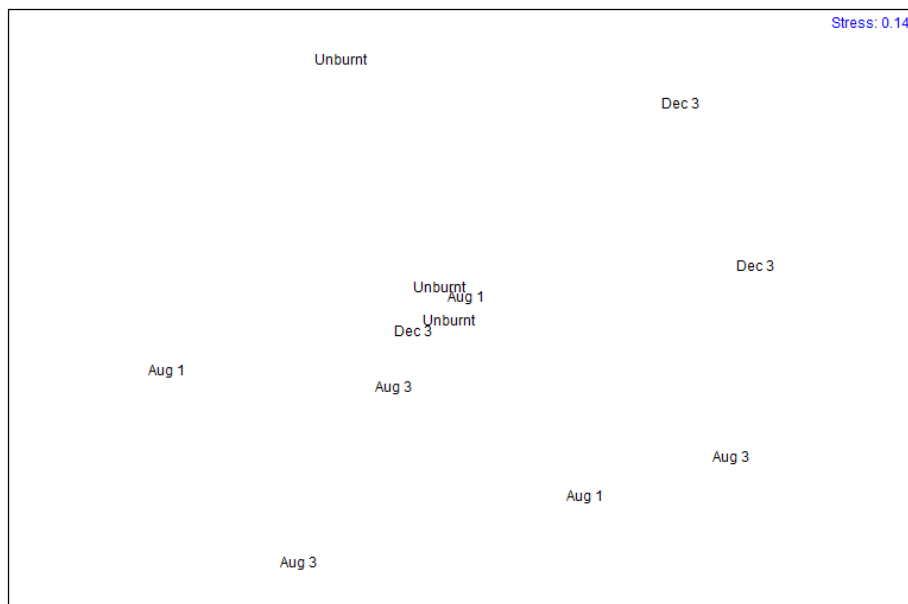


Figure 9. Multi-dimensional scaling plot comparing spider assemblages (with immature spiders included) across burning regimes at Mopani. Label abbreviations are as follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

A SIMPER analysis was used to investigate whether there were any species that were the main drivers of dissimilarity between burning regimes at each study area using both the adult-only dataset and the dataset including immature spiders (presence/absence dataset), but no species were found to do so. This is most likely again due to the high degree of species turnover (number of species per number of individuals), which we found.

Indicator species

An IndVal analysis conducted using the adult-only dataset showed slightly different results though (Table 4), although many of these results were not significant, most likely due to the small sample size of three, an inherent limitation of the experimental design. However, despite this, the IndVal results are still reported in order to show possible patterns that may exist. At

Pretoriuskop, using an IndVal threshold of 0.70, *Thomisus blandus* showed high levels of specificity and fidelity to the December 3 plots. Furthermore, three species were shown to be indicators at the unburnt plots, namely *Diaea puncta*, *Asemonea stella* and *Heliophanus orchestra*. When the IndVal threshold was reduced to 0.60, two new species emerged as indicators, namely *Monaeses quadrituberculatus* at the August 1 plots and *Tibellus minor* at the August 3 plots.

At Satara, a very different pattern was found (Table 4). Using a threshold of 0.70, *Oxyopes bothai* and *Neoscona moreli* were shown to be indicators at the August 1 plots. When the IndVal threshold was reduced to 0.60, two new species emerged as indicators at the August 1 plots, namely *Cheiracanthium furculatum* and *Oxyopes pallidecoloratus*. At this lower threshold, *Heliophanus insperatus* was found to be an indicator at the August 3 plots and *Cyrtophora citricola*, *Phoroncidia* sp. 1 and *Oxyopes angulitarsus* were found to be indicators at the December 3 plots. No species emerged as indicators at the unburnt plots.

Using a threshold of 0.70 for Mopani, Salticidae sp. 1 and *Hispo georgius* were shown to be indicators at the December 3 and unburnt plots, respectively (Table 4). At the lower threshold of 0.60, a new species, *Thyene thyenoides* emerged as an indicator at the December 3 plots and *Argyrodes zonatus* at the unburnt plots. *Stenaelurillus* sp. 2 emerged as an indicator at the August 1 plots using the lower threshold and *Hyllus argyrotoxus* and *Misc. Augacephalus* sp. were shown as indicators at the August 3 plots.

Table 4. Indicator species for the respective burning regimes across the three study areas. IndVals above the threshold of 0.70 are indicated in bold. Burning regime abbreviations are as follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

Study area and treatment	Species and family	IndVal	<i>p</i> -value
Pretoriuskop – Dec 3	<i>Thomisus blandus</i> (Thomisidae)	0.80	0.057
Pretoriuskop – Unburnt	<i>Diaea puncta</i> (Thomisidae)	1.00	0.015
Pretoriuskop – Unburnt	<i>Asemonea stella</i> (Salticidae)	0.75	0.013
Pretoriuskop – Unburnt	<i>Heliophanus orchestra</i> (Salticidae)	0.75	0.063
Pretoriuskop – Aug 1	<i>Monaeses quadrituberculatus</i> (Thomisidae)	0.67	0.188

Pretoriuskop – Aug 3	<i>Tibellus minor</i> (Philodromidae)	0.67	0.202
Satara – Aug 1	<i>Oxyopes bothai</i> (Oxyopidae)	1.00	0.038
Satara – Aug 1	<i>Neoscona moreli</i> (Araneidae)	0.83	0.056
Satara – Aug 1	<i>Cheiracanthium furculatum</i> (Miturgidae)	0.67	0.169
Satara – Aug 1	<i>Oxyopes pallidecoloratus</i> (Oxyopidae)	0.67	0.187
Satara – Aug 3	<i>Heliophanus insperatus</i> (Salticidae)	0.67	0.186
Satara – Dec 3	<i>Cyrtophora citricola</i> (Araneidae)	0.67	0.179
Satara – Dec 3	<i>Phoroncidia</i> sp. 1 (Theridiidae)	0.67	0.183
Satara – Dec 3	<i>Oxyopes angulitarsus</i> (Oxyopidae)	0.63	0.324
Mopani – Dec 3	Salticidae sp. 1 (Salticidae)	0.80	0.056
Mopani – Unburnt	<i>Hispo georgius</i> (Salticidae)	1.00	0.013
Mopani – Aug 1	<i>Stenaelurillus</i> sp. 2 (Salticidae)	0.67	0.162
Mopani – Aug 3	<i>Hyllus argyrotoxis</i> (Salticidae)	0.67	0.198
Mopani – Aug 3	Misc. <i>Augacephalus</i> sp. (Theraphosidae)	0.67	0.192
Mopani – Dec 3	<i>Thyene thyenoides</i> (Salticidae)	0.67	0.201
Mopani – Unburnt	<i>Argyrodes zonatus</i> (Theridiidae)	0.67	0.166

When investigating whether there were any species that were indicators for any of the respective burning regimes across the study areas (i.e. not separating the study areas) using the IndVal method, it was found that there were none either at a threshold of 0.70 or 0.60.

Functional traits

Vertical position/habitat

When the spiders were separated according to the vertical position in the vegetation where they occur (using the presence/absence dataset), markedly similar patterns in mean species density emerged across burning regimes at a study area and across study areas, with reductions in overall mean species density from the wettest study area (Pretoriuskop) to the driest study area (Mopani) (Fig. 10).

Spiders showing no specific preference for where they occur in the vertical structure; in other words 'habitat generalists' (the 'variable' category (VA)) were found to be most plentiful in terms of species followed by specialists of the grass/shrub layer (GS) (Fig. 10). Species grouped in the remaining categories (i.e. i) ground (GR); ii) ground, grass/shrub (GG); iii) ground, trees (under bark) (GB); iv) grass/shrub, tree (GT) and v) tree (TR)) occurred in relatively low number of species. No significant differences were found across burning regimes within a study area when considering each vertical position category separately.

Figure 11 illustrates how spiders were represented in the various vertical position categories in terms of mean abundance, using the adult-only dataset. Once again, these results reveal very similar patterns to those mentioned above, with no significant differences in mean abundance (within categories) across burning regimes within a study area. However, tree specialists were absent from the adult-only dataset.

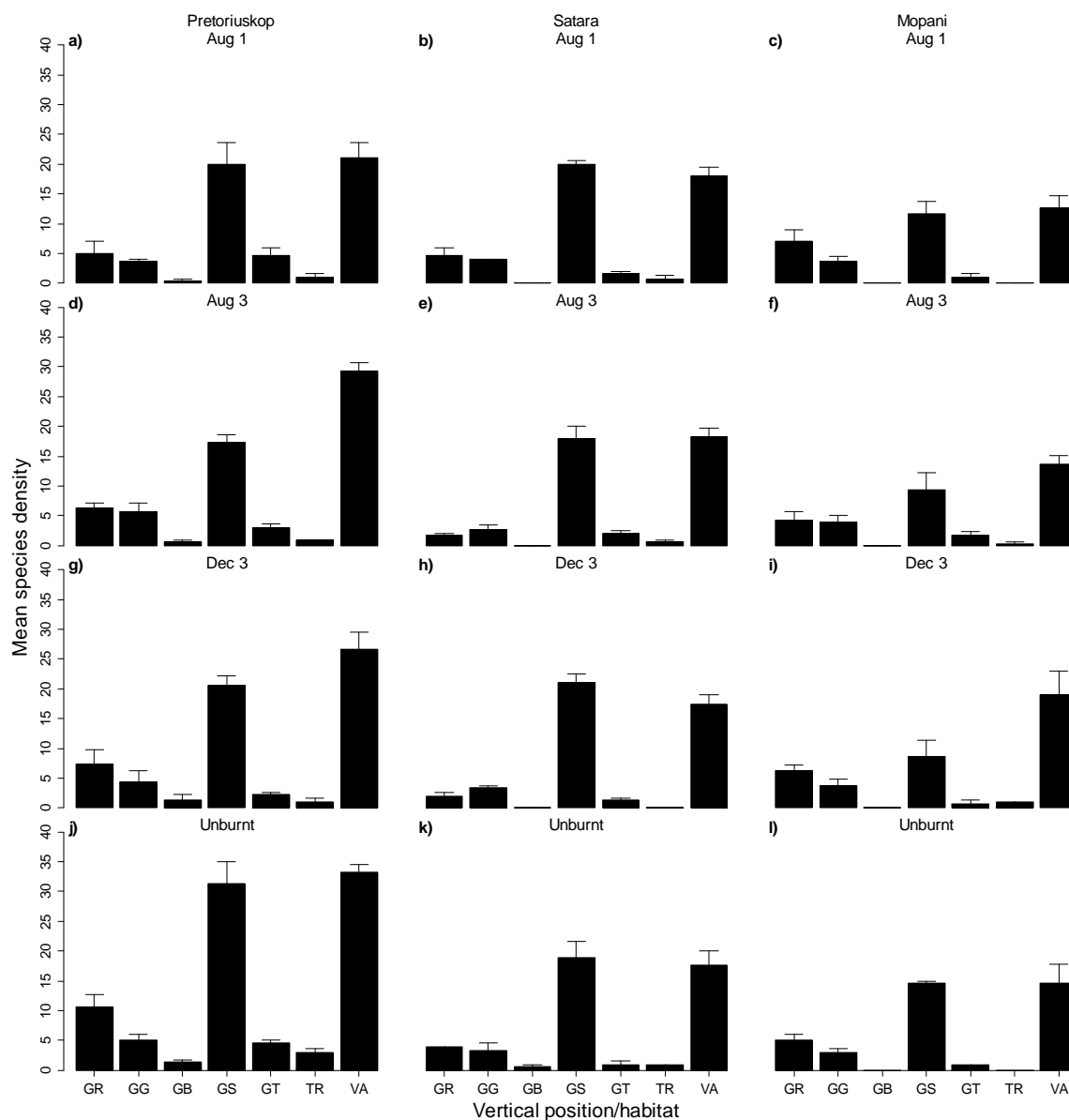


Figure 10. Mean species density of spiders from the presence/absence dataset grouped according to what part of the vertical habitat structure they occupy. Error bars indicate standard error. Category abbreviations are as follows: GR = ground; GG = ground, grass/shrub; GB = ground, trees (under bark); GS = grass/shrub; GT = grass/shrub, tree; TR = tree; VA = variable. Burning regime abbreviations are as follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

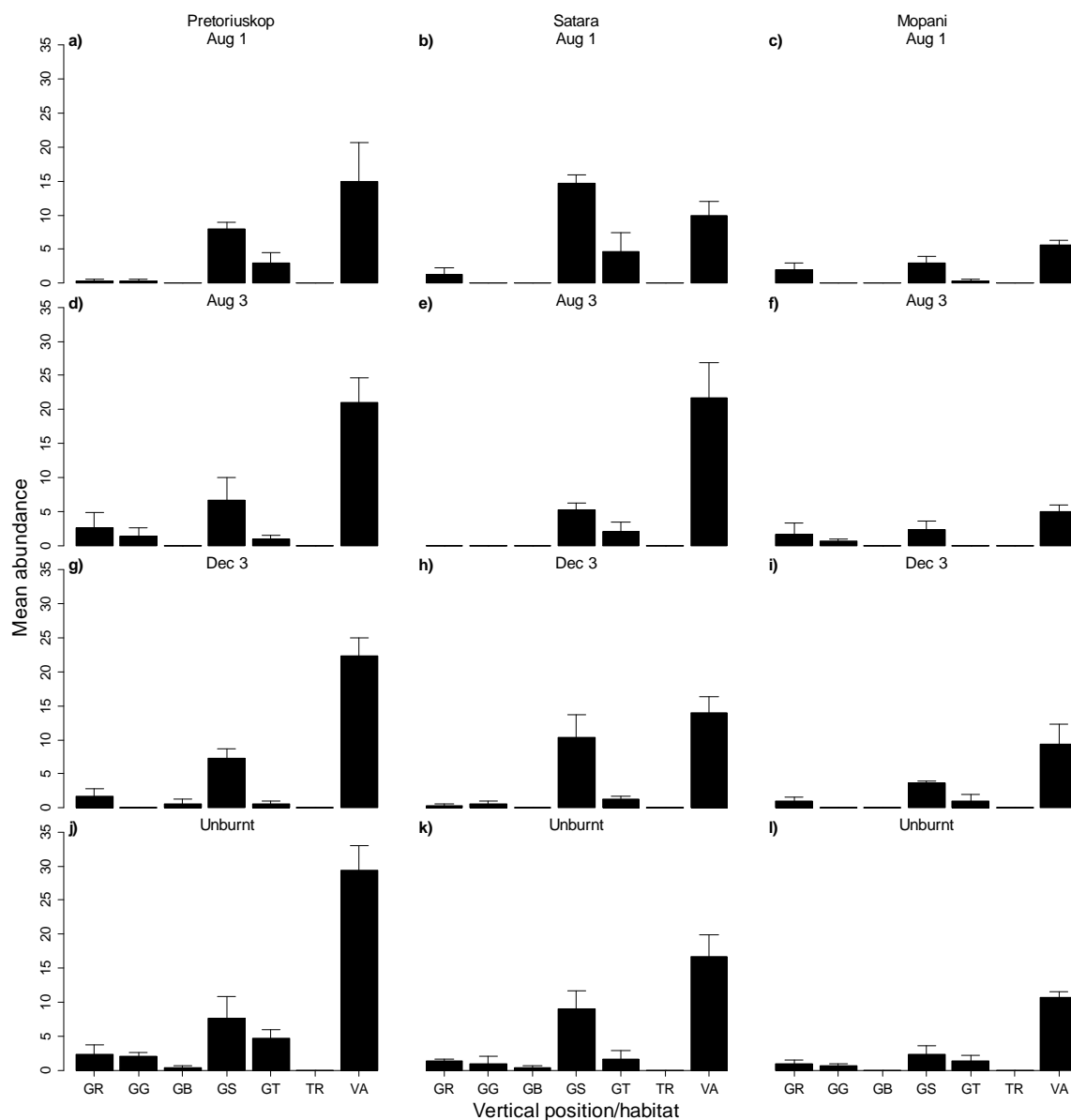


Figure 11. Mean abundance of adult spiders grouped according to what part of the vertical habitat structure they occupy. Error bars indicate standard error. Category abbreviations are as follows: GR = ground; GG = ground, grass/shrub; GB = ground, trees (under bark); GS = grass/shrub; GT = grass/shrub, tree; TR = tree; VA = variable. Burning regime abbreviations are as follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

Hunting strategy

When separating the spiders in this study according to hunting strategy, it is apparent that the majority of species represented employ an active hunting strategy (AC) followed by web specialists (WE), which strictly use webs to ensnare their prey (see Appendix 2). Very similar patterns in mean species density (using the presence/absence dataset) within each of the hunting strategy categories exist across burning regimes within a study area and across study areas, with reductions in overall mean species density along the rainfall gradient. No significant differences exist within each category across burning regimes at each study area.

Once again, mean spider abundance (using the adult-only dataset) was separated across the hunting strategy categories in a very similar fashion to that found when investigating mean species density (see Appendix 3) and no significant differences across burning regimes within a study area emerged.

Lifestyle

The bulk of spiders in this study tend to employ a free-living way of life (FR) when species were grouped according to lifestyle (using the presence/absence dataset; see Appendix 4). Strictly web-bound species (WB) were second most prevalent in terms of mean species density. Similar patterns in mean species density within lifestyle categories were found across burning regimes and study areas (with reduced density in drier areas). Almost identical patterns were found in mean abundance (see Appendix 5), where there were no significant differences within each lifestyle category across burning regimes at a study area for either mean species density or abundance.

Carapace sclerotisation

Most spider species in this study possessed no sclerotisation of the carapace. Where sclerotisation was present (be it completely, partially or only sometimes), it tended to be more prevalent in the unburnt plots. No significant differences existed in mean species density or mean abundance within a category across burning regimes at each study area respectively. Overall, the number of species and abundance of spiders decreased from the wetter to the drier study areas (Pretoriuskop to Mopani respectively).

Abdominal scutes/sclerotisation

As with carapace sclerotisation, the majority of spiders sampled exhibited no form of sclerotisation of the abdomen. Where sclerotisation did exist (either fully or in partial measures), more species with varying degrees of sclerotisation of the abdomen were found in the unburnt plots compared with the other burning regimes. Again, there were no significant differences within a category across burning regimes at each respective study area and overall species density and abundance decreased along the rainfall gradient in all cases.

Overall, in this study, the spider assemblages were largely dominated by free-living active hunters that were usually habitat generalists, not restricted to a specific section of the vertical habitat structure. However, these habitat generalists were sometimes as prevalent as the grass/shrub specialists were. Furthermore, the majority of spiders sampled had no form of sclerotisation, either on the carapace or on the abdomen.

Diet specialisation

When the spider assemblages were analysed in terms of spiders that specialise on ants as prey (to investigate whether these results corresponded with the results found in a previous study on ants at the same sampling sites; Parr *et al.* 2004), no specific trends in ant specialists emerged. This is likely due to the extremely low number of ant specialists encountered in this study.

Discussion

Changes in spider diversity across the rainfall gradient

Studies focusing on a range of faunal groups including both vertebrates and invertebrates have shown that species distribution patterns are often affected by environmental variables such as precipitation, known to set the upper limit of net primary productivity (NPP) especially in semi-arid environments such as southern Africa (O'Brien 1998; O'Brien *et al.* 2000; van Rensburg *et al.* 2002; Caylor *et al.* 2004 and references therein; Del Grosso *et al.* 2008). In addition, the species-energy hypothesis (Currie 1991) suggests that this change in NPP with rainfall would affect the abundance and diversity of fauna.

Species tend to decrease in abundance and richness in drier areas (e.g. O'Brien 1998; O'Brien *et al.* 2000; van Rensburg *et al.* 2002; Parr *et al.* 2004; Davies *et al.* 2012) and these general decreases in abundance and species richness were supported by the results of the current study in terms of spider abundance, species density and estimated species richness, which all decreased from the wettest Pretoriuskop area to the intermediate Satara area to the driest Mopani area.

Linking these decreases in abundance and species richness along rainfall gradients with the well tested species-energy hypothesis (Currie 1991), higher levels of productivity in higher rainfall areas correspond with more vegetation biomass (living, dead and decaying) (e.g. Scholes *et al.* 2002), which in turn acts as food for a variety of prey species (e.g. herbivorous insects; Collembola, which feed on detritus; termites, which feed on dead wood). In turn, these species (and species that prey on them, e.g. mantids) act as food for apex predators such as spiders. Therefore, higher rainfall resulting in higher NPP could result in a greater abundance of prey species, thus supporting a greater abundance of predator species (i.e. spiders in this case).

In addition, faunal assemblage composition (including spiders) is affected by habitat (vegetation) structure, heterogeneity and complexity (Andersen 1991; Tews *et al.* 2004; Warui *et al.* 2005; Jiménez-Valverde & Lobo 2007). More vegetation due to higher NPP is likely to create a wider diversity of habitat niches (due to greater habitat complexity), which could potentially support a greater diversity of spider species (see Tews *et al.* 2004 and references therein), requiring a variety of different microhabitats and habitat structural components. Greater habitat complexity could also create a larger habitat space, which could support a greater abundance of spiders (Tews *et al.* 2004 and references therein). The results of this current study support this

notion with higher spider abundance and species richness at the wettest study area, Pretoriuskop, which in general has a highly complex and dense vegetation structure compared to the drier study areas, Satara and Mopani, where vegetation structure decreases in complexity and density (personal observation and discussed below). Furthermore, Pretoriuskop and Satara supported relatively similar numbers of individuals however, whilst Mopani had significantly lower spider abundance than both.

Species density and estimated species richness showed a slightly different pattern though: Satara and Mopani were most similar and Pretoriuskop had significantly higher richness values from both. The latter could be a result of rainfall and NPP because Satara and Mopani only differ in rainfall by 100 mm per annum (Satara MAP = 550 mm; Mopani MAP = 450 mm) whereas Pretoriuskop receives much more rain (MAP 750 mm) and it can thus be reasoned that it has higher NPP thus leading to higher habitat heterogeneity by increased vegetation complexity (see above). The significant difference in abundance between Satara and Mopani however could indicate that although they are able to support the same number of species, the Satara area, with higher rainfall, is able to support a far greater abundance of spiders, similar to Pretoriuskop (see above). This intuitively makes sense because the three-dimensional habitat structure of Pretoriuskop (an open tree savanna) and Satara (a mixed *Acacia nigrescens* and *Sclerocarya birrea* savanna) is much more similar than this structure is between Satara and the relatively homogenous Mopani shrubveld that is characteristic of the Mopani area (Gertenbach 1983 and personal observation). A review by Tews *et al.* (2004) on studies linked to the ‘habitat heterogeneity hypothesis’, which predicts that higher habitat heterogeneity (driven by vegetation heterogeneity and structure) promotes higher species diversity showed that most fauna in the studies reviewed is indeed influenced in this way. Furthermore, many studies showed positive responses to habitat heterogeneity by spiders (see summary table in Tews *et al.* 2004).

A confounding factor in this argument is that the three study areas do not occur on the same soil type. The Pretoriuskop area is situated on granite-derived soils whereas the Satara and Mopani areas are situated on basalt-derived soils (Gertenbach 1983), which could potentially influence the results of this study, possibly through indirect effects via prey assemblages. This is a potential avenue for further research that could investigate the possible driving forces behind the differences and similarities in spider assemblage composition across the three study areas. One possibility to investigate this could be a comparison of spider assemblages between

experimental burn plots at the Skukuza area (part of the long-term burning experiment in KNP, which was not used in this study) and plots at the Satara area. Both areas receive approximately equal rainfall but differ in their underlying geologies (the Skukuza area is situated on granite-derived soils). In this way, the possible effect of soil-type could be investigated, while keeping rainfall (and presumably NPP) as a constant variable.

Effects of burning regime on spider assemblages

Given the often dramatic changes that burning regimes have on vegetation structure (discussed below and see Andersen *et al.* 2005, who summarise the effects of burning regimes at the Kapalga fire experiment in northern Australia), it is surprising how resistant and resilient (Pimm 1984) most fauna are to the effects of these burning regimes, especially in savannas (e.g. see Andersen & Müller 2000; Andersen *et al.* 2005; Teasdale *et al.* 2013 who show mostly no response by fauna to burning regimes). Some studies, however, have found that invertebrate assemblages are sensitive to burning regimes. For example, Orgeas & Andersen (2001) found that beetle abundance and species density actually increased in areas in northern Australian savannas subjected to early and late dry season fires, respectively, when compared to unburnt areas and that there was also a significant difference in assemblage composition between each of the two burning regimes and the unburnt areas, respectively. In the same part of Australia, Andersen & Müller (2000) found that some ground-dwelling invertebrates (ants, spiders, homopterans and silverfish) decreased in abundance quite substantially in areas subjected to burning compared to unburnt areas when analysed at the order level. Elsewhere, Freire & Motta (2011), in a study on the effects of burning regimes on cursorial arachnids in savannas in Brazil, found that abundance was lower in burnt areas than unburnt areas (with no difference among burnt areas), species richness tended to remain unchanged and diversity was elevated in burnt areas. These authors also found that the timing of the burning influenced diversity more than its frequency. A study on wildfire on ground spiders in a different type of habitat (deciduous forests in the Swiss Alps) (Moretti *et al.* 2002) found that species richness and abundance were higher in repeatedly burnt sites when compared to unburnt areas. Spider assemblages sampled in repeatedly burnt areas were also found to be distinctly different from those in unburnt areas.

The lack of differences across burning regimes in terms of spider abundance, species density and estimated species richness are in keeping with other studies focusing on the effects

of burning regime on invertebrates, especially a study by Parr *et al.* (2004) on ants sampled on the EBPs. They found no significant differences in mean ant species richness or abundance across burning regimes at the same study areas used in the current study, but did find significant differences between plots burnt annually in August and the unburnt plots at Pretoriuskop, as shown here. Similar results were found in ant assemblages in Australian savannas between annually burnt and unburnt plots by Andersen (1991), who found marked differences between the two burning regimes.

Furthermore, a study by Davies *et al.* (2012) showed little response in the assemblages of termites to the same burning regimes used in the current study in terms of abundance and species density. However, at Pretoriuskop they did find significantly greater species richness at August triennial plots compared to August annual plots and at Mopani, the December triennial plots had significantly higher abundance than the other plots (although these numbers were inflated due to the mass sporadic emergence of one species that coincided with the sampling period), both of which differed from the results of the current study.

Parr *et al.* (2004) found significant differences in assemblage composition between burnt and unburnt plots across the three study areas and found that these differences were most pronounced at the wettest savanna site, Pretoriuskop. The spider assemblage results in this current study only supported these results at Pretoriuskop where the greatest difference in assemblage composition was found between annually burnt August plots and the unburnt plots (but also between August annual and the December triennial plots). However, there were no major differences when comparing the other burnt plots with the unburnt plots. In the case of Satara and Mopani, the greatest differences in spider assemblage composition were not found between burnt and unburnt plots as in the case of Parr *et al.* (2004). At Satara for example, the greatest difference occurred between the August annual and August triennial plots and at Mopani, the greatest difference occurred between plots burnt triennially in August and December, respectively.

However, *R* statistic values (obtained from the ANOSIM results) were in general much higher at the wettest study area, Pretoriuskop, intermediate at Satara and lowest at the driest study area, Mopani. This suggests a greater response by spider assemblages in the wetter areas in keeping with the study by Parr *et al.* (2004). Similarly, in a study on termites comparing the same burning regimes as in this study, Davies *et al.* (2012) showed a greater response by termites

at Pretoriuskop (which had four pairs of burning regimes that were distinctly different) than at the drier study areas (Satara and Mopani), which each had three pairs of burning regimes that were very different (although the *R*-values at Satara and Mopani were in general higher than at Pretoriuskop possibly indicating a stronger response to the burning regimes than at the latter). In general, these results support the original hypothesis of the current study that areas with higher rainfall, and thus higher NPP, would exhibit greater changes in vegetation structure in response to burning regime (which becomes more important in structuring savannas in wetter areas following the reasoning in Sankaran *et al.* 2005) and thus affect spider assemblages to a greater extent than in drier areas.

The greater response of assemblages to disturbance in higher rainfall areas was further supported by the number of indicator species in this study that showed high IndVal scores (high specificity and fidelity to a certain locality) above 0.70 and were thus likely to be strong indicators of particular burning regimes at a study area. Pretoriuskop (wettest) had four of these indicator species whereas Satara and Mopani had only two each. At Pretoriuskop, three of these indicator species were identified for the unburnt plots, adding support for previous results discussed (for this study and others) that shown that unburnt localities tend to be different in assemblage composition when compared to burnt ones, especially in wetter areas.

An investigation into the natural history information of these indicator species yielded little to suggest why they were indicators of specific burning regimes at the respective study areas. The majority of the indicator species from Pretoriuskop were free-living (except for *Asemonea stella*, a largely free-living spider that also makes use of webs on some occasions) and generally grass/shrub dwellers (apart from *Asemonea stella*, which occurs in trees and the grass/shrub layer, and *Heliophanus orchestra*, which is not limited to any specific part of the vertical habitat structure). These indicator species use a wide (but by no means specialised) range of hunting strategies.

The indicator species from Satara were mostly free-living and about a third of them were web-bound. All but two (*Heliophanus insperatus* and *Phoroncidia* sp. 1, which utilise all parts of the vertical habitat structure) occur in the grass/shrub layer and utilise a variety of hunting strategies. Similarly, the indicator species from Mopani were almost all free-living (apart from the Misc. *Augacephalus* sp., which are burrow-bound and *Argyrodes zonatus*, which is semi web-bound) and all species but the Misc. *Augacephalus* sp. (which is restricted to the ground)

utilise all parts of the vertical habitat structure. No specialised hunting strategies existed for any of the indicator species.

When examining the distribution of these indicator species across burning regimes at each respective study area using the presence-absence dataset (in order to encompass all species sampled in order to find a plausible explanation for the results discussed above), most of them are actually common species, occurring on a wide variety of burn plots, and in many cases these species were found on almost all burn plots at a respective study area. This supports the generalist nature of the indicator species found in this study. It thus appears that the criteria of specificity and fidelity used in the IndVal analysis were an artefact of where adults of these indicator species were sampled instead of where the species were sampled in their entirety. More intensive sampling could possibly resolve this and yield more ecologically meaningful results.

Burning regimes and habitat structure

Understanding the effect that fire has on fauna, especially spiders in the case of this study, depends on understanding the role that fire has in shaping the habitat in which the spiders are found, especially vegetation (habitat) structure and complexity, as these have been shown to be vital factors that influence spider assemblages (Jiménez-Valverde & Lobo 2007 and references therein). Fire has been described as a large-scale, generalist herbivore and plays a critical role in shaping the structure and assemblage composition of vegetation in fire-prone ecosystems (Bond & Keeley 2005).

Changes in vegetation structure due to the effects of different burning regimes have been studied extensively on the KNP EBPs. Burning regime was outlined by Gill (1975) as being a combination of the intensity of the fire, its frequency and the season in which it occurs and these factors influence the effects that the burning regime will have on vegetation structure. Govender *et al.* (2006) investigated fire intensity using data from fires on the EBPs. They found that winter fires (August fires in the case of this study) had much higher intensities than summer fires (December fires in this study), which appeared to be mainly related to the moisture content of the grass (lowest in winter and highest in summer) rather than grass biomass. Furthermore, no significant differences existed in fire intensity between plots burnt annually and those burnt triennially (in this study, the August annual and triennial burns) despite fuel loads (grass biomass) being significantly higher at the plots burnt triennially. These authors also found that

the general intensity of fires was highest in the high rainfall area (Pretoriuskop) and decreased substantially along the rainfall gradient (Pretoriuskop to Satara to Mopani), being lowest at Mopani. They suggested that this was largely due to a rapid build-up of the unpalatable grasses that dominate the Pretoriuskop area (on granitic soils, which are nutrient-poor), whereas the lower rainfall areas (Satara and Mopani) occur on basalts (with nutrient-rich soils) and have a higher abundance of palatable grasses, which would be removed quicker by grazing, thus lowering the fuel load.

Various studies on the effects of burning regimes on vegetation structure at the KNP EBPs have yielded a variety of results but some general trends have emerged. The largest effects on vegetation structure due to burning occur in the highest rainfall area (Pretoriuskop) and lessen along the rainfall gradient to the driest area, Mopani, where differences between burnt and unburnt plots are less noticeable. Although the density of woody vegetation is not affected by the burning regimes in this study, August annual plots have a higher dominance of small trees (< 2 m) and December triennial plots have a slightly reduced dominance (Higgins *et al.* 2007). Woody canopy cover at a variety of height classes tends to be lowest at the August annual plots compared to the unburnt plots at Pretoriuskop with the smallest decrease in cover at the December triennial plots (Smit *et al.* 2010). At Satara and Mopani the greatest decrease occurs at the August annual plots whilst the smallest decrease occurs at the August triennial plots (Smit *et al.* 2010). Relative decrease in the same canopy cover compared to the unburnt plots shows greater relative decreases between burnt and unburnt plots at Satara and Mopani than at the highest rainfall area, Pretoriuskop (Smit *et al.* 2010). Considering all study areas together, a greater relative decrease occurs at the August annual plots than the August triennial plots (Smit *et al.* 2010). At Pretoriuskop, the density of vegetation at 51-150 cm is greater at the unburnt plots than the burnt plots (Parr *et al.* 2004). Similarly, at Satara, there is more tall vegetation (51-150 cm) on the unburnt plots than the burnt plots and the August annual plots have lower density, shorter vegetation than the other plots (Parr *et al.* 2004). At Mopani, there are no differences in complexity under 50 cm but the unburnt plots have taller and denser vegetation than the burnt plots (in the 51-150 cm height classes) (Parr *et al.* 2004). More bare ground exists on the burnt plots than the unburnt plots at Satara and Mopani (and the same appears to apply at Pretoriuskop (personal observation)) (Parr *et al.* 2004).

Functional traits and burning regimes

Analyses investigating whether spider functional traits were affected by the burning regimes yielded little differences across plots. In keeping with the response of spiders to rainfall and NPP, the functional trait results of this study indicated a decrease in individual abundance and species density within each trait across the rainfall gradient. However, the overall patterns that emerged in the distribution of spiders across the functional groups were similar across burning regimes and across study areas. This suggests that these distribution patterns may not be influenced by the effects of burning regime or rainfall (NPP) and it seems likely that they merely mirror the overall patterns found in the respective savanna habitats (A. S. Dippenaar-Schoeman, pers. comm.). The lack of response to burning regime supports the results of a study on spider functional traits and time since fire in Australia by Langlands *et al.* (2011) where little difference was found in the traits they investigated in relation to the post-fire ages of their study areas, furthermore supporting the notion that spider assemblages appear to be highly resistant to the effects of fire and burning regimes. It is possible that different patterns could have emerged if tree beating and pitfall trapping methods were included as this study as this would have allowed the tree-dwelling and ground-dwelling assemblages to be sampled more intensively.

Following the findings of Cardoso *et al.* (2011), more diverse or complex systems appear to have a high level of redundancy in species fulfilling specific functional roles in an ecosystem and are able to fill gaps in niches easier with species that are more tolerant to a certain disturbance, such as fire in the case of this study. African savannas have been associated with fire (including human-ignited fires) for a considerable length of time (Gowlett *et al.* 1981; Brain & Sillen 1988; Pennisi 1999) and fire-prone biomes in the region have existed for millions of years (Bond & Keeley 2005 and references therein). Furthermore, many studies have shown that the taxa in ecosystems that have a long evolutionary history with fire and burning are surprisingly resistant and resilient to its effects (see Anderson & Müller 2000; Orgeas & Anderson 2001; Parr *et al.* 2004; Bond & Keeley 2005; Davies *et al.* 2012). Considering this, savannas are likely to have evolved to cope with burning by the relevant functional groups being filled by various species that are able to cope with varying conditions caused by the disturbance. These different species would perform the same underlying roles in the savanna and would maintain it in various states of flux. This would form a patch mosaic type of system with a

variety of areas in different stages of succession, but the overall function and form of the savanna would remain constant because the same ecosystem processes are at work throughout.

It is thus possible that there are changes happening on a much finer scale than was addressed in this study where the same functional groups in a particular locality are being filled by the same number of species (for example), but the species composition is different and the resulting assemblage is able to survive the conditions in the modified habitat. This is a promising area for further research and it would be interesting to investigate whether functional diversity enables ecosystems to cope with disturbance in this way without their functioning being adversely affected.

Further considerations

The aforementioned possibility that spider assemblages may be affected at the individual species level rather than at broad scales (see above) should be noted and catered for in fire management policies because burning regimes could have important implications for more rare and fire-sensitive species (Andersen *et al.* 2005). In general however, the results of this study are promising, especially for conservation managers. They suggest that savanna spider assemblages are not particularly affected by varying burning regimes and appear not even to be affected much by whether an area burns or not.

A factor that could have prevented the emergence of significant differences in various assemblage parameters across burning regimes at the three study areas in this study could be the experimental layout of the KNP EBPs (outlined by Biggs *et al.* 2003). At the project's inception in 1954, only four replicates of each of the proposed burning regimes were implemented at the four study areas throughout the park (only three of the study areas were used in this study). In most studies, a fourth replicate at each of the study areas is excluded due to them being outliers in terms of soil type (Venter 1999), resulting in the use of only three replicates, as was the case in this current study. This low sample size reduces the statistical power of the statistical analyses conducted, which generally require larger sample sizes to increase the robustness of the tests. This is an unfortunate limitation in the experimental design, but the experiment is still the leading study on the effects of a variety of long-term burning regimes in the world to date (spanning almost 60 years) and this should not be discounted. Another aspect worth noting is the relatively small size of the individual plots, which are in general approximately 380 x 180 m (ca.

7 ha) in size. This relatively small size could possibly make recolonisation of the plots by spiders in the surrounding savanna matrix fairly easy, which could further mask changes that may occur in spider assemblages in areas subjected to different long-term burning regimes. Larger plot sizes could potentially mimic a more realistic system in which changes due to burning regimes could become more apparent.

When all potential shortcomings due to experimental design are considered, this study is still arguably one of the most comprehensive studies on savanna spiders (and the effects of long-term burning regimes on them) to-date in terms of spatial and temporal extent and intensity of sampling. In this study, where sampling was conducted over the space of a year (and sorting and identification of specimens took two-and-a-half years), a total of 1025 adult spiders from 334 species and 40 families were collected and in addition to this, an estimated three to five times more immature spiders. However, due to the enormous turn-over in species that is encountered when sampling spiders (especially when compared to other taxa, e.g. ants along an altitudinal gradient (W. Jansen unpublished MSc thesis 2013)) even the most rigorous sampling routines may not be adequate to comprehensively represent species richness and assemblage composition in a study area, as was the case in this study. There is likely to be considerable species turnover from year to year in these savannas, which could not be quantified in this study. Therefore, further research, especially sampling over several years and if possible, incorporating greater sampling intensity is necessary to reveal the patterns at play and help to better understand how savannas are so resistant and resilient to the effects of fire, especially from the perspective of the roles that invertebrates play in maintaining these systems.

Conclusion

Spiders were found to exhibit a high degree of resistance and resilience to the effects of the long-term burning regimes examined in this study in keeping with previous studies on invertebrates, contrary to the original hypotheses that predicted that spider diversity and abundance would be lower in plots subjected to high intensity, high frequency fires, which link to less complex habitat (vegetation) structure. However, there was a slight response in abundance between annually burnt and unburnt plots in the wettest savanna suggesting that spiders may have a more pronounced response to burning regimes in wetter savannas where the effect of burning regime on vegetation structure is greater. Furthermore, the distribution of spiders across different functional traits remained unchanged by burning regime and likely mirror the overall patterns found in savanna systems.

These results are promising for conservation managers as the effects of long-term burning regime do not appear to influence spiders, as with other invertebrate groups studied. There is however a desperate need for further research on the effects of long-term burning regimes on invertebrates, but especially spiders because it is possible that the extremely high species turnover of spiders may mask more subtle effects that burning regimes may have on their assemblages, possibly to the detriment of rarer species that may prove vital to ecosystem functioning and stability. This remains an exciting field of study and many opportunities still exist to further investigate the way in which invertebrates continue to drive ecosystem processes despite major disturbances such as fire. More interesting results are likely to be uncovered in future studies compared to what is only the tip of the iceberg, regarding research conducted so far.

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Appendix 1

List of the spider species sampled in the study. The abbreviation ‘Misc.’ indicates miscellaneous species from a Family or genus that were grouped together. It was not possible to identify these species further and these were generally species where only immature spiders were sampled.

Family	Species
Agelenidae	<i>Benoitia ocellata</i>
	Misc. <i>Benoitia</i> sp.
Amaurobiidae	<i>Pseudauximus</i> sp.
Araneidae	Araneidae sp. 1
	Araneidae sp. 6
	Araneidae sp. 7
	Araneidae sp. 8
	Misc. Araneidae sp.
	Misc. Araneidae? sp.
	Misc. <i>Araneilla</i> sp.
	<i>Araneus holzapfelae</i>
	<i>Araneus</i> sp.
	<i>Araneus strupifer</i>
	<i>Argiope australis</i>
	<i>Argiope lobata</i>
	Misc. <i>Argiope</i> sp.
	<i>Argiope?</i> sp.
	<i>Argiope trifasciata</i>
	<i>Caerostris sexcupidata</i>
	<i>Chorizopes</i> sp.
	<i>Cyclosa</i> sp.
	<i>Cyphalonotus larvatus</i>
	<i>Cyrtophora citricola</i>
	<i>Cyrtophora</i> sp.
	<i>Hypsosinga lithyphantoides</i>
	<i>Hypsosinga</i> sp. 1
	<i>Hypsosinga</i> sp. 2
	Misc. <i>Hypsosinga</i> sp.
	<i>Larinia?</i> sp. 1
	<i>Lipocrea longissima</i>
	<i>Nemoscolus cotti</i>
	<i>Nemoscolus virgintipunctatus</i>
	<i>Nemoscolus</i> sp. 1
	<i>Nemoscolus</i> sp. 2
	<i>Neoscona blondeli</i>

	<i>Neoscona moreli</i>
	<i>Neoscona quincasea</i>
	Misc. <i>Neoscona</i> sp.
	<i>Neoscona?</i> sp.
	<i>Neoscona subfusca</i>
	<i>Pararaneus cyrtoscapus</i>
	Misc. <i>Pararaneus</i> sp.
	<i>Prasonica</i> sp. 1
	Misc. <i>Prasonica</i> sp.
	<i>Pycnacantha tribulis</i>
	<i>Singa albodorsata</i>
Caponiidae	Misc. <i>Caponia</i> sp.
Clubionidae	Misc. <i>Clubiona</i> sp.
Corinnidae	<i>Cambalida fulvipes</i>
	<i>Castianeira</i> sp.
	Misc. Corinnidae sp.
	<i>Fuchiba aquilonia</i>
	<i>Merenius alberti</i>
	<i>Orthobula radiata</i>
	Trachelinae gen. nov. sp. nov.
Ctenidae	<i>Ctenus gulosus</i>
	Misc. <i>Ctenus</i> sp.
Cyatholipidae	<i>Cyatholipus isolatus</i>
Cyrtoucheniidae	<i>Ancylotrypha</i> sp.
Dictynidae	Misc. <i>Archaeodictyna</i> sp.
	<i>Dictyna</i> sp.
	Misc. Dictynidae sp.
	Misc. Dictynidae? sp.
	<i>Mashimo leleupi</i>
Eresidae	<i>Dresserus</i> sp.
	<i>Stegodyphus dumicola</i>
	<i>Stegodyphus mimosarum</i>
Gnaphosidae	<i>Aphantaulux</i> sp.
	<i>Asemesthes ceresicola</i>
	<i>Asemesthes reflexus</i>
	Misc. <i>Asemesthes</i> sp.
	Misc. <i>Camillina</i> sp.
	Misc. <i>Drassodes</i> sp.
	Drassodinae sp.
	Misc. Gnaphosidae sp.
	Misc. <i>Micaria</i> sp.
	<i>Setaphis</i> sp.

	<i>Setaphis subtilis</i> <i>Xerophaeus</i> sp. <i>Zelotes caldarius</i> Misc. <i>Zelotes</i> sp. <i>Zelotes tuckeri</i>
Hahniidae	Misc. <i>Hahnia</i> sp.
Hersiliidae	<i>Hersilia sericea</i>
Linyphiidae	Erigoninae sp. Linyphiidae sp. 2 Misc. Linyphiidae sp. Linyphiidae? sp. <i>Meioneta habra</i> <i>Meioneta</i> sp. <i>Microlinypha</i> sp. <i>Ostearius melanopygius</i>
Liocranidae	<i>Liocranidae</i> sp.
Lycosidae	<i>Amblyothele</i> sp. 1 <i>Evippomma squamulatum</i> Misc. <i>Geolycosa</i> sp. <i>Hippasa australis</i> <i>Hippasa</i> sp. <i>Hogna</i> sp. 1 Misc. <i>Hogna</i> sp. <i>Lycosa</i> sp. Lycosidae sp. 1 Misc. Lycosidae sp. Lycosidae? sp. <i>Minicosa neptuna</i> <i>Pardosa crassipalpis</i> <i>Pardosa</i> sp. 1 <i>Pardosa</i> sp. 2 Misc. <i>Pardosa</i> sp. <i>Trabea</i> sp. 1 Misc. <i>Trabea</i> sp.
Mimetidae	<i>Mimetus natalensis</i> <i>Mimetus</i> sp.
Miturgidae	<i>Cheiracanthium africanum</i> <i>Cheiracanthium furculatum</i> Misc. <i>Cheiracanthium</i> sp. <i>Cheiramiona krugerensis</i> Misc. <i>Cheiramiona</i> sp.
Nephilidae	<i>Nephila senegalensis</i>

	<i>Nephila</i> sp.
Oecobiidae	<i>Oecobius navus</i>
Oonopidae	<i>Gamasomorpha humicola</i>
Oxyopidae	<i>Hamataliwa kulczynski</i> <i>Hamataliwa</i> sp. 2 Misc. <i>Hamataliwa</i> sp. <i>Oxyopes affinis</i> <i>Oxyopes angulitarsus</i> <i>Oxyopes bothai</i> <i>Oxyopes hoggi</i> <i>Oxyopes jacksoni</i> <i>Oxyopes pallidecoloratus</i> <i>Oxyopes russoi</i> Misc. <i>Oxyopes</i> sp. <i>Oxyopes vogelsangeri</i> Misc. <i>Peucetia</i> sp. <i>Peucetia striata</i> <i>Peucetia viridis</i>
Palpimanidae	<i>Diaphorocellus</i> sp. 1 Misc. <i>Palpimanus</i> sp. <i>Palpimanus transvaalicus</i>
Philodromidae	<i>Philodromus browningi</i> <i>Philodromus</i> sp. 1 <i>Philodromus</i> sp. 2 <i>Philodromus</i> sp. 3 <i>Philodromus</i> sp. 4 Misc. <i>Philodromus</i> sp. <i>Suemus punctatus</i> <i>Thanatus dorsilineatus</i> Misc. <i>Thanatus</i> sp. <i>Tibellus armatus</i> <i>Tibellus flavipes</i> <i>Tibellus minor</i> <i>Tibellus</i> sp. 1 Misc. <i>Tibellus</i> sp.
Pholcidae	<i>Leptopholcus</i> sp. <i>Smeringopus natalensis</i>
Phyxelididae	Phyxelididae sp.
Pisauridae	<i>Afropisaura rothiformis</i> <i>Euprosthopsis pulchella</i> <i>Maypacijs bilineatus</i> <i>Perenethis simoni</i>

Prodidomidae	<i>Theuma fusca</i>
Salticidae	Misc. <i>Asemonea</i> sp. <i>Asemonea stella</i> <i>Brancus</i> sp. 1? <i>Cyrba boveyi</i> <i>Cyrba nigrimana</i> Misc. <i>Cyrba</i> sp. <i>Evarcha alba</i> <i>Evarcha dotata</i> <i>Evarcha prosimilis</i> Misc. <i>Evarcha</i> sp. <i>Evarcha striolata</i> <i>Evarcha vittula</i> <i>Festucula festuculaeformis</i> <i>Festucula lawrencei</i> <i>Fuchiba aquilonia</i> <i>Harmochirus</i> sp. 1 <i>Heliophanus debilis</i> <i>Heliophanus insperatus</i> <i>Heliophanus orchestra</i> <i>Heliophanus pygmaeus</i> <i>Heliophanus pygmaeus?</i> Misc. <i>Heliophanus</i> sp. <i>Hispo georgius</i> <i>Hyllus argyrotoxis</i> <i>Langelurillus krugeri</i> <i>Langona pilosa</i> <i>Langona</i> sp. 2 <i>Langona tortuosa</i> <i>Merenius alberti</i> <i>Menemerus</i> sp. <i>Mexcala elegans</i> <i>Myrmarachne</i> sp. 1 <i>Myrmarachne</i> sp. 2 <i>Myrmarachne</i> sp. 3 <i>Natta chionogastra</i> <i>Natta horizontalis</i> <i>Natta</i> sp. (probably <i>N. chionogastra</i>) <i>Natta</i> sp. (probably <i>N. horizontalis</i>) Misc. <i>Natta</i> sp. <i>Nigorella hirsuta</i> <i>Oelurillus</i> sp.

	<i>Pellenes bulawayoensis</i>
	<i>Pellenes tharinae</i>
	<i>Phintella</i> sp.
	<i>Phlegra bresnieri</i>
	<i>Phlegra certa</i>
	<i>Phlegra certa?</i>
	Misc. <i>Phlegra</i> sp.
	<i>Pignus simoni</i>
	<i>Pseucidius dentatus</i>
	<i>Pseucidius</i> sp. 1
	<i>Pseudicius</i> sp.
	<i>Rhene pinguis</i>
	Salticidae sp. 1
	Salticidae sp. 2
	Salticidae sp. 3
	Misc. Salticidae sp.
	Misc. <i>Sibianor</i> sp.
	<i>Sibianor victoriae</i>
	<i>Stenaelurillus guttiger</i>
	<i>Stenaelurillus natalensis</i>
	<i>Stenaelurillus</i> sp. 2
	<i>Stenaelurillus</i> sp.
	<i>Tanzania mkomaziensis</i>
	<i>Thyene coccineovittata</i>
	<i>Thyene imperialis</i>
	<i>Thyene inflata</i>
	<i>Thyene semiargentea</i>
	Misc. <i>Thyene</i> sp.
	<i>Thyene thyenoides</i>
	<i>Thyenula aurantiaca</i>
	<i>Thyenula</i> sp.
	<i>Tusitala barbata</i>
	<i>Veisella durbani</i>
Scytodidae	<i>Scytodes caffra</i>
	<i>Scytodes constellata</i>
	<i>Scytodes ocellates</i>
Segestriidae	<i>Ariadna corticola</i>
	Misc. <i>Ariadna</i> sp.
Sicariidae	<i>Loxosceles spiniceps</i>
Sparassidae	<i>Olios correvoni</i>
	<i>Olios machadoi</i>
	<i>Olios</i> sp. 1

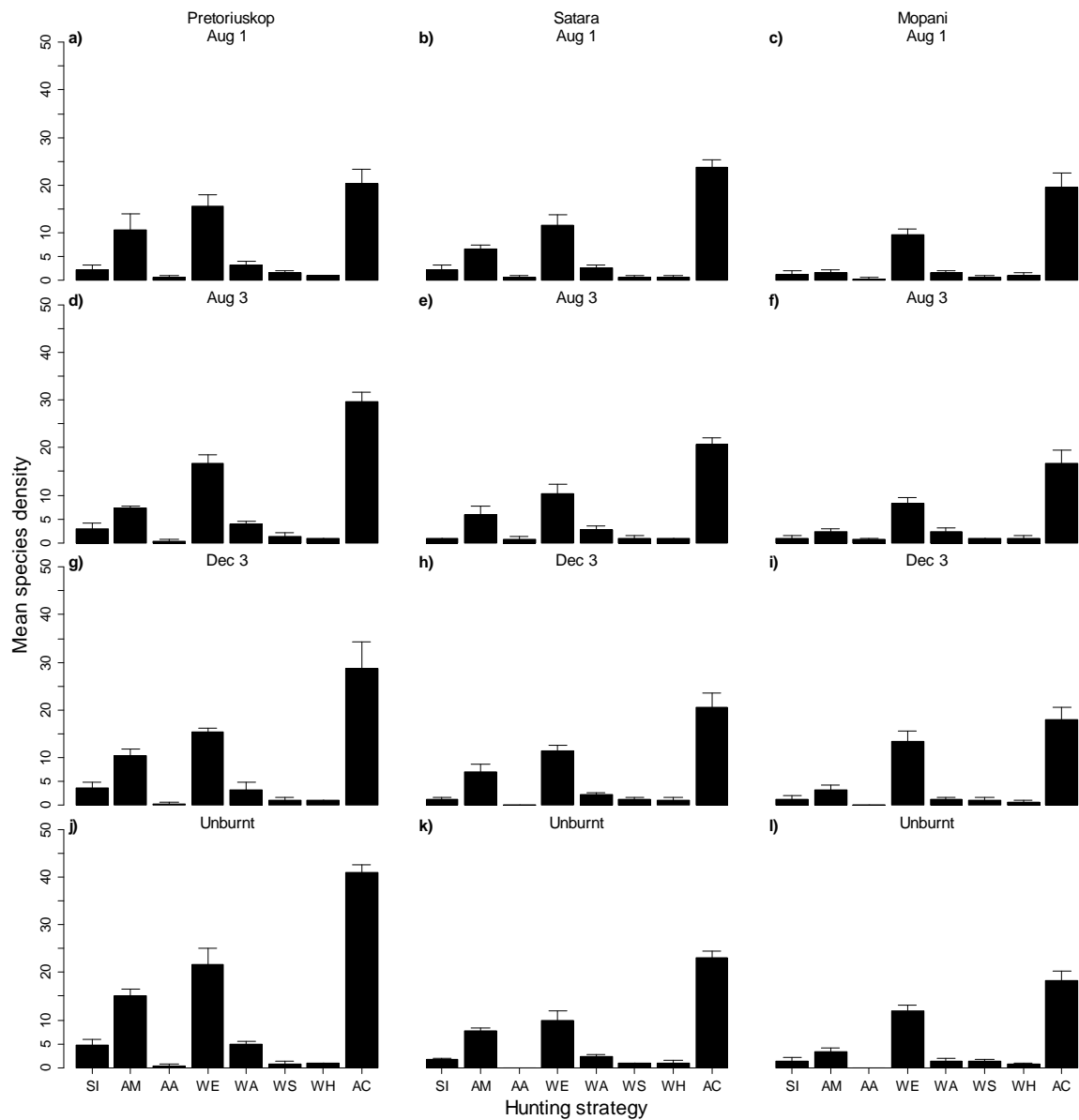
	<i>Olios</i> sp. 2 Misc. <i>Olios</i> sp. <i>Pseudomicrommata longipes</i>
Tetragnathidae	<i>Leucauge auronotum</i> <i>Leucauge festiva</i> <i>Leucauge levanderi</i> Misc. <i>Leucauge</i> sp.
Theraphosidae	Misc. <i>Augacephalus</i> sp. <i>Ceratogyrus</i> sp. <i>Harpactirella</i> sp. Unknown Theraphosidae
Theridiidae	<i>Argyrodes convivians</i> Misc. <i>Argyrodes</i> sp. <i>Argyrodes zonatus</i> <i>Chorizopella tragardhi</i> <i>Dipenura</i> sp. 1 <i>Dipoena</i> sp. 1 <i>Dipoena</i> sp. 2 <i>Dipoena</i> sp. <i>Enoplognatha</i> sp. <i>Euryopsis</i> sp. 1 <i>Euryopsis</i> sp. <i>Latrodectus geometricus</i> <i>Latrodectus renivulvatus</i> <i>Phoroncidia eburnea</i> <i>Phoroncidia</i> sp. 1 Misc. <i>Phoroncidia</i> sp. <i>Rhomphaea nasica</i> <i>Steatoda</i> sp. 2 Misc. <i>Steatoda</i> sp. Theridiidae sp. 1 Theridiidae sp. <i>Theridion purcelli</i> <i>Theridion</i> sp. 1 Misc. <i>Theridion</i> sp.
Thomisidae	<i>Ansiea tuckeri</i> <i>Diaea puncta</i> <i>Firmicus bragantinus</i> <i>Heriaeus crassispinus</i> Misc. <i>Heriaeus</i> sp. <i>Hewittia gracilis</i> <i>Misumenops rubrodecoratus</i>

Monaeses australis
Monaeses austrinus
Monaeses gibbus
Monaeses pustulosus
Monaeses quadrituberculatus
Misc. *Monaeses* sp.
Oxytate argenteooculata
Pherecydes carinae
Platythomisus deserticola
Pycnacantha tribulus
Runcinia aethiops
Runcinia flavida
Simorcus cotti
Stiphropus bisilligatus
Stiphropus sp.
Synema decens
Synema diana
Synema imitator
Synema marlothi
Synema nigrotibiale
Thomisops melanopes
Thomisops pupa
Thomisops senegalensis
Thomisops sp.
Thomisops sulcatus
Thomismus blandus
Thomismus daradioides
Thomismus granulatus
Thomismus scrupeus
Misc. *Thomismus* sp.
Tmarus africanus
Tmarus cameliformis
Tmarus foliatus
Misc. *Tmarus* sp.
Misc. *Xysticus* sp.

Uloboridae *Miagrammopes brevicaudus*
Miagrammopes longicaudus
Misc. Uloboridae sp.
Uloborus lugubris
Uloborus planepedius
Uloborus plumipes
Misc. *Uloborus* sp.

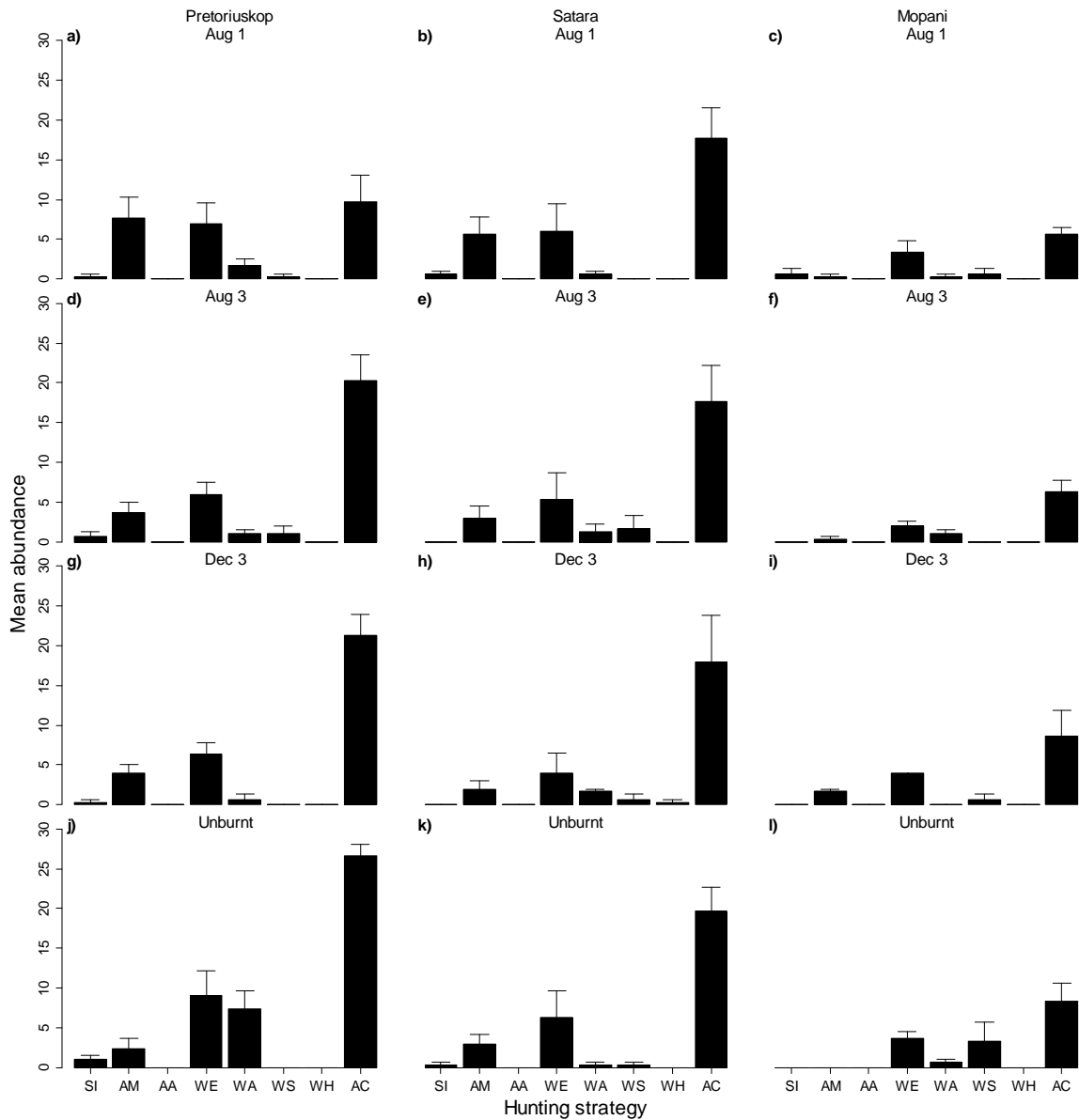
Zodariidae Misc. *Cicynethus* sp.
 Misc. *Cydrela* sp.
 Misc. *Diores* sp.
 Misc. *Heradida* sp.
 Systemoplacis fagei

Appendix 2



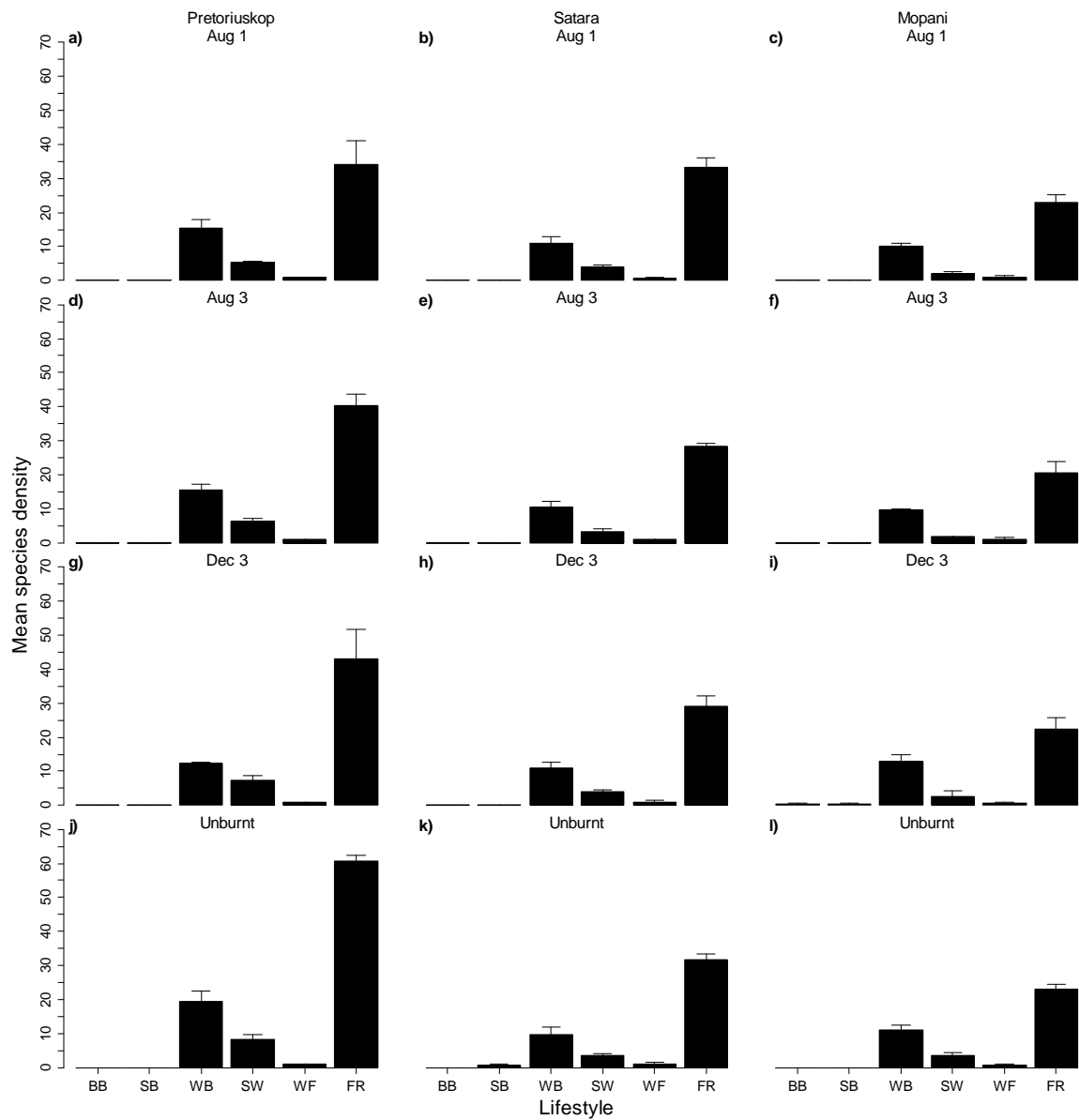
Mean species density of spiders from the presence/absence dataset grouped according to hunting strategy. Error bars indicate standard error. Category abbreviations are as follows: SI = sit-and-wait; AM = ambush; AA = ambush/active hunter; WE = web; WA = web/ambush; WS = web/semi-active hunter; WH = web/ambush or active hunter; AC = active hunter. Burning regime abbreviations are as follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

Appendix 3



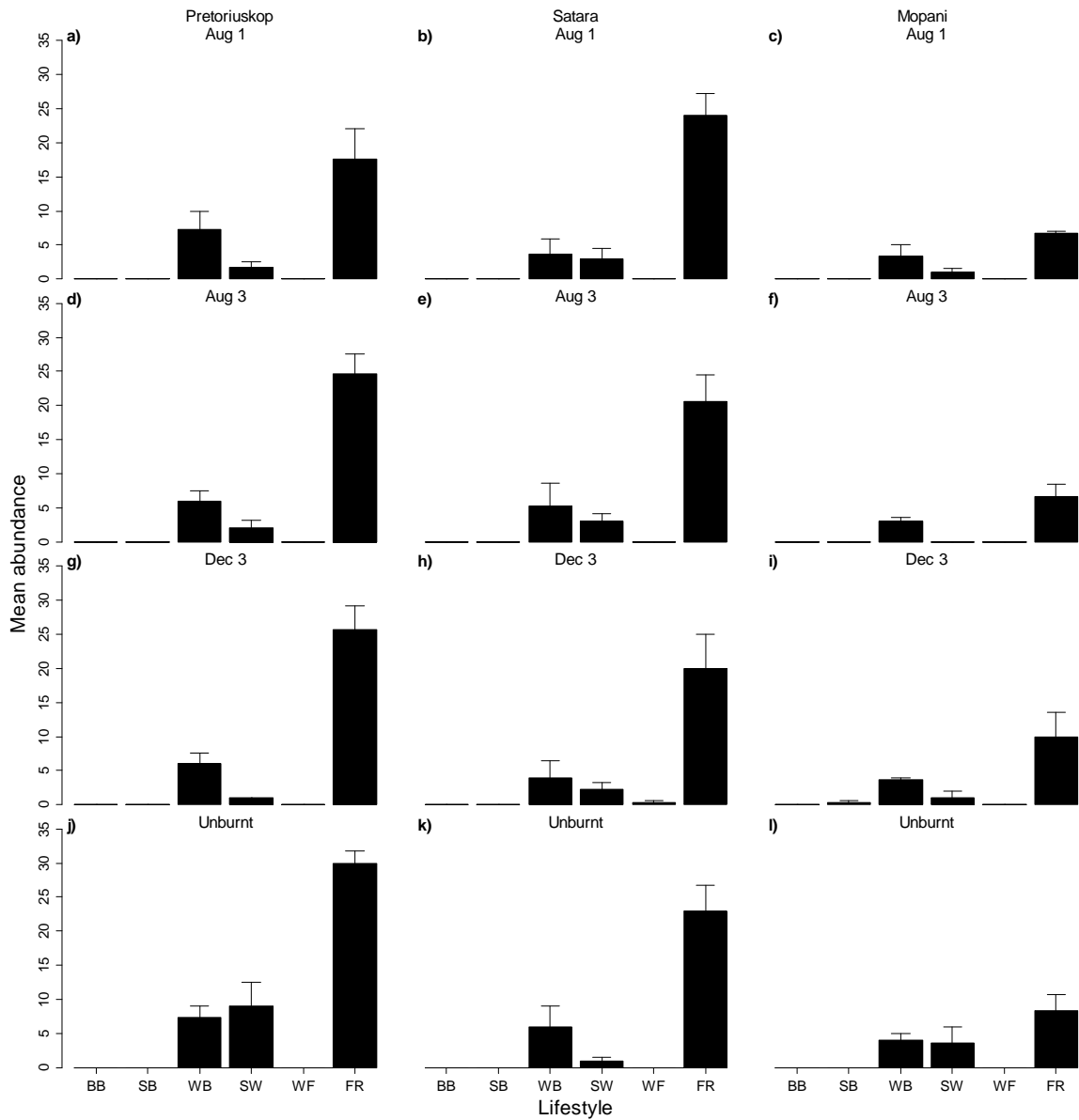
Mean abundance of adult spiders grouped according to hunting strategy. Error bars indicate standard error. Category abbreviations are as follows: SI = sit-and-wait; AM = ambush; AA = ambush/active hunter; WE = web; WA = web/ambush; WS = web/semi-active hunter; WH = web/ambush or active hunter; AC = active hunter. Burning regime abbreviations are as follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

Appendix 4



Mean species density of spiders from the presence/absence dataset grouped according to lifestyle. Error bars indicate standard error. Category abbreviations are as follows: BB = burrow-bound; SB = semi burrow-bound; WB = web-bound; SW = semi web-bound; WF = semi web-bound or free-living; FR = free-living. Burning regime abbreviations are as follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.

Appendix 5



Mean abundance of adult spiders grouped according to lifestyle. Error bars indicate standard error. Category abbreviations are as follows: BB = burrow-bound; SB = semi burrow-bound; WB = web-bound; SW = semi web-bound; WF = semi web-bound or free-living; FR = free-living. Burning regime abbreviations are as follows: Aug 1 = annual burns in August, Aug 3 = triennial burns in August, Dec 3 = triennial burns in December and Unburnt = unburnt plots.