

# Effects of a fast-burning spring fire on the ground-dwelling spider assemblages (Arachnida: Araneae) in a central South African grassland habitat

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Fire is widely used as a management strategy in grasslands to maintain vegetation structure and improve grazing quality for large herbivores. The impacts of burning on invertebrates in South Africa remain poorly understood. A study was initiated in spring 2005 to determine the impact of a fast hot burn on ground-dwelling spider assemblages in a grassland habitat in the central Free State. Pitfall traps were set out at six sites in the reserve, with three sites each in the burnt and unburnt areas, to sample spiders over a 12-month period. A total of 5 253 spiders were collected, representing 33 families and 120 species. Spider abundance was significantly lower in the burnt ( $n = 1\ 956$ ) than unburnt sites ( $n = 3\ 297$ ), and burnt sites had, on average, considerably fewer species than unburnt sites. The dominant families in the burnt sites were Lycosidae (29.5%), Gnaphosidae (16.9%), Ammoxenidae (9.6%) and Zodariidae (5.7%), whereas Ammoxenidae (22.7%), Lycosidae (20.6%), Gnaphosidae (15.3%) and Amaurobiidae (10.2%) dominated the unburnt sites. Of the nine most abundant families collected, only Caponiidae were more abundant in the burnt than unburnt sites. Our data suggest that fast-burning hot spring fires cause a considerable initial post-fire decline in spider abundance, and have a negative influence on the abundance as well as the resistance of assemblages to disturbances other than fire (e.g. rain). However, most of the dominant families had abundances comparable to unburnt areas within a year post-burn.

**Keywords:** abundance, Free State, management, resistance, season, species richness

## Introduction

Fires, both naturally and anthropogenically initiated, are widely viewed as important ecological disturbance events (Hartley et al. 2007). They play a critical role in removing dead plant biomass from terrestrial ecosystems (Blair 1997) and restricting the expansion of woody vegetation into grassland ecosystems (Ford and McPherson 1996; White et al. 2006; Hartley et al. 2007). Fire is widely used as a management tool to improve grazing quality and to stimulate fresh plant growth (Barratt et al. 2006, 2009).

Fire-prone grassland and savanna ecosystems in southern Africa are often managed through a prescribed burning system based on a diverse fire regime that comprises three basic elements (Govender et al. 2006; Smith et al. 2013): frequency, season and intensity, which largely determine the effects on the biota (Mucina and Rutherford 2006). Furthermore, fires affect the net primary productivity of plants and their vegetative cover (Blair 1997; Carbutt et al. 2011), soil nutrient composition and susceptibility to soil erosion (White et al. 2006). Effects on plants depend on the amount, vertical level and rate at which heat energy is released (Trollope et al. 2002), which varies between habitats of different vegetation structure

and composition (e.g. Smit et al. 2010; Levick et al. 2012), influencing other organisms directly.

Conservation biologists are increasingly recognising the importance of invertebrates in the functioning of healthy ecosystems, particularly since they are the largest component of terrestrial biodiversity (Zhang 2011). It is therefore critical to consider the effects that different disturbances may have on them (Gerlach et al. 2013). Even though some invertebrates have adaptations to fire by, for example, being able to flee or seek refuge (Uys et al. 2006; Pryke and Samways 2012), there may be considerable short-term (Hartley et al. 2007) and long-term (Nekola 2002; Lubin and Crouch 2003; Elia et al. 2012) local declines of invertebrate species. Notably, the season of fires may significantly affect some macroarthropods (Ford 2007; Johnson et al. 2008), but has little effect on microarthropods such as mites and springtails (Barratt et al. 2006; Hugo-Coetzee and Avenant 2011).

As predatory arthropods, spiders are not directly dependent on the vegetation as a food source, but assemblage composition can vary due to changes in vegetation structure during succession. For example, Podgaiski

et al. (2013) found an initial post-fire increase in hunting spiders and a decrease in web-builders due to the low vegetation density, but six months later orb-web spiders increased and hunters decreased due to increases in vegetation density.

Little is known of the influence of ecological factors on spider assemblages in South African grasslands, including fire (Haddad et al. 2013). Two species of the social spider genus *Stegodyphus* Simon, 1873 (Eresidae) showed contrasting responses to fire in grassland due to differences in their spatial distribution, ecology and life history (Lubin and Crouch 2003), whereas fire frequency and grazing intensity had no significant effects on spider abundance, species richness and assemblage structure in moist Mpumalanga grasslands (Jansen et al. 2013).

In September 2005, a project was initiated in the semi-arid grasslands of the Free State province in central South Africa to determine the impact of a fast hot spring fire on various faunal groups, including spiders, mites, insects and small mammals. Taking a multiple taxon approach to assess fire effects is critical, as different groups show contrasting responses and a variety of taxa can better indicate overall responses of compositional biodiversity than single taxa (Pryke and Samways 2012). The focus of the current study was to assess the effects on the ground-dwelling spider communities in the reserve; data on mites (Hugo-Coetzee and Avenant 2011) and small mammals (Avenant and Schulze 2012) have been dealt with separately.

This study aimed to investigate the response of spiders to fire in a grassland, and we hypothesised that (1) widespread mortality as a consequence of fire will result in lower spider abundance and species richness in burnt sites, (2) differences in vegetation density and structure at the ground level post-burn will result in clear differences in spider assemblages of burnt and unburnt areas, (3) burning affects rare species more than common species, and (4) seasonality plays a significant role in spider diversity. The biodiversity data generated in this study contributes to the South African National Survey of Arachnida in the Grassland Biome (Dippenaar-Schoeman et al. 2013; Haddad et al. 2013).

## Materials and methods

### Study area and period

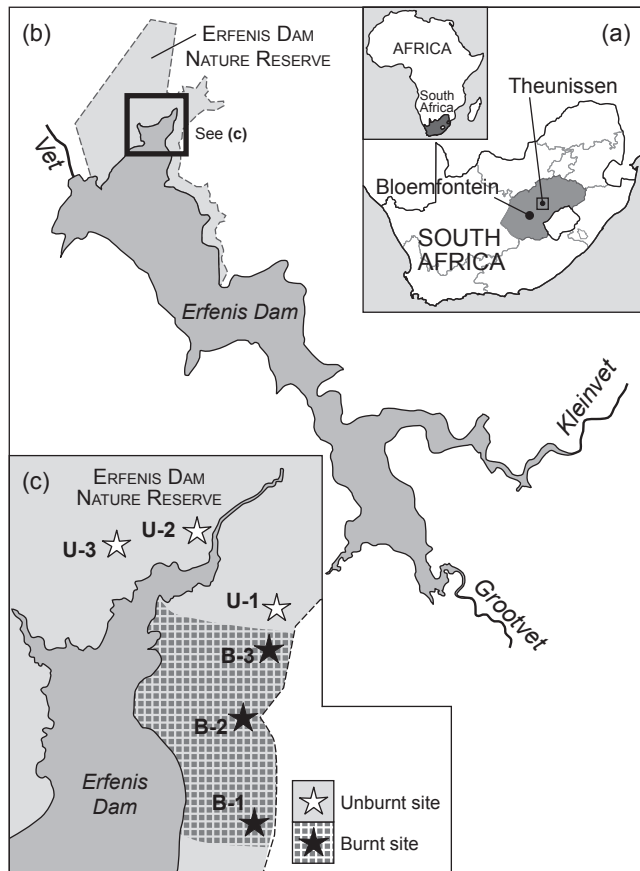
The Erfenis Dam Nature Reserve (EDNR) is located in the central part of the Free State province, approximately 13 km south-east of Theunissen. The dam is located at the confluence of the Kleinvet and Grootvet rivers, which form the Vet River downstream from the dam wall. The reserve extends approximately 4 000 ha, of which 3 300 ha comprises the dam (Hugo-Coetzee and Avenant 2011), and the remainder grassland on the north-western shores of the dam (Figures 1a and b).

Pitfall traps were initially set out the day following a prescribed fire on 28 September 2005 that formed part of EDNR's conservation management policy. The fire took place early in spring when there was a considerable load of dry grass following winter, a moderate wind of approximately 15 km h<sup>-1</sup> and ambient temperatures above 30 °C. As such, it could be considered as a fast, hot fire

that burnt an area of approximately 80 ha (Hugo-Coetzee and Avenant 2011).

Two clear shortcomings were identified prior to this study. First, the burn did not take place within a defined burning plot, as has been the case in studies comparing different fire regimes in savanna, for example Parr et al. (2004) and Reynolds (2014), and thus the extent of the burn was not predetermined. Consequently, the collecting sites within and beyond the burn area could not be identified prior to the burn having occurred. Second, as a consequence, no pre-fire samples could be taken to provide a pre-burn control within the burnt and unburnt grassland, nor could differences in soil types and plant species composition be identified prior to the burning having occurred, and compensated for in site selections. Thus, the data generated here were all post-burn comparisons.

The traps were set out at six different sites in the reserve, with three of the sites located in the burnt (B) area and the other three sites in the unburnt (U) area (Figure 1c). Sites are referred to hereafter by their codes. Sites B-1 and B-3 were located 50 m from the southern and northern burn margins, respectively, and all three burnt sites were set approximately 50 m from the eastern burn margin to avoid



**Figure 1:** Location of the study area. (a) Theunissen district in the central Free State province, South Africa. (b) Erfenis Dam Nature Reserve (shaded area) on the north-western side of the Erfenis Dam. (c) Part of the reserve with three study sites in the burnt grassland (B), indicated by horizontal stripes, and three sites in the unburnt grassland (U)

edge effects. Site U-1 was placed 50 m north of the eastern burn margin, whereas U-2 and U-3 were located on the opposite side of the dam (Figure 1c).

The soils at the six sites could be grouped into two main types: the burnt sites were composed of dark vertic clay-loamy soils, with a relatively high content of loam. In contrast, the unburnt sites were of the vertic clay-sandy type, with a relatively high sand content (Appendix 1). Sites B-1, B-3 and U-3 had considerable amounts of loose gravel on the surface, whereas only site U-3 had patches of loose sand on the soil surface.

The dominant grasses at most of the sites (plant classification follows Germishuizen et al. 2006) included *Eragrostis* spp., *Aristida congesta* Roem. & Schult., *Cymbopogon pospischilii* (K.Schum.) C.E.Hubb., *Enneapogon cenchroides* (Roem. & Schult.) C.E.Hubb., *Setaria pumila* (Poir.) Roem. & Schult., *Sporobolus fimbriatus* (Trin.) Nees and *Tragus berteronianus* Schult. At sites B-1, U-1 and U-2 there was also considerable coverage of red grass, *Themeda triandra* Forssk., which was largely absent from the other three sites. There was a general absence of woody plants in the sampled grasslands, with a single *Ziziphus mucronata* Willd. tree approximately 15 m from the pitfall grids at sites U-1 and U-3, and a single *Searsia lancea* (L.f.) F.A.Barkley tree approximately 30m from the U-3 pitfall grid. It is unlikely that these trees would have had an influence on the ground-dwelling spider assemblages at these sites.

Traps were emptied every 30 d to ensure consistency in the monthly sampling effort. During February 2006, six pitfalls were lost at site B-2 due to heavy rainfall, which filled them with silt, making it impossible to locate them. These lost pitfalls were immediately replaced. Rainfall records were provided by the management of the EDNR.

### Sampling methods

Ten pitfall traps (diameter 8 cm) were set out at each of the six sites, arranged in a 5 × 2 grid with 5 m separating each trap. The traps were buried flush with the soil surface and 100 ml of ethanediol was added monthly as a preservative. The collected samples were sieved through a fine sieve and preserved in 70% ethanol. In the laboratory, spiders were sorted from the remaining material and preserved in fresh 70% ethanol, after which they were identified to family level and morphospecies, and tallied.

All of the material collected during the study has been deposited in the National Collection of Arachnida at the Agricultural Research Council-Plant Protection Research Institute in Pretoria (NCA) and the National Museum in Bloemfontein (NMBA).

### Statistics

We assumed that it is possible to estimate richness of samples taken in a systematic way, being restricted to areas of reasonably homogenous habitat (Magurran 2004). Sample completeness was measured as sample coverage; this is the fraction of the total number of individuals in the community represented by the species in a sample (Chao and Jost 2012). Unique species, rarefied and estimated species richness (Chao 2) was calculated for each site with the vegan package in R (Oksanen et al. 2007).

Generalised linear mixed models and the bias-corrected Akaike information criterion with Poisson error structures were used to assess the extent to which spider abundance and species density were related to fire and seasonality. Season and burnt vs unburnt were coded as binary variables. Numeric predictors were centred around their mean and standardised to allow for the interpretation of coefficients (Schielzeth 2010). Soil variables were tested for collinearity with Pearson product moment correlations. When two variables were significantly correlated with coefficients larger than 0.5, the one that was considered biologically significant was retained. Soil characteristics were included as random effects to account for variation explained by differences in soil characteristics of sites. Modelling was done using the lme4 package in R (Bates et al. 2013) that includes maximum likelihood estimation. Variation explained by fixed effects season and burning as well as their interaction ( $R^2_m$ ) and variation due to fixed and random effects ( $R^2_c$ ) were calculated (Nakagawa and Schielzeth 2013).

The role of burning, time (months) and soil in explaining spider assemblage structure was done through redundancy analysis using the vegan package in R (Oksanen et al. 2007). Variables that explained significant amounts of variation were identified through forward selection in 'packfor' and then used in variation partitioning that identifies the contribution of soil, burning and time (month) in explaining spider assemblage structure.

Repeated-measures analysis of variance (ANOVA) was used to test for differences in the monthly abundance of the nine most abundant spider families between the burnt and unburnt sites. The treatment term in the repeated-measures ANOVA was burnt vs unburnt and the error term was treatment within family, partialling out the family variability. If burning had a significant effect, Tukey HSD will not run on this model, and we used a pair-wise *t*-test with adjusted *p*-values (Holm-Bonferroni method) to determine the families for which burning had a significant effect. A significance level of 0.05 was applied. The analyses were carried out in R 3.1.0 using the stats package (R Development Core Team 2014).

## Results

### Abundance and richness patterns

During the 12-month period a total of 5 253 spiders were collected, representing 33 families and 120 species (Appendix 2). Twenty of these species are new to science, of which five have been described recently. Total spider abundance and species richness was higher in the three unburnt sites ( $n = 3\ 297$ , 117 spp.) than the burnt sites ( $n = 1\ 956$ , 101 spp.).

Sample coverage for the entire study was very similar for all sites (0.88–0.90). This suggests that observed richness can be used when comparing species densities between sites. Chao 2 estimates of species richness were lower for the burnt sites (80–104 spp.) than most of the unburnt sites (102–111 spp.). Sites B-2 and B-3 also had the lowest number of unique species (Table 1).

In the unburnt grassland, Ammoxenidae ( $n = 747$ , 22.7%), Lycosidae ( $n = 679$ , 20.6%), Gnaphosidae ( $n = 505$ , 15.3%) and Amaurobiidae ( $n = 336$ , 10.2%) were the most

abundant families, while the burnt grassland sites were dominated by Lycosidae ( $n = 577$ , 29.5%), Gnaphosidae ( $n = 331$ , 16.9%), Ammoxenidae ( $n = 187$ , 9.6%) and Zodariidae ( $n = 111$ , 5.7%). Of the 33 families collected, 24 were more abundant in the unburnt area than in the burnt area. Furthermore, all 33 families were collected in the unburnt grasslands, whereas seven families were absent from the burnt sites (Appendix 2).

Unburnt sites generally had more spiders than burnt

**Table 1:** Total number of species observed, sample coverage, Chao 2 estimator of species richness and number of unique species of ground-dwelling spiders captured by pitfall trapping from three burnt (B) and three unburnt (U) sites in the Erfenis Dam Nature Reserve, Free State province, from October 2005 to September 2006

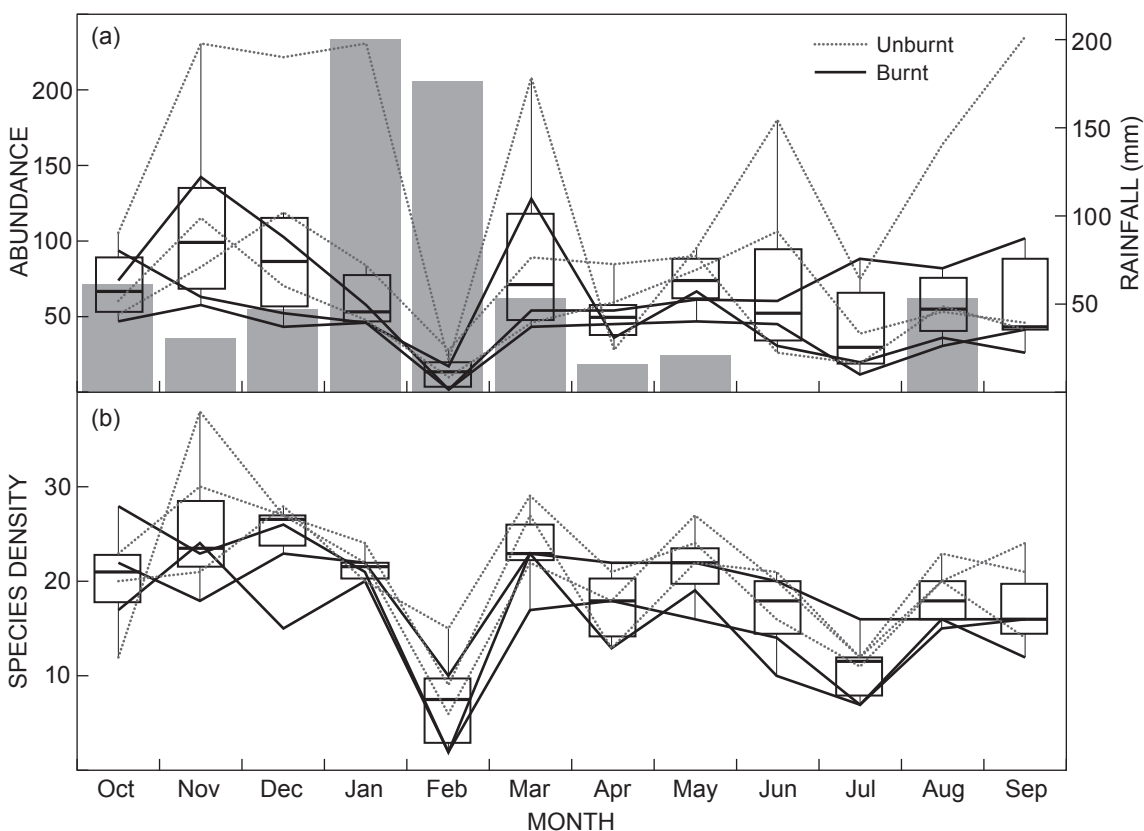
| Site          | Total species | Coverage | Chao 2 | Unique species |
|---------------|---------------|----------|--------|----------------|
| B-1           | 81            | 0.89     | 104    | 3              |
| B-2           | 71            | 0.88     | 85     | 0              |
| B-3           | 66            | 0.90     | 80     | 1              |
| U-1           | 79            | 0.89     | 102    | 3              |
| U-2           | 85            | 0.89     | 108    | 6              |
| U-3           | 85            | 0.89     | 111    | 6              |
| Total species | 120           | –        | –      | 19             |

sites (Figure 2), and U-3 consistently had more spiders than the other unburnt sites. Overall, burning did not have a significant impact on spider abundance in the final model (Table 2), but did interact with month to affect abundance. This interaction was evident in the months soon after the fire (November, December and January), but was still significant over the last two months of the study (Table 2). Spider abundance was also strongly linked to the month in which trapping was done (Figure 2). Although making a small contribution to conditional  $R^2$  of the abundance model (Table 2), soil characteristics did affect spider abundance observed and covaried positively with percentage sand and potassium (K) in the soil.

Most of the variation in species density was explained by month and the interaction between time and the treatment (burnt vs unburnt) (Table 2). This is mainly the result of the large drop in species richness observed during the month of February and its significantly larger impact on the burnt sites.

### Assemblage structure

Spider assemblage structure was largely explained by variation in assemblages over time (months), whereas soil and the burning treatment explained very little variation (Table 3). Partitioning the variation suggested that 31.6% was due to temporal variation, whereas 11.4% could be explained by soil characteristics, more specifically



**Figure 2:** Seasonal abundance (a) and species density (b) of spiders captured by pitfall trapping from three burnt and three unburnt sites in the Erfenis Dam Nature Reserve, Free State province, from October 2005 to September 2006. Grey blocks indicate monthly rainfall; white blocks are boxplots indicating the 25th (bottom) and 75th (top) percentiles and the median (horizontal line) for each month. Line plots detail trends in abundance (a) and species density (b) in each of the six replicates – three unburnt (dashed lines) and three burnt (bold solid lines)

**Table 2:** Summary of generalised linear mixed models linking spider species density and abundance to time (month) and burning.  $R^2_m$  (marginal) explained by fixed effects only,  $R^2_c$  (conditional) explained by fixed and random effects

| Response        | Model   | $R^2_m$ | $R^2_c$ |
|-----------------|---|---------|---------|
| Species density | ~February*** + July* + February:Unburnt*<br>Model equation: $Y = e^{2.9 - 1.3 \times \text{February} - 0.6 \times \text{July} + 0.8 \times \text{February:Unburnt}}$  | 0.735   | 0.74    |
| Abundance       | October*** + November*** + December*** + February*** + March*** + May* + December:Unburnt***<br>+ January:Unburnt*** + February:Unburnt** + June:Unburnt*** + August: Unburnt* +<br>September:Unburnt**<br>Model equation: $Y = e^{3.8 + 0.5 \times \text{October} + 0.7 \times \text{November} + 0.4 \times \text{December} - 1.9 \times \text{February} + 0.5 \times \text{March} + 0.3 \times \text{May} + 0.5 \times \text{December:Unburnt} + 0.6 \times \text{January:Unburnt} + 0.8 \times \text{February:Unburnt} + 0.6 \times \text{June:Unburnt} + 0.4 \times \text{August:Unburnt} + 0.4 \times \text{September:Unburnt}}$ | 0.63    | 0.77    |

\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

**Table 3:** Forward selected environmental variables (soil, time [month] and burn treatment) and their adjusted  $R^2$  values in a redundancy analysis that explained significant amounts of the variation in spider assemblage structure

| Factor  | No. | Environmental variable | Adj. $R^2$ cum. | $F$ | $p$    |
|---------|-----|------------------------|-----------------|-----|--------|
| Soil    | 1   | CEC                    | 0.04            | 4.3 | 0.0001 |
|         | 2   | Ca.Mg                  | 0.06            | 2.4 | 0.0021 |
|         | 3   | P                      | 0.08            | 2.3 | 0.0019 |
|         | 4   | Sand                   | 0.08            | 1.7 | 0.0267 |
| Time    | 1   | June                   | 0.08            | 7.1 | 0.0001 |
|         | 2   | May                    | 0.12            | 3.9 | 0.0001 |
|         | 3   | February               | 0.15            | 3.7 | 0.0001 |
|         | 4   | July                   | 0.17            | 3   | 0.0002 |
|         | 5   | April                  | 0.19            | 2.5 | 0.0002 |
|         | 6   | September              | 0.21            | 2.6 | 0.0007 |
|         | 7   | August                 | 0.24            | 3   | 0.0003 |
|         | 8   | March                  | 0.26            | 2.8 | 0.0006 |
|         | 9   | October                | 0.27            | 1.9 | 0.0146 |
|         | 10  | November               | 0.28            | 1.6 | 0.0388 |
| Burning | 1   | Unburnt                | 0.015           | 2.1 | 0.006  |

cation exchange capacity (CEC), calcium, magnesium, phosphorus and sand content. Whereas the effect of burning only accounted for 1.2% (Figure 3), 1% is the result of the soil characteristics associated with the burnt and unburnt sites, respectively.

### Spider phenology

Heavy rainfall during January and February 2006 caused considerable declines in spider abundance at most sites. During March there was a return to high abundances, but a week of very cold weather during April again caused a depression in spider abundance at two of the sites. Throughout the winter months spider abundance remained relatively constant for all of the sites except U-3, where there were regular fluctuations between months (Figure 2).

An assessment of the phenologies of the nine most abundant families (Figure 4) showed that during the year following the burn the activity densities of most spider families was lower in the burnt sites, with the exception of Caponiidae and, on occasion, Lycosidae and Zodariidae, however this was not statistically significant (repeated-measures ANOVA,  $F_{1,7} = 4.025$ ,  $P = 0.08$ ). Pair-wise comparisons with adjusted  $P$ -values did, however, suggest that there were moderate negative effects of fire on

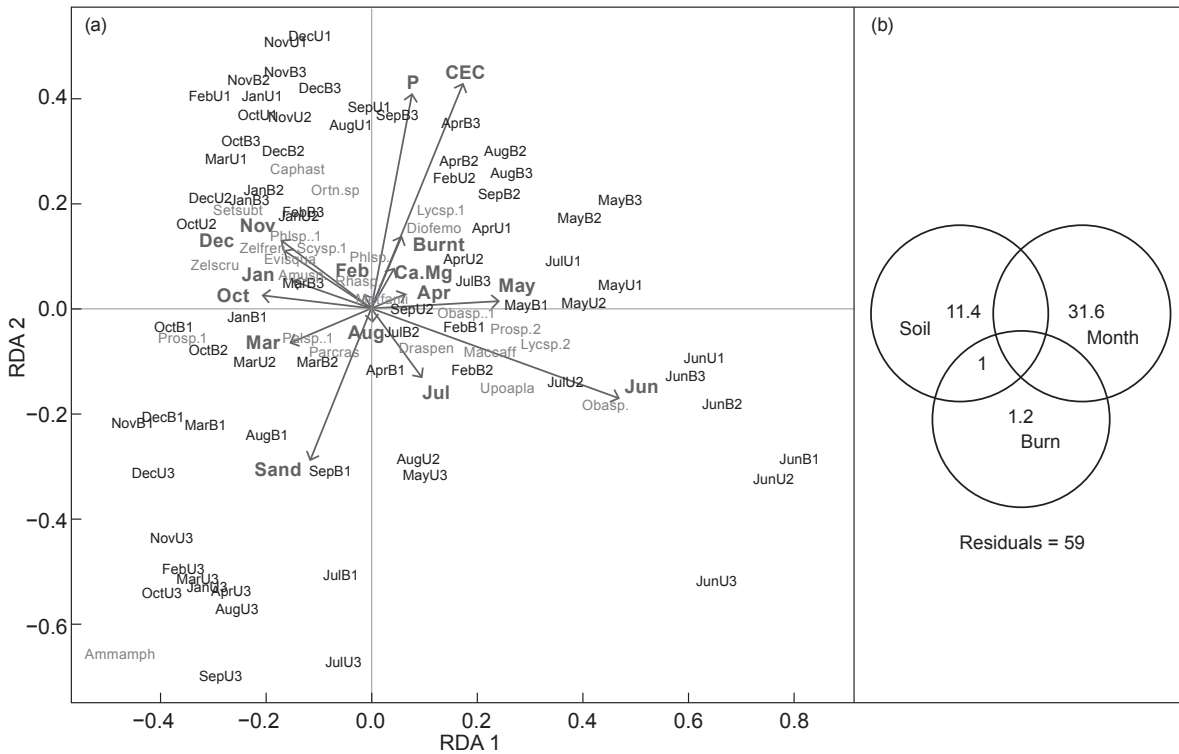
Amoxenidae ( $P = 0.046$ ) and Linyphiidae ( $P = 0.04$ ) abundance, and very strong effects on Corinnidae ( $P = 0.0083$ ) and Gnaphosidae ( $P = 0.0087$ ). While most of the families showed a reduction in spider abundance during winter, the abundance of Lycosidae remained relatively stable during the colder months. Two families clearly show greater abundance levels during autumn and winter, viz. Amaurobiidae and Linyphiidae (Figure 4).

### Discussion

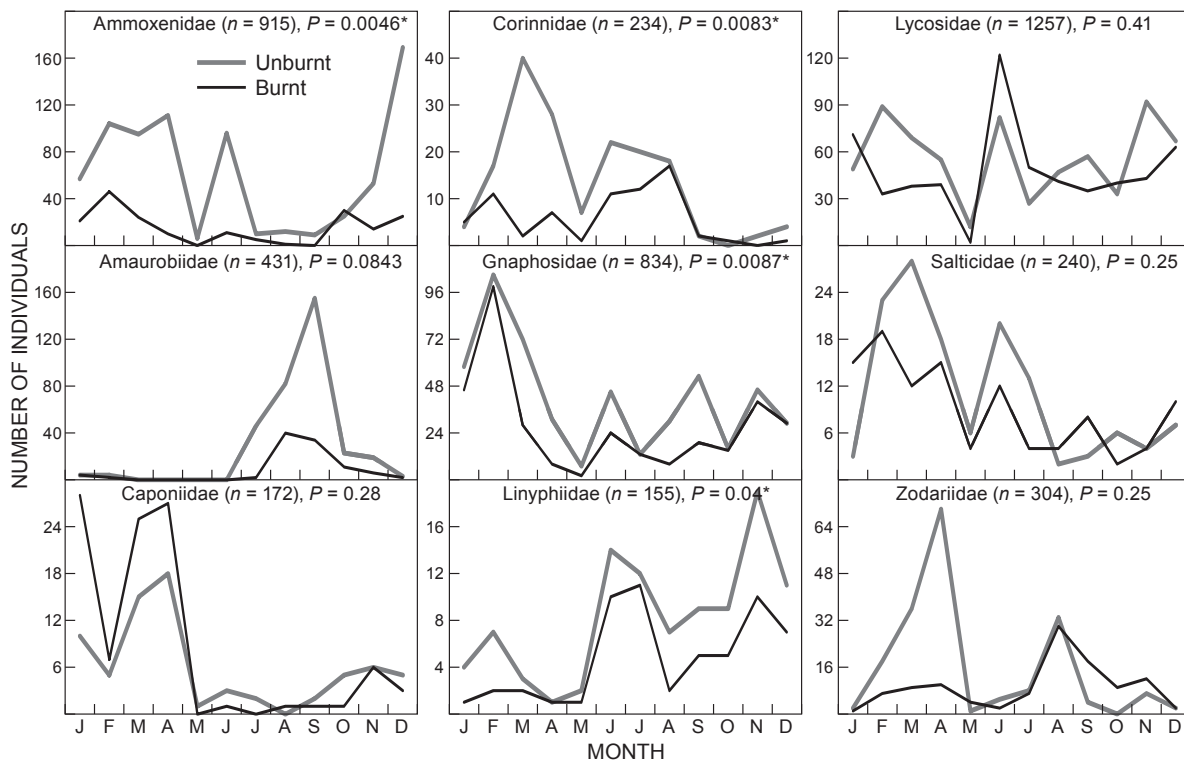
Fires play a critical role in the ecology of terrestrial ecosystems, yet their effects on the invertebrate fauna of South Africa, particularly spiders, remains poorly studied. Pryke and Samways (2012) suggested that fires in grasslands require arthropods to recolonise or re-emerge over a much larger spatial scale, as most of the above-ground biomass is removed. We found that, although fire interacts with time to affect spider abundance and richness, there was little evidence to suggest that this fire had a significant large-scale impact on spider diversity. Other South African studies have come to the same conclusions (Jansen et al. 2013; Reynolds 2014).

The present study showed that both species richness and abundance of spiders in semi-arid grasslands of central South Africa were negatively affected by fire, and that contrasting assemblages occurred in burnt and unburnt grasslands. Furthermore, although the three dominant families from the two treatments were the same (Amoxenidae, Lycosidae and Gnaphosidae), the relative abundance of each differed considerably between treatments.

Malumbres-Olarte et al. (2014) found that recolonisation of New Zealand tussock grasslands by spiders following fire was facilitated by two strategies: smaller spiders (e.g. linyphiids) colonised rapidly because of their ability to disperse by ballooning, although effects differed between spring and summer, whereas larger spiders could colonise burnt areas because they could travel longer distances on the ground. For at least the first five months post-burn all of the nine most abundant families, excluding Caponiidae, showed lower abundances in the burnt sites, but later in the study the abundance of several groups was comparable between the treatments (Figure 4). In the case of winter-active Amaurobiidae and Linyphiidae, both families of small web-building spiders, fire had a prolonged effect on these groups until the end of the 12-month study. Our data



**Figure 3:** (a) Triplot of redundancy analysis (RDA) and (b) variation partitioning of ground-dwelling spider assemblages captured by pitfall trapping from three burnt (B) and three unburnt (U) sites in the Erfenis Dam Nature Reserve, Free State province, from October 2005 to September 2006. In (a) arrows represent environmental and temporal variables that explained significant amounts of variation in spider assemblage structure and the length of the arrow represents their influence; sample units are in black and species are in grey



**Figure 4:** Phenology of the nine most abundant spider families collected by pitfall trapping in the Erfenis Dam Nature Reserve, Free State province, from October 2005 to September 2006 in burnt (black lines) and unburnt (grey lines) grasslands (pooled data of three sites each). Significance values for pair-wise *t*-test with Holm–Bonferroni adjusted *p*-values of spider abundance are indicated for each family, with significantly different values indicated with an asterisk

suggests that some spider groups that colonise the burnt areas in spring are able to build up populations that reach similar densities to those in unburnt areas within a few months. This rapid colonisation could be partly attributed to the relative proximity of the sampling sites to the burn edge (~50 m), which would have allowed spiders to colonise by walking on the ground or ballooning. Uys et al. (2006) found that in sites close to the burn edge, changes in invertebrate communities were evident within two weeks, and that species richness, abundance and homogeneity recovered after 12 weeks. Had sites been placed towards the centre of the burn area in this study (Figure 1c), spider populations would likely have taken considerably longer to recover.

An important factor in post-fire faunal recovery is whether species are fire tolerant or not, i.e. are able to exploit microrefugia to escape fires. While insects can escape fires through flight, non-flying arthropods are dependent on other strategies to survive, including exploiting microrefugia such as bush clumps, rocks and marshy areas (Uys et al. 2006; Pryke and Samways 2012), burrows (Dippenaar-Schoeman 2002) or moving beneath the soil surface (Villani et al. 1999). Temperatures in the soil stay relatively low, even when there is a fire, enabling survival of soil invertebrates (Tainton and Mentis 1984). In the current study, the observed fire impacts could largely be attributed to the complete destruction of the above-ground vegetation and lack of rocks in the burnt area, removing the possibility for such escape. Therefore, most of the spiders collected during the first month post-fire must have sought refuge in cracks in the soil, a common characteristic of vertic clays (Bredenkamp et al. 2002; Fey 2010; Liu et al. 2010) displayed in the study area, or in self-constructed burrows. Based on our data, families such as Amaurobiidae, Caponiidae, Lycosidae, Salticidae and Zodariidae may be considered fire-resilient in grasslands, whereas Ammoxenidae, Corinnidae, Gnaphosidae and Linyphiidae are significantly reduced due to fire effects.

Pitfall trapping has limited value in providing absolute estimates of spider abundance, as the capture efficiency is affected by factors including abundance and activity of individual species (Topping and Sunderland 1992; Holland and Smith 1999), vegetation density (Melbourne 1999), trap size (Work et al. 2002) and trampling by large mammals (Oxbrough et al. 2006). Consequently, some taxa can be overestimated while other taxa can be underestimated (Lang 2000). However, they remain the most practical sampling method to acquire suitable data on the species richness of ground-dwelling invertebrates (Uetz and Unzicker 1976; Sabu and Shiju 2010), including grasslands.

Future use of fire management in grasslands requires a more thorough investigation into the effects of season (and by implication, fire intensity) and fire frequencies on faunal assemblages, to ascertain fire regimes that can minimise impacts on the ground-dwelling fauna, while optimising grassland biodiversity and vegetation management.

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**Appendix 1:** Chemical and physical characteristics of soil samples taken by an auger from each of the three burnt (B) and three unburnt (U) sites in Erfenis Dam Nature Reserve, Free State province. Values in parentheses indicate percent cation proportion in each sample. Abbreviations: AS = acid saturation, CEC = cation exchange capacity, EA = exchangeable acidity

| Variable/site                             | B-1        | B-2        | B-3        | U-1        | U-2        | U-3        |
|---|------------|------------|------------|------------|------------|------------|
| pH (KCl)                                  | 5.8        | 5.4        | 5.4        | 5.6        | 5.4        | 5.3        |
| P (mg kg <sup>-1</sup> )                  | 3.9        | 3          | 4.8        | 5.2        | 1.3        | 1.3        |
| K (mg kg <sup>-1</sup> )                  | 277.1 (4)  | 305.6 (4)  | 351.2 (5)  | 169.5 (3)  | 244.6 (4)  | 194.2 (7)  |
| Ca (mg kg <sup>-1</sup> )                 | 2 441 (75) | 2 328 (67) | 2 461 (67) | 1 478 (57) | 1 876 (61) | 686 (47)   |
| Mg  | 411.6 (21) | 616.6 (29) | 632.1 (28) | 600.7 (38) | 641.4 (34) | 398.3 (45) |
| Na (mg kg <sup>-1</sup> )                 | 6.1 (0)    | 4.7 (0)    | 5.6 (0)    | 46.5 (2)   | 6.5 (0)    | 10.7 (1)   |
| EA  | 0          | 0          | 0          | 0          | 0          | 0          |
| AS (%)                                    | 0          | 0          | 0          | 0          | 0          | 0          |
| Ca/Mg                                     | 3.62       | 2.3        | 2.37       | 1.5        | 1.78       | 1.05       |
| (Ca+Mg)/K                                 | 21.98      | 21.36      | 19.47      | 28.4       | 23.4       | 13.48      |
| CEC (cmol <sub>c</sub> kg <sup>-1</sup> ) | 16.31      | 17.49      | 18.41      | 12.95      | 15.29      | 7.24       |
| Sand (%)                                  | 28         | 21         | 28         | 43         | 44         | 53         |
| Clay (%)                                  | 18         | 18         | 22         | 20         | 16         | 14         |
| Loam (%)                                  | 54         | 61         | 50         | 37         | 40         | 33         |

**Appendix 2:** Species diversity and abundance of spiders collected from six sites (three burnt [B] and three unburnt [U] sites) in Erfenis Dam Nature Reserve (EDNR) in the Free State province from October 2005 until September 2006. Symbols: † = new species, ‡ = species for which EDNR is the type locality, ? = dubious identification

| Family/species  | B-1 | B-2 | B-3 | U-1 | U-2 | U-3 | Total | % of total |
|---|-----|-----|-----|-----|-----|-----|-------|------------|
| <b>AGELENIDAE</b>   |     |     |     |     |     |     |       |            |
| <i>Benoitia ocellata</i> (Pocock, 1900)                       | 0   | 0   | 0   | 0   | 0   | 1   | 1     | 0.02       |
| <b>AMAUROBIIDAE</b>   |     |     |     |     |     |     |       |            |
| <i>Macrobnus caffer</i> (Simon, 1898)?                        | 16  | 14  | 3   | 1   | 26  | 18  | 78    | 1.48       |
| <i>Obatala</i> sp. 1†   | 28  | 4   | 5   | 48  | 73  | 96  | 254   | 4.84       |
| <i>Obatala</i> sp. 2†   | 11  | 1   | 5   | 5   | 28  | 7   | 57    | 1.09       |
| <i>Pseudauximus</i> sp. 1†                                    | 3   | 3   | 8   | 12  | 15  | 9   | 48    | 0.91       |
| <b>AMMOXENIDAE</b>  |     |     |     |     |     |     |       |            |
| <i>Ammoxenus amphalodes</i> Dippenaar & Meyer, 1980           | 172 | 14  | 1   | 2   | 8   | 737 | 934   | 17.78      |
| <b>ARANEIDAE</b>  |     |     |     |     |     |     |       |            |
| <i>Hypsosinga lithyphantoides</i> Caporiacco, 1947            | 1   | 0   | 0   | 0   | 1   | 0   | 2     | 0.04       |
| <i>Kilima decens</i> (Blackwall, 1866)                        | 2   | 2   | 4   | 4   | 4   | 1   | 17    | 0.32       |
| <i>Neoscona moreli</i> (Vinson, 1863)                         | 0   | 1   | 0   | 2   | 0   | 0   | 3     | 0.06       |
| <i>Pararaneus cyrtoscapus</i> (Pocock, 1898)?                 | 0   | 1   | 3   | 1   | 0   | 0   | 5     | 0.10       |
| <b>ATYPIDAE</b>   |     |     |     |     |     |     |       |            |
| <i>Calommata meridionalis</i> Fourie, Haddad & Jocqué, 2011†‡ | 1   | 5   | 0   | 1   | 0   | 1   | 8     | 0.15       |
| <b>CAPONIIDAE</b>   |     |     |     |     |     |     |       |            |
| <i>Caponia hastifera</i> Purcell, 1904                        | 32  | 31  | 37  | 61  | 3   | 8   | 172   | 3.27       |
| <b>CORINNIDAE</b>   |     |     |     |     |     |     |       |            |
| <i>Cambalida fulvipes</i> (Simon, 1896)                       | 1   | 0   | 0   | 3   | 1   | 0   | 5     | 0.10       |
| <i>Graptartia mutillica</i> Haddad, 2004                      | 5   | 1   | 7   | 2   | 7   | 4   | 26    | 0.49       |
| <i>Orthobula</i> sp. 1†                                       | 15  | 6   | 34  | 69  | 44  | 30  | 198   | 3.77       |
| <i>Pochelas striatus</i> Haddad & Lyle, 2008                  | 0   | 0   | 0   | 0   | 1   | 1   | 2     | 0.04       |
| <i>Thysanina absolvo</i> Lyle & Haddad, 2006                  | 1   | 0   | 0   | 0   | 1   | 1   | 3     | 0.06       |
| <b>CTENIDAE</b>   |     |     |     |     |     |     |       |            |
| <i>Anahita</i> sp. 1  | 1   | 3   | 2   | 1   | 3   | 1   | 11    | 0.21       |
| <b>CTENIZIDAE</b>   |     |     |     |     |     |     |       |            |
| <i>Stasimopus oculus</i> Pocock, 1897                         | 4   | 2   | 6   | 3   | 0   | 3   | 18    | 0.34       |
| <i>Stasimopus</i> sp. 2                                       | 5   | 1   | 0   | 2   | 2   | 1   | 11    | 0.21       |
| <b>CYRTAUCHENIIDAE</b>  |     |     |     |     |     |     |       |            |
| <i>Ancylotrypa nigriceps</i> (Purcell, 1902)                  | 0   | 0   | 4   | 1   | 0   | 2   | 7     | 0.13       |
| <i>Ancylotrypa pretoriae</i> (Hewitt, 1913)                   | 2   | 0   | 2   | 10  | 1   | 13  | 28    | 0.53       |
| <i>Ancylotrypa</i> sp. 3                                      | 0   | 0   | 3   | 2   | 5   | 5   | 15    | 0.29       |
| <b>ERESIDAE</b>   |     |     |     |     |     |     |       |            |
| <i>Dresserus kannemeyeri</i> Tucker, 1920                     | 0   | 2   | 0   | 0   | 2   | 1   | 5     | 0.10       |
| <b>GNAPHOSIDAE</b>  |     |     |     |     |     |     |       |            |
| <i>Amusia</i> sp. 1   | 19  | 12  | 14  | 11  | 28  | 16  | 100   | 1.90       |
| <i>Camillina cordifera</i> (Tullgren, 1910)                   | 0   | 2   | 1   | 0   | 3   | 6   | 12    | 0.23       |
| <i>Drassodes splendens</i> Tucker, 1923                       | 17  | 3   | 17  | 5   | 6   | 21  | 69    | 1.31       |
| <i>Drassodes stationis</i> Tucker, 1923                       | 1   | 0   | 0   | 0   | 0   | 2   | 3     | 0.06       |
| <i>Echemus</i> sp. 1  | 4   | 1   | 0   | 4   | 1   | 2   | 12    | 0.23       |
| <i>Micaria</i> sp. 1  | 0   | 1   | 0   | 2   | 1   | 5   | 9     | 0.17       |
| <i>Pterotricha varia</i> (Tucker, 1923)                       | 1   | 0   | 0   | 0   | 1   | 3   | 5     | 0.10       |
| <i>Setaphis subtilis</i> (Simon, 1897)                        | 37  | 22  | 33  | 48  | 24  | 33  | 197   | 3.75       |
| <i>Trachyzelotes</i> sp. 1                                    | 0   | 0   | 0   | 1   | 0   | 0   | 1     | 0.02       |
| <i>Trephopoda</i> sp. 1                                       | 1   | 0   | 0   | 2   | 0   | 1   | 4     | 0.08       |
| <i>Upognampa aplanita</i> Tucker, 1923                        | 5   | 1   | 8   | 2   | 12  | 28  | 56    | 1.07       |
| <i>Xerophaeus aridus</i> Purcell, 1907                        | 3   | 4   | 0   | 0   | 0   | 1   | 8     | 0.15       |
| <i>Zelotes frenchi</i> Tucker, 1923                           | 26  | 17  | 18  | 34  | 29  | 31  | 155   | 2.95       |
| <i>Zelotes fuliginus</i> (Purcell, 1907)                      | 0   | 1   | 0   | 2   | 3   | 4   | 10    | 0.19       |
| <i>Zelotes sclateri</i> Tucker, 1923                          | 1   | 0   | 1   | 2   | 0   | 0   | 4     | 0.08       |
| <i>Zelotes scrutatus</i> (O. P.-Cambridge, 1872)              | 22  | 4   | 6   | 32  | 44  | 31  | 139   | 2.65       |
| <i>Zelotes zonognathus</i> (Purcell, 1907)                    | 2   | 1   | 0   | 1   | 4   | 3   | 11    | 0.21       |
| <i>Zelotes</i> sp. 6  | 7   | 1   | 1   | 0   | 0   | 0   | 9     | 0.17       |
| <i>Zelotes</i> sp. 7  | 5   | 9   | 2   | 4   | 8   | 4   | 32    | 0.61       |
| <b>HAHNIIDAE</b>  |     |     |     |     |     |     |       |            |
| <i>Hahnia tabulicola</i> Simon, 1898                          | 0   | 0   | 0   | 0   | 1   | 0   | 1     | 0.02       |
| <b>HERSILIIDAE</b>  |     |     |     |     |     |     |       |            |
| <i>Tyrotama australis</i> (Simon, 1893)                       | 0   | 0   | 0   | 0   | 0   | 6   | 6     | 0.11       |
| <b>IDIOPIDAE</b>  |     |     |     |     |     |     |       |            |
| <i>Galeosoma</i> sp. 1  | 0   | 1   | 0   | 0   | 2   | 0   | 3     | 0.06       |

| Family/species   | B-1 | B-2 | B-3 | U-1 | U-2 | U-3 | Total | % of total |
|--|-----|-----|-----|-----|-----|-----|-------|------------|
| <i>Segregara monticola</i> Hewitt, 1916                  | 0   | 0   | 0   | 0   | 1   | 0   | 1     | 0.02       |
| LINYPHIIDAE  |     |     |     |     |     |     |       |            |
| <i>Meioneta habra</i> Lockett, 1968                      | 2   | 4   | 9   | 8   | 18  | 6   | 47    | 0.89       |
| <i>Meioneta</i> sp. 2                                    | 0   | 1   | 3   | 0   | 6   | 0   | 10    | 0.19       |
| <i>Metaleptyphantes familiaris</i> Jocqué, 1984          | 17  | 9   | 2   | 11  | 19  | 6   | 64    | 1.22       |
| <i>Ostearius melanopygius</i> (O. P.-Cambridge, 1879)    | 2   | 2   | 0   | 0   | 4   | 3   | 11    | 0.21       |
| <i>Pelecopsis janus</i> Jocqué, 1984                     | 2   | 1   | 0   | 2   | 8   | 1   | 14    | 0.27       |
| Linyphiidae sp. 1  | 0   | 2   | 1   | 1   | 2   | 1   | 7     | 0.13       |
| Linyphiidae sp. 2  | 0   | 0   | 0   | 0   | 1   | 0   | 1     | 0.02       |
| Linyphiidae sp. 3  | 0   | 0   | 0   | 0   | 1   | 0   | 1     | 0.02       |
| LIOCRANIDAE  |     |     |     |     |     |     |       |            |
| <i>Rhaeboctesis secundus</i> Tucker, 1920                | 0   | 11  | 3   | 15  | 6   | 3   | 38    | 0.72       |
| <i>Rhaeboctesis</i> sp. 2                                | 10  | 13  | 8   | 22  | 6   | 11  | 70    | 1.33       |
| LYCOSIDAE  |     |     |     |     |     |     |       |            |
| <i>Allocosa tuberculipalpa</i> (Caporiacco, 1940)        | 0   | 0   | 0   | 0   | 3   | 0   | 3     | 0.06       |
| <i>Amblyothele albocincta</i> Simon, 1910                | 0   | 2   | 0   | 2   | 3   | 4   | 11    | 0.21       |
| <i>Evippomma squamulatum</i> (Simon, 1898)               | 15  | 5   | 9   | 22  | 2   | 41  | 94    | 1.79       |
| Lycosinae sp. 1  | 62  | 65  | 32  | 26  | 11  | 6   | 202   | 3.85       |
| Lycosinae sp. 2  | 6   | 4   | 11  | 5   | 19  | 36  | 81    | 1.54       |
| Pardosinae sp. 1   | 3   | 0   | 0   | 0   | 2   | 3   | 8     | 0.15       |
| <i>Pardosa crassipalpis</i> Purcell, 1903                | 1   | 4   | 1   | 1   | 14  | 30  | 51    | 0.97       |
| <i>Proevippa</i> sp. 1†                                  | 0   | 0   | 1   | 1   | 0   | 0   | 2     | 0.04       |
| <i>Proevippa</i> sp. 2†                                  | 130 | 36  | 151 | 60  | 84  | 274 | 735   | 13.99      |
| <i>Proevippa</i> sp. 3†                                  | 9   | 18  | 5   | 4   | 9   | 10  | 55    | 1.05       |
| <i>Zenonina mystacina</i> Simon, 1898                    | 4   | 1   | 2   | 2   | 0   | 5   | 14    | 0.27       |
| MIMETIDAE  |     |     |     |     |     |     |       |            |
| <i>Ero</i> sp. 1   | 0   | 0   | 0   | 0   | 0   | 1   | 1     | 0.02       |
| MITURGIDAE   |     |     |     |     |     |     |       |            |
| <i>Cheiramiona florisbadensis</i> Lotz, 2003             | 11  | 8   | 4   | 0   | 1   | 0   | 24    | 0.46       |
| ORSOLOBIDAE  |     |     |     |     |     |     |       |            |
| <i>Afrilobus</i> sp. 1†                                  | 0   | 0   | 1   | 2   | 0   | 0   | 3     | 0.06       |
| <i>Azanielobus</i> sp. 1†                                | 8   | 0   | 9   | 10  | 1   | 13  | 41    | 0.78       |
| OXYOPIDAE  |     |     |     |     |     |     |       |            |
| <i>Oxyopes</i> sp. 1                                     | 0   | 0   | 0   | 0   | 0   | 1   | 1     | 0.02       |
| PALPIMANIDAE   |     |     |     |     |     |     |       |            |
| <i>Palpimanus</i> sp. 1                                  | 10  | 9   | 13  | 11  | 2   | 5   | 50    | 0.95       |
| PHILODROMIDAE  |     |     |     |     |     |     |       |            |
| <i>Suemus</i> sp. 1?                                     | 0   | 3   | 1   | 1   | 2   | 5   | 12    | 0.23       |
| <i>Suemus</i> sp. 2?                                     | 1   | 0   | 0   | 0   | 3   | 2   | 6     | 0.11       |
| <i>Thanatus vulgaris</i> Simon, 1870                     | 0   | 0   | 0   | 0   | 0   | 2   | 2     | 0.04       |
| <i>Tibellus minor</i> Lessert, 1919                      | 1   | 0   | 0   | 1   | 2   | 0   | 4     | 0.08       |
| PHYXELIDIDAE   |     |     |     |     |     |     |       |            |
| <i>Vidole sothoana</i> Griswold, 1990                    | 5   | 0   | 0   | 0   | 6   | 10  | 21    | 0.40       |
| PISAUROIDAE  |     |     |     |     |     |     |       |            |
| <i>Euprosthenops</i> sp. 1                               | 0   | 0   | 0   | 1   | 0   | 1   | 2     | 0.04       |
| PRODIDOMIDAE   |     |     |     |     |     |     |       |            |
| <i>Theuma capensis</i> Purcell, 1907                     | 1   | 0   | 0   | 0   | 1   | 0   | 2     | 0.04       |
| <i>Theuma fusca</i> Purcell, 1907                        | 2   | 3   | 2   | 0   | 5   | 1   | 13    | 0.25       |
| <i>Theuma schreineri</i> Purcell, 1907                   | 0   | 2   | 0   | 0   | 1   | 0   | 3     | 0.06       |
| SALTICIDAE   |     |     |     |     |     |     |       |            |
| <i>Evarcha vittula</i> Haddad & Wesolowska, 2011†‡       | 0   | 0   | 0   | 3   | 0   | 0   | 3     | 0.06       |
| <i>Langona hirsuta</i> Haddad & Wesolowska, 2011†‡       | 15  | 10  | 9   | 21  | 14  | 8   | 77    | 1.47       |
| <i>Nigorella hirsuta</i> Wesolowska, 2009                | 4   | 4   | 0   | 2   | 0   | 6   | 16    | 0.30       |
| <i>Pellenes bulawayoensis</i> Wesolowska, 1999           | 0   | 0   | 1   | 0   | 1   | 1   | 3     | 0.06       |
| <i>Pellenes geniculatus</i> (Simon, 1868)                | 1   | 0   | 1   | 0   | 0   | 2   | 4     | 0.08       |
| <i>Pellenes modicus</i> Wesolowska & Russell-Smith, 2000 | 1   | 0   | 0   | 1   | 0   | 2   | 4     | 0.08       |
| <i>Pellenes tharinae</i> Wesolowska, 2006                | 4   | 6   | 2   | 3   | 1   | 9   | 25    | 0.48       |
| <i>Phlegra bresnieri</i> (Lucas, 1846)                   | 5   | 5   | 1   | 15  | 2   | 0   | 28    | 0.53       |
| <i>Phlegra karoo</i> Wesolowska, 2006                    | 14  | 7   | 8   | 21  | 9   | 7   | 65    | 1.24       |
| <i>Pignus simoni</i> (Peckham & Peckham, 1903)           | 2   | 2   | 5   | 0   | 1   | 3   | 13    | 0.25       |
| <i>Tanzania meridionalis</i> Haddad & Wesolowska, 2011†‡ | 2   | 0   | 0   | 2   | 0   | 0   | 4     | 0.08       |
| SCYTODIDAE   |     |     |     |     |     |     |       |            |
| <i>Scytodes</i> sp. 1                                    | 7   | 3   | 8   | 19  | 11  | 8   | 56    | 1.07       |

| Family/species  | B-1 | B-2 | B-3 | U-1 | U-2 | U-3   | Total | % of total |
|---|-----|-----|-----|-----|-----|-------|-------|------------|
| THERIDIIDAE   |     |     |     |     |     |       |       |            |
| <i>Anelosimus</i> sp. 1   | 1   | 0   | 0   | 0   | 0   | 0     | 1     | 0.02       |
| <i>Coscinida</i> sp. 1  | 7   | 1   | 0   | 2   | 0   | 5     | 15    | 0.29       |
| <i>Enoplognatha molesta</i> O. P.-Cambridge, 1904?                  | 0   | 0   | 1   | 0   | 0   | 0     | 1     | 0.02       |
| <i>Enoplognatha</i> sp. 2   | 5   | 0   | 1   | 0   | 1   | 0     | 7     | 0.13       |
| <i>Euryopsis</i> sp. 1  | 2   | 6   | 3   | 9   | 4   | 5     | 29    | 0.55       |
| <i>Euryopsis</i> sp. 2  | 0   | 0   | 0   | 4   | 0   | 0     | 4     | 0.08       |
| <i>Steatoda capensis</i> Hann, 1990                                 | 1   | 1   | 4   | 0   | 0   | 1     | 7     | 0.13       |
| <i>Steatoda</i> sp. 2   | 3   | 5   | 2   | 8   | 7   | 2     | 27    | 0.51       |
| <i>Steatoda</i> sp. 3   | 0   | 0   | 0   | 0   | 2   | 0     | 2     | 0.04       |
| <i>Theridion</i> sp. 1  | 5   | 0   | 0   | 1   | 1   | 0     | 7     | 0.13       |
| Theridiidae sp. 1   | 1   | 0   | 0   | 0   | 0   | 0     | 1     | 0.02       |
| THERIDIOSOMATIDAE   |     |     |     |     |     |       |       |            |
| Theridiosomatidae sp. 1   | 0   | 0   | 0   | 8   | 3   | 0     | 11    | 0.21       |
| THOMISIDAE  |     |     |     |     |     |       |       |            |
| <i>Heriaeus allenjonesi</i> van Niekerk & Dippenaar-Schoeman, 2013† | 3   | 0   | 2   | 4   | 2   | 4     | 15    | 0.29       |
| <i>Monaeses quadrituberculatus</i> Lawrence, 1927                   | 1   | 1   | 0   | 0   | 2   | 0     | 4     | 0.08       |
| <i>Stiphropus affinis</i> Lessert, 1923                             | 0   | 1   | 0   | 4   | 1   | 0     | 6     | 0.11       |
| <i>Xysticus natalensis</i> Lawrence, 1938                           | 9   | 4   | 6   | 3   | 12  | 1     | 35    | 0.67       |
| <i>Xysticus urbensis</i> Lawrence, 1952                             | 10  | 1   | 11  | 4   | 1   | 0     | 27    | 0.51       |
| ZODARIIDAE  |     |     |     |     |     |       |       |            |
| <i>Akyttara</i> sp. †   | 0   | 0   | 0   | 0   | 0   | 1     | 1     | 0.02       |
| <i>Cydrela</i> sp. 1 †  | 3   | 10  | 6   | 2   | 0   | 2     | 23    | 0.44       |
| <i>Cydrela</i> sp. 2 †  | 2   | 2   | 6   | 2   | 12  | 3     | 27    | 0.51       |
| <i>Diores femoralis</i> Jocqué, 1990                                | 12  | 16  | 43  | 41  | 2   | 14    | 128   | 2.44       |
| <i>Diores poweri</i> Tucker, 1920                                   | 2   | 0   | 0   | 0   | 0   | 0     | 2     | 0.04       |
| <i>Diores</i> sp. 3 †   | 0   | 0   | 2   | 2   | 0   | 2     | 6     | 0.11       |
| <i>Palfuria</i> sp. 1 †   | 4   | 1   | 1   | 2   | 9   | 80    | 97    | 1.85       |
| <i>Ranops</i> sp. 1 †   | 1   | 0   | 0   | 1   | 2   | 9     | 13    | 0.25       |
| TOTAL   | 880 | 460 | 616 | 772 | 733 | 1 792 | 5 253 | 100        |