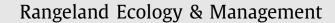
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# Responses of Ground-Dwelling Arthropods to Long-Term Prescribed Fire Regimes in a Savanna-Protected Area<sup>\*</sup>



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#### ABSTRACT

In savanna ecosystems, fire is common, yet little is known on the direct and long-term effects of prescribed burns on arthropod abundance, richness, diversity, and composition. To understand the impact of fire on arthropods at Kruger National Park (KNP), standardized pitfall traps and active searches were used to collect arthropods at unburnt, annually burnt, and triennially burnt plots of the long-term experimental burnt plots (EBPs). Abundance, richness, diversity, and assemblage composition of arthropods were compared across EBPs. Results showed that arthropods from the order Hymenoptera, particularly those in the family Formicidae, were the most abundant (76.4%), followed by Coleoptera (18.6%), Araneae (3%), Orthoptera (1%), and other small/less dominant orders (1%). However, the species richness of arthropods from Coleoptera was high (30.2%) compared with Formicidae (24.6%), Araneae (24.6%), and Orthoptera (4%). Abundance, richness, diversity, and assemblage composition of multitaxon and Formicidae were significantly different among EBPs. Although the abundance of multitaxon and Formicidae was significantly high at unburnt plot, species richness and diversity were low while the assemblage composition was unique at this plot compared with the annually and triennially burnt. Furthermore, the assemblage of arthropods in annually burnt EBP differed compared with those collected at unburnt and triennially burnt EBPs. We conclude that the frequency of prescribed fires improves the richness, diversity, and assemblage composition of arthropods with a significant reduction of abundances. Thus, fire can be used as a conservation tool for arthropods in the protected savanna of KNP.

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## Introduction

The savanna biome is a landscape dominated by grasses and scattered trees (Scholes and Archer 1997). Globally, savannas sustain diverse plant, vertebrate, invertebrate, and pathogenic species (Vaz et al. 2012; Botha et al. 2017; Leeuwis et al. 2018). In South Africa, savanna is the largest biome, covering more than one-third of the total land surface area (Low and Rebelo 1998). Savanna is

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among the renowned reserves of biodiversity, which is prone to anthropogenic and climatic disturbances (Low and Rebelo 1996; Mbenoun et al. 2017). A change in the composition of one or more communities of arthropods affects the abundance and diversity of other organisms within the trophic cascade and functioning of this ecosystem (Low and Rebelo 1996; Siemann et al. 1997; Layme et al. 2004; Uehara-Prado et al. 2010; Mbenoun et al. 2017; Soto-Shoender et al. 2018). This may lead to a dysfunctional and imbalanced ecosystem, thus compromising the provision of essential ecological services.

Arthropods are the most dominant group of organisms in savannas and are sensitive to ecological changes (Blaum et al. 2009; Botha et al. 2016; LeClare et al. 2020). They account for more than 80% of the identified species from the Animalia Kingdom

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(Friend and Richardson 1986; Stork 2018). Their contribution toward ecosystem services includes organic matter decomposition, nutrient cycling, pollination, seed dispersal, maintenance of biome density, and food resources for other organisms within savanna landscapes (Kunz and Krell 2011; Botha et al. 2016; Del-Claro et al. 2019; LeClare et al. 2020). However, arthropod abundance, richness, and composition are affected by anthropogenic disturbances and climate change (Gebeyehu and Samways 2003; Parr et al. 2012; Jerrentrup et al. 2014; Mauda et al. 2018). Changes in the composition of species within savanna ecosystems do not only interrupt the ecological processes and functions but also disrupt trophic interactions (Mauda et al. 2018; Maia et al. 2019; Scheiter et al. 2019).

The common disturbances within savanna ecosystems include mammal herbivory/grazing, fuelwood extraction, and veld fires (Siemann et al. 1997; Andersen and Muller 2000; Mograbi et al. 2019; Butler et al. 2021). Although these three activities exert pressure on the composition of plants and arthropods, fire has been widely used to maintain the balance between the coexisting plant communities by impeding the dense encroachment of shady tree species but also promote coppicing of ground covering grass species and forbs (Trollope 1980; Trollope et al. 1998; Higgins et al. 2000; Gordijn and Ward 2010; Mukwevho et al. 2023). Thus, fire plays a pivotal role in savanna community assembly and subsequent ecosystem function (Coetsee et al. 2010; Smith et al. 2013; Butler et al. 2021). The influence of fires on the diversity of organisms, particularly arthropods and ecosystem processes in savanna biomes, has received minimal attention. Yet this knowledge is crucial in the conservation of biodiversity and management of protected conservancy reserves.

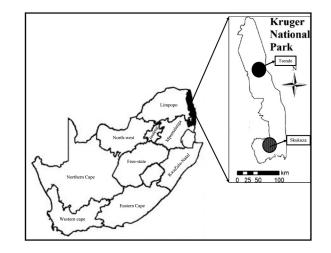
In South Africa, one of the largest protected areas, Kruger National Park (hereafter referred to as KNP), pioneered the long-term fire trials in 1954, following the amendment of the fire suppression policy in 1948 (Biggs et al. 2003; Van Wilgen et al. 2004). The experimental burnt plots (EBPs) were initiated with the intention of documenting the impact of fire on fauna and flora of a savanna ecosystem. However, the response of arthropods to different fire frequencies and intensities has received less attention (Parr et al. 2004; Horak et al. 2006; Wittkuhn et al. 2011; D'Souza et al. 2021).

Studies reported that ground-dwelling arthropods endure fires better than the active and soil-nesting ones (Warren et al. 1987; Higgins et al. 2014; Thom et al. 2015; Butler et al. 2021; Certini et al. 2021). Furthermore, the elimination of plants by direct fire affects the arthropods inhabiting and feeding on the eliminated plants, and these impacts cascade through the food chain (Haddad et al. 2009). Therefore, this study aimed at quantifying the longterm impacts of prescribed fires on the abundance, species richness, and diversity of arthropods within the EBPs of KNP. We hypothesized that long-term prescribed burns (annual and triennial) negatively affect abundance, species richness, diversity, and community structure of arthropods in KNP.

# **Material and Methods**

# Study area

KNP is among the largest protected areas (i.e.,  $\sim 2$  million ha) in South Africa and is located along the northeastern boarder of the country (Carruthers 1995; Biggs et al. 2003). The park extends from Mpumalanga to Limpopo provinces, with its northern demarcation bordering Mozambique and Zimbabwe. The park is located in a subtropical region with the annual rainfall ranging between 350 and 750 mm per annum along the geographic regions dominated by granite and basalt soils (Biggs et al. 2003; Wigley-Coetsee et al. 2022). Furthermore, the monthly minimum and maximum temperatures range between 15.7°C and 28.0°C during



**Figure 1.** South African map displaying the geographic location of Kruger National Park and two selected experimental burnt plots, namely Tsende (*shaded circle*) and Skukuza (*dotted circle*).

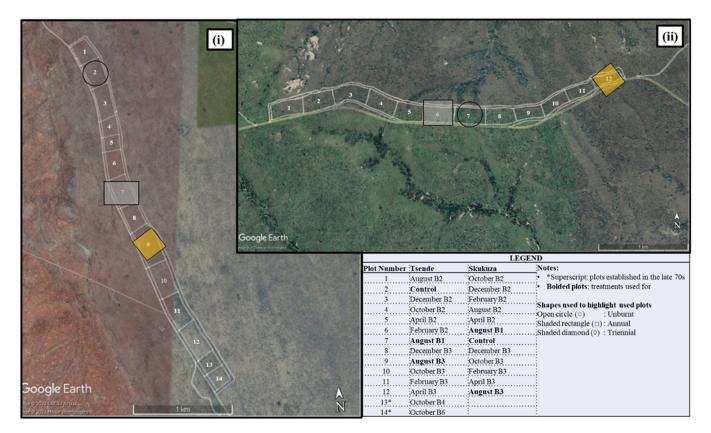
the cooler winter (June–August) and warmer summer (December– March) seasons, respectively, at KNP (Zambatis 2006). For this study, Tsende (23°27.319'S; 31°23.197'E; 370 m a.s.l) and Skukuza (25°5.870'S; 31°27.891'E; 430 m a.s.l) EBPs, which are located in the northern and southern parts of KNP, respectively, were selected (Fig. 1). Tree species dominating the landscapes include *Colophospermum mopane, Vachellia* sp. (i.e., formally known as *Acacia*), *Combretum*, and *Sclerocarya* sp. at Tsende, while *Combretum collinum* and *Combretum zeyheri* dominated Skukuza EBPs (Biggs et al. 2003; Smith et al. 2013). However, grasses such as *Enneapogon cenchroides, Urochloa mosambicensis*, and *Bothriochloa radicans* were dominant at Tsende, while *Digitaria eriantha, Setaria sphacelate*, and *Panicum maximum* dominated the Skukuza (Smith et al. 2013).

## Experimental plots

At both Tsende and Skukuza, strings of EBPs constituted 12 plots at the initial establishment in 1954 (Biggs and Potgieter 1999; Biggs et al. 2003). The late summer biennial and triennial plots at Tsende were divided in the late 70s with the intention of introducing the spring quadrennial and sexennial EBPs, respectively (Biggs et al. 2003). The division caused an increase in the number of subplots to 14; however, the two new treatments were not used in this experiment. Each plot was approximately 7 ha and the strings of EBPs, or individual plots, were demarcated using a double firebreak to protect them from incidental fires (Fig. 2). In the current experiment, plots that were annually and triennially burnt during the Austral Spring season (i.e., August) were selected. Hence, the unburnt plots were used as a control. The unburnt and annually, biennially, triennially, quadrennially, and sexennial burnt plots were haphazardly arranged along the string of EBPs, so the distance between unique treatment plots varied (see Fig. 2).

# Arthropod sampling

A combination of passive and active arthropods capturing techniques were used to optimize the sampling effort of arthropods from different taxa following previous studies (Garcia et al. 1982; Eckert 2017; Yekwayo et al. 2018). In brief, arthropods were first collected using pitfall traps and later active searches within the transects during Austral winter (between June and August 2019). At each of the 100-m transects, 10 pitfall traps were temporarily laid at a  $2 \times 5$  grid transect with a trap set (two individual pitfall traps) placed 2 m apart (Munyai and Foord 2015). The first pair of pitfall



**Figure 2.** Aerial images showing the layout of Tsende (i) and Skukuza (ii) strings of experimental burnt plots. Treatment plots on both strings were described, and those used for the experiments (i.e., Unburnt  $[\circ]$ , annually  $[\Box]$  and triennially  $[\diamond]$ ) were highlighted.

traps were placed at least 20 m from the fire break to avoid the boundary effect. The distance between pitfall traps was maintained at 20 m, and the experiment was replicated three times (i.e., with replicates demarcated at  $\pm$  250 m apart) for each of the unburnt, annually burnt, and triennially burnt plots (Ward et al. 2001). During sampling, a 500-mL plastic pitfall trap (8-cm diameter and 10cm height) was buried with its rim flushing the soil surface. The pitfall trap was half-filled with ethylene glycol, and the traps were left open during arthropod sampling for 5 consecutive d (Borgelt and New 2006; Chikowore et al. 2021). Intensive active searches were conducted within the 100 × 2 m transect for 30 min. The less mobile arthropods inhabiting the dung, dwelling under rocks and those inhabiting specific host plants, were actively captured. Data collected through both methods were pooled for each transect.

Samples from traps were washed before arthropod preservation. Collected arthropods were transferred from ethylene glycol to 70% ethanol and preserved at the University of Mpumalanga laboratory, Mbombela, South Africa for subsequent identification. In the laboratory, representative specimens were sorted on the basis of their distinctive morphological characteristics (i.e., morphospecies), and where possible, identified to the lowest taxonomic level (e.g., genus or species) using relevant guides (Scholtz and Holm 1985; Picker 2012; Gutteridge 2017; Dippenaar-Schoeman 2023). Voucher specimens were housed and cataloged at the University of Mpumalanga, Biocontrol and Applied Entomology Laboratory.

## Data analyses

Data collected at the unburnt, triennially burnt, and annually burnt plots of Tsende and Skukuza were pooled and analyzed using PAleontological STatistics software (PAST) version 4.09 (Hammer et al. 2001), STATISTICA 13.3 (TIBCO Software Inc.), and PRIMER 6. Using EstimateS version 9.1.0 (Gotelli and Colwell 2011), nonparametric estimators were used to predict the asymptotic species richness of arthropods sampled at the unburnt, annually burnt, and triennially burnt plots. The robust, accurate, and reliable coveragebased estimator of species richness, namely Incidence-based Coverage Estimator (ICE), was used to measure adequacy of sampling effort. Furthermore, Chao2, Jacknife2, Bootstramp, and Michaelis-Menten (MM) means estimators were used to provide the least biased estimates of the sampled arthropods (Gotelli and Colwell 2011). Samples were randomized 100 times.

Following Shapiro-Wilk's test, data for the abundance, species richness, and diversity of Araneae, Coleoptera, Formicidae, and Orthoptera did not meet the assumptions for analyses of variance. As a result, generalized linear models (GLZ) (in R software [R Core Team 2021]), which are less sensitive to homogeneity of variance and normality assumptions, were used assuming a Poisson distribution with a log-linear function. Significant differences were then determined using the Wald  $\chi^2$  test statistic. The diversity metrices for Orthoptera was not computed due to lack of sufficient data. For arthropod groups whose abundance, species richness, and diversity were statistically different, Dunn's tests were used for multiple comparisons among undisturbed, triennially burnt, and annually burnt plots.

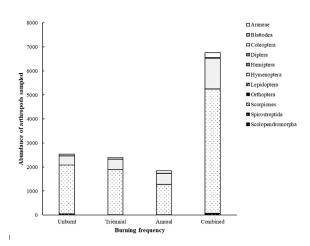
Using PRIMER 6, permutational multivariate analysis of variance (PERMANOVA) was used to determine the assemblage composition of arthropod sampled at the unburnt, triennially burnt, and annually burnt EBPs. Data were first transformed using square root matrix, and the assemblage composition was calculated using 9999 permutations. Thereafter, pairwise PERMANOVA models were used to determine the differences in the species composition of arthropods at different EBPs. Lastly, multivariate analysis consisting of a group-average hierarchical cluster analysis with similarity profile (SIMPROF) permutation tests was used to compare the

#### Table 1

Abundance, species richness, and estimators of arthropods sampled from unburnt, triennially burnt, and annually burnt plots in the long-term experimental burnt plots of Kruger National Park.

| Arthropod species                | Frequency of burns |                |                  |              |  |
|----------------------------------|--------------------|----------------|------------------|--------------|--|
|                                  | Unburnt            | Triennial      | Annual           | Combined     |  |
| No. of arthropods sampled        | 2 532              | 2 391          | 1 842            | 6 765        |  |
| Percentage of arthropods sampled | 37.4               | 35.3           | 27.2             | 100          |  |
| No. of species sampled           | 69                 | 65             | 87               | 126          |  |
| Percentage of species sampled    | 54.8%              | 51.6%          | 69.1%            | 100%         |  |
| ICE <sup>1</sup>                 | 93.4               | 73.7           | 117.8            | 169          |  |
| Chao2                            | 93.6 ± 13.1        | $69.6 \pm 3.7$ | $110.8 \pm 11.4$ | 161.3 ± 14.7 |  |
| Jackknife2                       | 107.3              | 76.04          | 129.3            | 184.7        |  |
| Bootstramp                       | 78                 | 71.7           | 100.7            | 144.2        |  |
| MM means                         | 83.5               | 78.2           | 104.6            | 132.2        |  |

<sup>1</sup> ICE indicates incidence-based coverage estimator; MM, Michaelis-Menten.



**Figure 3.** Abundance of arthropods sampled at the unburnt, annually burnt, and triennially burnt experimental burnt plots, solely and combined.

composition of species sampled among transects within unburnt, triennially burnt, and annually burnt EBPs. To visualize the separation of arthropod communities among EBPs, a non-metric multidimensional scaling (nMDS) was performed at a stress value of 0.14. Multivariate analyses were carried out using the Bray-Curtis similarity resemblance matrix.

#### Results

# Species abundance and richness

A total of 6 765 individual arthropods representing 126 morphospecies were collected from unburnt, annually burnt, and triennially burnt plots (Table 1). From the sampled arthropod species, the Formicidae were the dominant group contributing 5 168 (76.4%), followed by Coleoptera 1 255 (18.6%), while 342 (5%) individual arthropods were recorded from the remaining groups, namely Orthoptera, Araneae, Blattodea, Diptera, Hemiptera, Lepidoptera, Scorpiones, Spirostreptida, and Scolopendromorpha (Fig. 3; Table S1, available online at ...). The high number of arthropods (multitaxon) were captured at the unburnt plots with a total of 2 532 (37.4%). Furthermore, the abundance of multitaxon declined by 0.9 and 0.7 folds at triennially burnt and annually burnt compared with the unburnt plot; thus, a total of 2 391 (35.4 %) and 1 842 (27.2 %) arthropods were captured from each plot, respectively (see Fig. 3 and Table 1).

The abundance of multitaxon was significantly different ( $\chi^2 = 117.025$ , df = 2, P < 0.001) among the unburnt, triennially burnt, and annually burnt plots. When analyzed separately, the abundance of Formicidae ( $\chi^2 = 194.498$ , df = 2, P < 0.001) and

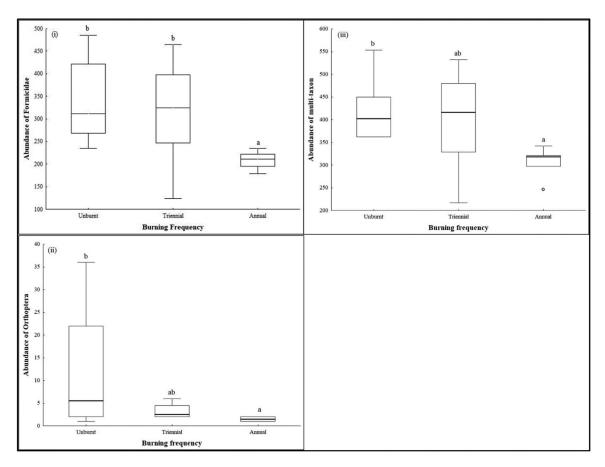
Orthoptera ( $\chi^2 = 35.243$ , df = 2, P < 0.001) was significantly different among the unburnt, triennially burnt, and annually burnt EBPs at KNP. The abundances of multitaxon, Formicidae, and Orthoptera were significantly high at the unburnt and triennially burnt compared with the annually burnt EBPs (Fig. 4). Contrasting results showed no statistical differences in the abundance of Araneae ( $\chi^2 = 14.131$ , df = 2, P = 0.224) and Coleoptera ( $\chi^2 = 8.423$ , df = 2, P = 0.701).

Despite the noticeably high abundance of arthropods sampled at the long-term EBPs of KNP, the species richness did not reach asymptotic estimations at the annually burnt, triennially burnt, and unburnt plots either solely or combined. Of the 126 morphospecies collected, 87 morphospecies were captured at the annually burnt plots; hence, 69 and 65 morphospecies were recorded at the unburnt and triennially burnt plots, respectively (see Table 1). From these plots, the overall number of morphospecies sampled was high for Coleoptera (30.2%), Hymenoptera: Formicidae (24.6%), Araneae (24.6%), and Blattodea (5.6%), while less species-rich groups (Diptera, Hemiptera, Lepidoptera, Orthoptera, Scorpiones, Spirostreptida, and Scolopendromorpha) contributed 4% (Fig. 5).

Species richness of multitaxon was significantly higher  $(\chi^2 = 8.733, df = 2, P = 0.013)$  at the annually burnt plot compared with triennially burnt and unburnt plots. It increased by 0.1 and 0.2 folds in triennially and annually burnt plots, respectively. Similarly, the species richness of Formicidae ( $\chi^2 = 5.841$ , df = 2, P = 0.045) was significantly high at the annually burnt compared with the unburnt plot. Species richness of multitaxon and Formicidae was significantly low at the unburnt compared with the annually burnt plots. Species richness of Formicidae recorded at the triennially burnt plot was not significantly different compared with those recorded at either unburnt or annually burnt plots. However, species richness of multitaxon at the triennially burnt plot was not significantly different compared with the unburnt plot (Fig. 6). Furthermore, the species richness of other groups arthropods such as Araneae ( $\chi^2 = 1.603$ , df = 2, P = 0.449), Coleoptera  $(\chi^2 = 2.365, df = 2, P = 0.307)$ , and Orthoptera  $(\chi^2 = 1.837, df = 2, P = 0.307)$ df = 2, P = 0.399) did not significantly vary among the three EBPs.

## Diversity metrices

Shannon diversity index showed that there was significant variation in the diversity of multitaxon ( $\chi^2 = 16.204$ , df = 2, P < 0.001) and Formicidae ( $\chi^2 = 7.585$ , df = 2, P = 0.023). The diversity of Formicidae and multitaxon was significantly high at the annually burnt compared with unburnt plots, not with the triennially burnt plots (Fig. 7). However, there was no significant variation in the diversity of Araneae ( $\chi^2 = 1.116$ , df = 2, P = 0.572) and Coleoptera ( $\chi^2 = 1.901$ , df = 2, P = 0.387) among the unburnt, triennially burnt,



**Figure 4.** Boxplots showing the abundance of Formicidae (i), Orthoptera (ii), and multitaxon (iii) arthropods collected at the unburnt, triennially burnt, and annually burnt experimental burnt plots of Kruger National Park. Different letters above the bars show significant differences between treatments (Dunn's test: P < 0.05).

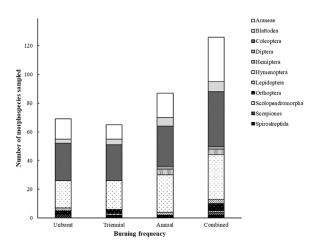


Figure 5. Number of arthropod species sampled at the unburnt triennially and annually burnt plots solely and combined.

and annually burnt EBPs. Of the 126 morphospecies of arthropods collected in the current study, 30.2% of the species was shared among the three plots. Less than 4.8% of the multitaxon was shared between burnt (i.e., either annual or triennial) and unburnt plots. The high number of species (7.1%) was shared between annually burnt and triennially burnt plots. Lastly, 16.7%, 11.1%, and 27% of the species were distinct to the unburnt, triennially burnt, and annually burnt plots, respectively (see Table S1).

Species similarity and composition

Cluster analysis identified four groups: group 1-annual 3; group 2-triennial 1-3, unburnt 1-3, and annual 1-2; group 3-unburnt 4-6 and triennial 4-6; and group 4-annual 4-6. Within groups 2 and 3, assemblage communities were similar for each type of EBP (e.g., in group 3, the unburnt 4-6 and triennial 4-6 formed different subgroups. However, a subgroup in group 2 had annual 1-2 and triennial 1 grouped together, suggesting similarities (Fig. 8). The species composition was significantly different (PERMANOVA: pseudo-F=2.0568, df=2, P=0.002) among the unburnt and annually burnt plots; hence, there were no marked differences between the triennially burnt and other EBPs of KNP (Table 2). Similarly, the two-dimensional representation of the nMDS showed that the arthropod communities in unburnt plots were separated from those of the annually and triennially burnt plots, while there was an overlap between the triennial and annual plots (Fig. 9). Crematogester sp. and Carabidae sp. 8 characterized the unburnt plots, whereas Pyramica sp. 01 and Gyrinidae sp. 6 were common in the triennial plots. Lastly, Carabidae sp. 10 was common in the annually burnt plot (see Fig. 9).

# Discussion

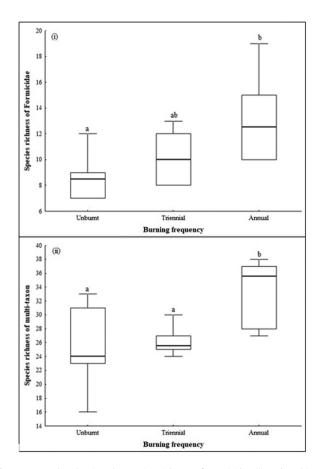
The current study reported the significant impact of prescribed burns (i.e., annual and triennial) on the abundance, species richness, diversity, and assemblages of the multitaxon sampled at the long-term experimental burnt plots of KNP. Findings also demonstrated the sensitivity of Formicidae and Orthoptera, through

#### Table 2

Pairwise comparisons showing similarity in species composition of arthropods sampled at the unburnt, triennially burnt, and annually burnt plots of Kruger National Park. Bolded *P* value shows statistically significant dissimilarity of species composition between experimental burnt plot combinations.

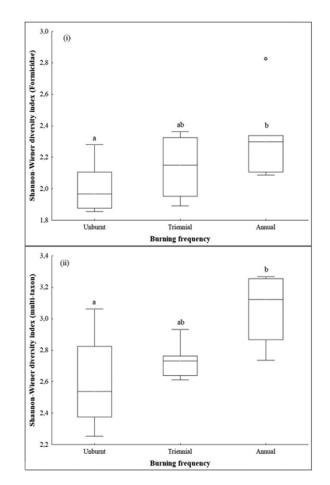
| Combinations of plots compared |           | Statistics |         |                        |  |
|--------------------------------|-----------|------------|---------|------------------------|--|
|                                |           | t value    | P value | Composition similarity |  |
| Unburnt                        | Triennial | 1.336      | 0.0629  | =1                     |  |
|                                | Annual    | 1.7222     | 0.0024  | $\neq$                 |  |
| Triennial                      | Annual    | 1.1929     | 0.1324  | =                      |  |

 $^{1}$  = indicates similarity;  $\neq$ , dissimilarity.



**Figure 6.** Boxplot showing the species richness of Formicidae (i) and multitaxon (ii) sampled at the annually, triennially burnt, and unburnt plots of Kruger National Park. Different letters above the bars show significant differences between treatments (Dunn's test: P < 0.05).

reduced abundances with the increased frequency of fires. Emulating the pattern of multitaxon, the species richness and diversity of Formicidae increased with the frequency of fires. Multitudes of studies also demonstrated the impact of predetermined and accidental fires on the abundance, species richness, diversity and assemblages of arthropods in the forests, fynbos, grasslands, and oak savanna landscapes in the Americas, Australasia, and South Africa (Siemann et al. 1997; Andersen and Muller 2000; Ferrenberg et al. 2006; Vasconcelos et al. 2009; Calcaterra et al. 2014; Haddad et al. 2015; Yekwayo et al. 2018). Formicidae, Coleoptera, Araneae, and Orthoptera were recorded among the most abundant groups of arthropods recorded at the long-term EBPs protected Afrotropic region of KNP. Four groups were also listed among dominating orders of arthropods sampled in fire experiments conducted at the Brazilian savannas (Uehara-Pradoa et al. 2009; Vasconcelos et al. 2009; Uehara-Prado et al. 2010), Peninsula fynbos (Pryke and Samways 2012; Yekwayo et al. 2018) and Ceuta (Spain) forests (EL Khayati et al. 2023). Furthermore, studies cataloging the common arthro-



**Figure 7.** Boxplot showing the diversity (Shannon-Wiener diversity index) of arthropods (i.e., Formicidae [i] and multitaxon [ii]), sampled at the unburnt, annually burnt, and triennially burnt experimental burnt plots of Kruger National Park. Different letters above the bars show significant differences between treatments (Dunn's test: P < 0.05).

pod groups and those conducted at the grazed exclosures documented similar orders as dominant at the savanna and grassland landscapes (Jonsson et al. 2010; Gerlach et al. 2013; Botha et al. 2017; Mavasa et al. 2022; Mukwevho et al. 2023).

Here, we showed that the abundance of multitaxon, Formicidae, and Orthoptera significantly declined with the increasing frequency of fires. The results showed that the abundance of arthropods (i.e., multitaxon and Formicidae and Orthoptera) was significantly lower at the annually burnt plot (i.e., sampled at least 11 mo post fire) compared with the unburnt plot. Results corroborate with those reported by da Silva et al. (2020), Ferrenberg et al. (2006), Lazarina et al. (2017), Paolucci et al. (2017), and Siemann et al. (1997) that documented the short-term impacts of fires, time post fire, and frequency of prescribed burns on arthropod abundances. The studies reported high abundance of multitaxon and unique groups on the undisturbed/infrequently burnt plots compared with the

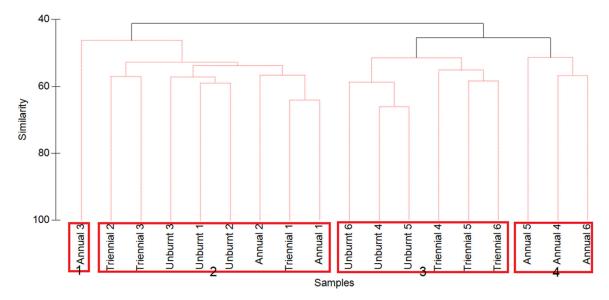
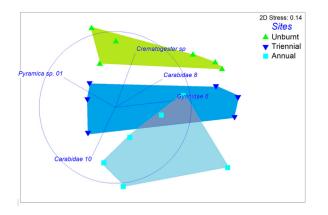


Figure 8. Classification tree showing arthropod assemblage similarities across unburnt, triennially burnt, and annually burnt plots at Kruger National Park. The group-average linking on Bray-Curtis species similarities was used to measure the similarities.



**Figure 9.** Nonmetric multidimensional scaling (nMDS) ordination showing the resemblance of arthropod species across unburnt, triennially burnt, and annually burnt plots surveyed at KNP. Polygons represent different plots, namely unburnt (green), triennially (dark blue), and annually burnt (light blue).

intensively burnt or those assessed promptly after burns (Siemann et al. 1997; Ferrenberg et al. 2006; Lazarina et al. 2017; Paolucci et al. 2017; da Silva et al. 2020).

The notable difference in the abundance of Formicidae and Orthoptera among plots reflects their sensitivity to late winter fires of KNP. The sensitivity of Formicidae and Orthoptera to ecological disturbance (i.e., fire) at the EBPs of KNP illustrates their renowned use as reliable ecological indicators. Similarly, studies have reported that the significant reduction in the abundance of Formicidae and Orthoptera to fires was not surprising since they are known to be a ubiquitous group contributing to a variety of ecological functions in grasslands and savannas (Porter and Redak 1996; Underwood and Fisher 2006; Bell 2009; Graham et al. 2009; Van Schalkwyk et al. 2019; da Silva et al. 2020). Underground nests and influxing abilities of Formicidae (i.e., ants) and Orthoptera may be associated with the resilience of the group to frequent predetermined fires (i.e., annually) at KNP.

The decline of multitaxon and unique orders of arthropods within different trophic cascades may be associated with the direct and indirect effects of fire at KNP. Ground-dwelling and immature developmental stages of flying invertebrates inhabiting combustible live (e.g., plants) or dead material (e.g., litter) are highly prone to fires and may be burnt during veld fires (Vasconcelos et al. 2009; Kwok and Eldridge 2015; Kwok et al. 2016). As such, the destruction of various habitats such as the live plants, leaf litter, and dung during burning is speculated to have directly reduced the numbers of arthropods dwelling at these microhabitats on annually burnt plots of KNP. Furthermore, limited food resources for pollinators indirectly impact the abundance of prestigious ecological facilitators, while the trophic cascade and ecological functions are disrupted by the elimination of arthropods at any trophic level (Scherber et al. 2010; van Dam and Heil 2011; Seibold et al. 2018).

The species richness and diversity of multitaxon and Formicidae significantly differed between the unburnt and annually burnt plots, while the overlap was noticeable between triennially burnt and unburnt EBPs of KNP. Some studies (Ferrenberg et al. 2006; Graham et al. 2009; Pryke and Samways 2012; Valkó et al. 2016; Yekwayo et al. 2018) showed that the richness and diversity of arthropods sampled at the burnt plots from at least 6 months (up to 10 years) after incidental or prescribed fires does not statistically differ with that on the unburnt plot at different protected areas across landscapes. Due to the noticeable significant increase in the species richness and diversity of multitaxon and Formicidae between the unburnt and annually burnt sites, we speculate that the accelerated recovery and diversity of plants during the rainy season could have encouraged influxes and recovery of arthropods at the annually burnt plot. The abundance of diverse food resources (i.e., from plants to predators) within trophic cascades could have improved the species richness and diversity of multitaxon and Formicidae at the annually burnt plot at KNP (Scherber et al. 2010; van Dam and Heil 2011; Ebeling et al. 2018; Seibold et al. 2018; Maia et al. 2019).

While Yekwayo et al. (2018) reported low species richness and diversity of multitaxon, the current study reported contrasting results with the significantly high richness and diversity recorded in the annually burnt plots. However, a study by Pryke and Samways (2012) reported that the diversity of multitaxon is significantly higher at a recently burnt plot (i.e., 3 mo post fire) compared with those sampled 1–3 yr after fires.

The assemblages of multitaxon were distinct for the unburnt plots while the slight overlap was recorded between the triennially and annually burnt plots. The pattern emphasizes the impact of fires and its role in shifting the assemblage in the ecosystem. The level of overlaps explains that a low proportion is resilient to different frequencies of fires; hence, distinct groups have different levels of fire tolerances. Studies conducted at the Afrotropical savannas reported resilience of arthropods assemblages to prescribed and accidental fires; however, the assemblages' compositions were associated with the vegetation structure and complexity (Parr et al. 2004; Davies et al. 2012). Because fire was reported as a major driver of grass and tree diversity at KNP (Smit et al. 2010; Smit et al. 2013), we assume that the assemblages of arthropods could be associated with vegetation structures at the unburnt, triennially burnt, and annually burnt EBPs.

The current study reported that the abundance, species richness, and diversity of multitaxon emulated that of the dominating group of arthropods, Formicidae. Likewise, Siemann et al. (1997) reported that the abundance, species richness, and diversity of dominating group of arthropods was similar to that of multitaxa combined at different burnt plots at the oak savanna of Cedar Creek Natural History Area, Minnesota. Moreover, Yekwayo et al. (2018) demonstrated that the abundance, species richness, and diversity of the most abundant group of arthropods (i.e., Formicidae) was similar to that of the multitaxon in a study that measured the impact of fire on arthropods at the Cape Winelands and Kogelberg Biosphere Reserves, Western Cape, South Africa.

The current study shed some light on the long-term benefits of late summer prescribed burns on the conservation of arthropod species and biodiversity in the savanna landscape of KNP. Results of the current study filled a gap outlined by Parr et al. (2004), which emphasized the need to assess the overall response of arthropods (i.e., multitaxon) at the protected areas where late fires have been constantly used as a veld management tool. The current study reported that the impact of the late winter fire is temporal and the abundance of Formicidae, Orthoptera and multitaxon significantly improved with the reduction in the frequency of fires. Contrarily, the species richness, diversity, and composition improved with the frequency of fires at Kruger National Park. The abundance, species richness, diversity, and composition of arthropods at the long-term EBPs emulate that of the plots where shortterm fires (e.g., those incurred post burn or incidental fires). In conclusion, burning during late winter season should be encouraged, although it has temporal impact on the abundance of arthropods inhabiting savanna landscape of KNP. The intensity of ongoing prescribed burns at the protected reserve of KNP encouraged the conservation of arthropod species for more than 67 yr; thus, the disruption of functions and ecological services rendered by arthropods may be largely at acute temporal scales.

## **Declaration of Conflicts of Interest**

The authors Ludzula Mukwevho, Mduduzi Ndlovu, Gerald Chikowore, Tatenda Dalu, Reyard Mutamiswa, and Frank Chidawanyika declare no conflict of interest.

# **CRediT** authorship contribution statement

Ludzula Mukwevho: Conceptualization, Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. Mduduzi Ndlovu: Formal analysis, Methodology, Supervision, Writing – review & editing. Gerald Chikowore: Investigation, Methodology, Software, Writing – review & editing. Tatenda Dalu: Validation, Writing – review & editing. Reyard Mutamiswa: Visualization, Writing – review & editing. Frank Chidawanyika: Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing.

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## **Supplementary materials**

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2024.04.008.

#### References

- Andersen, A.N., Muller, W.J., 2000. Arthropod responses to experimental fire regimes in an Australian tropical savannah: ordinal-level analysis. Australian Ecology 25, 199–209.
- Bell, D., 2009. Indirect effects of mammalian herbivores on invertebrates in a river gradient of the Kruger National Park, South Africa.
- Biggs, H., Potgieter, A., 1999. Overview of the fire management policy of the Kruger National Park. Koedoe 42, 101–110.
- Biggs, R., Biggs, H., Dunne, T., Govender, N., Potgieter, A., 2003. Experimental burn plot trial in the Kruger National Park: history, experimental design and suggestions for data analysis. Koedoe 46, 1–15.
- Blaum, N., Seymour, C., Rossmanith, E., Schwager, M., Jeltsch, F., 2009. Changes in arthropod diversity along a land use driven gradient of shrub cover in savanna rangelands: identification of suitable indicators. Biodiversity and Conservation 18, 1187–1199.
- Borgelt, A., New, T., 2006. Pitfall trapping for ants (Hymenoptera, Formicidae) in mesic Australia: what is the best trapping period? Journal of Insect Conservation 10, 75–77.
- Botha, M., Siebert, S., Van den Berg, J., Ellis, S., Dreber, N., 2017. Plant functional types differ between the grassland and savanna biomes along an agro-ecosystem disturbance gradient in South Africa. South African Journal of Botany 113, 308–317.
- Botha, M., Siebert, S.J., Van den Berg, J., 2016. Do arthropod assemblages fit the grassland and savanna biomes of South Africa? South African Journal of Science 112, 1–10.
- Butler, A., Davis, C.A., Fuhlendorf, S.D., Wilder, S.M., 2021. Effects of fire on ground-dwelling arthropods in a shrub-dominated grassland. Ecology and Evolution 11, 427–442.
- Calcaterra, L.A., Di Blanco, Y., Srur, M., Briano, J., 2014. Fire effect on ground-foraging ant assemblages in northeastern Argentina. Journal of Insect Conservation 18, 339–352.
- Carruthers, J., 1995. The Kruger National Park: a social and political history. University of Natal Press, Natal, South Africa.
- Certini, G., Moya, D., Lucas-Borja, M.E., Mastrolonardo, G., 2021. The impact of fire on soil-dwelling biota: a review. Forest Ecology and Management 488, 118989.
- Chikowore, G., Martin, G.D., Chidawanyika, F., 2021. An assessment of the invasive alien tree, *Robinia pseudoacacia* canopy traits and its effect on grassland microclimates and subsequent arthropod assemblages. Journal of Insect Conservation 25, 429–439.
- Coetsee, C., Bond, W.J., February, E.C., 2010. Frequent fire affects soil nitrogen and carbon in an African savanna by changing woody cover. Oecologia 162, 1027–1034.
- D'Souza, M.L., van der Bank, M., Shongwe, Z., Rattray, R.D., Stewart, R., van Rooyen, J., Govender, D., Hebert, P.D, 2021. Biodiversity baselines: tracking insects in Kruger National Park with DNA barcodes. Biological Conservation 256, 109034.
- da Silva, C.V.C., da Silva Goldas, C., Dattilo, W., Dröse, W., de Souza Mendonça Jr., M., Podgaiski, L.R., 2020. Effects of time-since-fire on ant-plant interactions in southern Brazilian grasslands. Ecological Indicators 112, 106094.
- Davies, A.B., Eggleton, P., Van Rensburg, B.J., Parr, C.L., 2012. The pyrodiversity-biodiversity hypothesis: a test with savanna termite assemblages. Journal of Applied Ecology 49, 422–430.
- Del-Claro, K., Rodriguez-Morales, D., Calixto, E., Martins, A., Torezan-Silingardi, H., 2019. Ant pollination of *Paepalanthus lundii* (Eriocaulaceae) in Brazilian savanna. Annals of Botany 123, 1159–1165.
- Dippenaar-Schoeman, A., 2023. Field guide to the spiders of South Africa. Penguin Random House South Africa, Parkwood, South Africa.
- Ebeling, A., Rzanny, M., Lange, M., Eisenhauer, N., Hertzog, L.R., Meyer, S.T., Weisser, W.W., 2018. Plant diversity induces shifts in the functional structure and diversity across trophic levels. Oikos 127, 208–219.

- Eckert, M., 2017. The diversity and distribution of topsoil and leaf litter arthropods in timber plantation landscape mosaics. Stellenbosch University, Stellenbosch, South Africa, p. 98.
- EL Khayati, M., Chergui, B., Barranco, P., Fahd, S., Ruiz, J.L., Taheri, A., Santos, X., 2023. Assessing the response of different soil arthropod communities to fire: a case study from northwestern. Africa. Fire 6, 206.
- Ferrenberg, S.M., Schwilk, D.W., Knapp, E.E., Groth, E., Keeley, J.E., 2006. Fire decreases arthropod abundance but increases diversity: early and late season prescribed fire effects in a Sierra Nevada mixed-conifer forest. Fire Ecology 2, 79–102.
- Friend, J.A., Richardson, A.M.M., 1986. Biology of terrestrial amphipods. Annual Review of Entomology 31, 25–48.
- Garcia, A., Gonzalez, D., Leigh, T., 1982. Three methods for sampling arthropod numbers on California cotton. Environmental Entomology 11, 565–572.
- Gebeyehu, S., Samways, M.J., 2003. Responses of grasshopper assemblages to long-term grazing management in a semi-arid African savanna. Agriculture. Ecosystems & Environment 95, 613–622.
- Gerlach, J., Samways, M., Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. Journal of Insect Conservation 17, 831–850.
- Gordijn, P.J., Ward, D., 2010. The role of fire in bush encroachment in Ithala Game Reserve. University of KwaZulu-Natal, Pietermaritzburg, South Africa, p. 124.
- Gotelli, N.J., Colwell, R.K., 2011. Estimating species richness. Biological Diversity: Frontiers in Measurement and Assessment 12, 35.
- Graham, J.H., Krzysik, A.J., Kovacic, D.A., Duda, J.J., Freeman, D.C., Emlen, J.M., Zak, J.C., Long, W.R., Wallace, M.P., Chamberlin-Graham, C., 2009. Species richness, equitability, and abundance of ants in disturbed landscapes. Ecological Indicators 9, 866–877.
- Gutteridge, L., 2017. Invertebrates of Southern Africa and their tracks and signs. Jacana Media, Johannesburg, South Africa.
- Haddad, C.R., Foord, S.H., Fourie, R., Dippenaar-Schoeman, A.S., 2015. Effects of a fast-burning spring fire on the ground-dwelling spider assemblages (Arachnida: Araneae) in a central South African grassland habitat. African Zoology 50, 281–292.
- Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M., Tilman, D., 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12, 1029–1039.
- Hammer, Ø., Harper, D.A., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 9.
- Higgins, J.W., Cobb, N.S., Sommer, S., Delph, R.J., Brantley, S.L., 2014. Ground-dwelling arthropod responses to succession in a pinyon-juniper woodland. Ecosphere 5, 1–29.
- Higgins, S.I., Bond, W.J., Trollope, W.S., 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88, 213–229.
- Horak, I., Gallivan, G., Spickett, A., Potgieter, A., 2006. Effect of burning on the numbers of questing ticks collected by dragging. Onderstepoort Journal of Veterinary Research 73, 163–174.
- Jerrentrup, J.S., Wrage-Mönnig, N., Röver, K.U., Isselstein, J., 2014. Grazing intensity affects insect diversity via sward structure and heterogeneity in a long-term experiment. Journal of Applied Ecology 51, 968–977.
- Jonsson, M., Bell, D., Hjältén, J., Rooke, T., Scogings, P., 2010. Do mammalian herbivores influence invertebrate communities via changes in the vegetation? Results from a preliminary survey in Kruger National Park, South Africa. African Journal of Range & Forage Science 27, 39–44.
- Kunz, B.K., Krell, F.T., 2011. Habitat differences in dung beetle assemblages in an African savanna–forest ecotone: implications for secondary seed dispersal. Integrative Zoology 6, 81–96.
- Kwok, A.B., Eldridge, D.J., 2015. Does fire affect the ground-dwelling arthropod community through changes to fine-scale resource patches? International Journal of Wildland Fire 24, 550–559.
- Kwok, A.B., Wardle, G.M., Greenville, A.C., Dickman, C.R., 2016. Long-term patterns of invertebrate abundance and relationships to environmental factors in arid Australia. Australian Ecology 41, 480–491.
- Layme, V.M.G., Lima, A.P., Magnusson, W.E., 2004. Effects of fire, food availability and vegetation on the distribution of the rodent *Bolomys lasiurus* in an Amazonian savanna. Journal of Tropical Ecology 20, 183–187.
- Lazarina, M., Sgardelis, S.P., Tscheulin, T., Devalez, J., Mizerakis, V., Kallimanis, A.S., Papakonstantinou, S., Kyriazis, T., Petanidou, T., 2017. The effect of fire history in shaping diversity patterns of flower-visiting insects in post-fire Mediterranean pine forests. Biodiversity and Conservation 26, 115–131.
- LeClare, S.K., Mdluli, M., Wisely, S.M., Stevens, N., 2020. Land-use diversity within an agricultural landscape promotes termite nutrient cycling services in a southern African savanna. Global Ecology and Conservation 21, e00885.
  Leeuwis, T., Peel, M., De Boer, W.F., 2018. Complexity in African savannas: direct,
- Leeuwis, T., Peel, M., De Boer, W.F., 2018. Complexity in African savannas: direct, indirect, and cascading effects of animal densities, rainfall and vegetation availability. PLOS ONE 13, e0197149.
- Low, A., Rebelo, A., 1996. Vegetation of South Africa. Department of Environmental Affairs and Tourism, Lesotho and Swaziland. Pretoria, South Africa.
- Low, A.B., Rebelo, A.G., 1998. Vegetation of South Africa, Lesotho and Swaziland: a companion to the vegetation map of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria, South Africa.
- Maia, L., França, F., Nascimento, A.R., Faria, L.B., 2019. Do community and food-web metrics temporally change in tropical systems? Responses from a four-trophic level food web. Arthropod-Plant Interactions 13, 895–903.
- Mauda, E.V., Joseph, G.S., Seymour, C.L., Munyai, T.C., Foord, S.H., 2018. Changes in landuse alter ant diversity, assemblage composition and dominant func-

tional groups in African savannas. Biodiversity and Conservation 27, 947–965.

- Mavasa, R., Yekwayo, I., Mwabvu, T., Tsvuura, Z., 2022. Preliminary patterns of seasonal changes in species composition of surface-active arthropods in a South African savannah. Australian Ecology 47, 1222–1231.
- Mbenoun, M., Garnas, J.R., Wingfield, M.J., Boyogueno, A.D.B., Roux, J., 2017. Metacommunity analyses of Ceratocystidaceae fungi across heterogeneous African savanna landscapes. Fungal Ecology 28, 76–85.
- Mograbi, P.J., Witkowski, E.T, Erasmus, B.F., Asner, G.P., Fisher, J.T., Mathieu, R., Wessels, K.J., 2019. Fuelwood extraction intensity drives compensatory regrowth in African savanna communal lands. Land Degradation & Development 30, 190–201.
- Mukwevho, L., Dalu, T., Chidawanyika, F., 2023. Long-term mammal herbivory on arthropod assemblages at Kruger National Park, South Africa. PLOS ONE 18, e0286396.
- Munyai, T.C., Foord, S.H., 2015. An inventory of epigeal ants of the western Soutpansberg Mountain Range. South Africa. Koedoe, South Africa: African Protected Area Conservation and Science 57, 1–12.
- Paolucci, L.N., Schoereder, J.H., Brando, P.M., Andersen, A.N., 2017. Fire-induced forest transition to derived savannas: cascading effects on ant communities. Biological Conservation 214, 295–302.
- Parr, C.L., Gray, E.F., Bond, W.J., 2012. Cascading biodiversity and functional consequences of a global change–induced biome switch. Diversity and Distributions 18, 493–503.
- Parr, C.L., Robertson, H.G., Biggs, H.C., Chown, S.L., 2004. Response of African savanna ants to long-term fire regimes. Journal of Applied Ecology 630–642.
- Picker, M., 2012. Field guide to insects of South Africa. Penguin Random House South Africa, Parkwood, South Africa.
- Porter, E.E., Redak, R.A., 1996. Short-term recovery of the grasshopper communities (Orthoptera: Acrididae) of a California native grassland after prescribed burning. Environmental Entomology 25, 987–992.
- Pryke, J.S., Samways, M.J., 2012. Importance of using many taxa and having adequate controls for monitoring impacts of fire for arthropod conservation. Journal of Insect Conservation 16, 177–185.
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Scheiter, S., Schulte, J., Pfeiffer, M., Martens, C., Erasmus, B.F., Twine, W.C., 2019. How does climate change influence the economic value of ecosystem services in savanna rangelands? Ecological Economics 157, 342–356.
- Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D., Roscher, C., Weigelt, A., Allan, E., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468, 553–556.
- Scholes, R.J., Archer, S., 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 517–544.
- Scholtz, C.H., Holm, E., 1985. Insects of Southern Africa. Butterworths, Durban, South Africa, p. 502.
- Seibold, S., Cadotte, M.W., Maclvor, J.S., Thorn, S., Müller, J., 2018. The necessity of multitrophic approaches in community ecology. Trends in Ecology and Evolution 33, 754–764.
- Siemann, E., Haarstad, J., Tilman, D., 1997. Short-term and long-term effects of burning on oak savanna arthropods. American Midland Naturalist 349–361.
- Smit, I.P., Asner, G.P., Govender, N., Kennedy-Bowdoin, T., Knapp, D.E., Jacobson, J., 2010. Effects of fire on woody vegetation structure in African savanna. Ecological Applications 20, 1865–1875.
- Smit, I.P., Petersen, R., Riddell, E.S., Cullum, C., 2013. Kruger National Park research supersites: establishing long-term research sites for cross-disciplinary, multiscaled learning. Koedoe: African Protected Area Conservation and Science 55, 1–7.
- Smith, M.D., van Wilgen, B.W., Burns, C.E., Govender, N., Potgieter, A.L., Andelman, S., Biggs, H.C., Botha, J., Trollope, W.S., 2013. Long-term effects of fire frequency and season on herbaceous vegetation in savannas of the Kruger National Park, South Africa. Journal of Plant Ecology 6, 71–83.
- Soto-Shoender, J.R., McCleery, R.A., Monadjem, A., Gwinn, D.C., 2018. The importance of grass cover for mammalian diversity and habitat associations in a bush encroached savanna. Biological Conservation 221, 127–136.
- Stork, N.E., 2018. How many species of insects and other terrestrial arthropods are there on earth? Annual Review of Entomology 63, 31–45.
- Thom, M.D., Daniels, J.C., Kobziar, L.N., Colburn, J.R., 2015. Can butterflies evade fire? Pupa location and heat tolerance in fire prone habitats of Florida. PLOS ONE 10, e0126755.
- Trollope, W., 1980. Controlling bush encroachment with fire in the savanna areas of South Africa. Proceedings of the Annual Congresses of the Grassland Society of southern Africa 15, 173–177.
- Trollope, W., Trollope, L., Biggs, H., Pienaar, D., Potgieter, A., 1998. Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. Koedoe 41, 103–112.
- Uehara-Prado, M., Bello, A.M., Fernandes, J.O., Santos, A.J., Silva, I.A., Cianciaruso, M.V., 2010. Abundance of epigaeic arthropods in a Brazilian savanna under different fire frequencies. Zoologia (Curitiba) 27, 718–724.
- Uehara-Pradoa, M., de Moura Bellob, A., Fernandesc, J.O., Santosd, A.J., Silvae, I.A., Cianciarusof, M.V., 2009. Capítulo 3–abundance of soil epigaeic arthropods in a Brazilian savanna under different fire frequencies. Ficha Catalográfica Elaborada Pela Biblioteca Do Instituto De Biologia–Unicamp 93.
- Underwood, E.C., Fisher, B.L., 2006. The role of ants in conservation monitoring: if, when, and how. Biological Conservation 132, 166–182.

- Valkó, O., Deák, B., Magura, T., Török, P., Kelemen, A., Tóth, K., Horváth, R., Nagy, D.D., Debnár, Z., Zsigrai, G., 2016. Supporting biodiversity by prescribed burning in grasslands—a multi-taxa approach. Science of the Total Environment 572, 1377–1384.
- van Dam, N.M., Heil, M., 2011. Multitrophic interactions below and above ground: en route to the next level. Journal of Ecology 99, 77–88.
  Van Schalkwyk, J., Pryke, J., Samways, M., 2019. Contribution of common vs. rare
- Van Schalkwyk, J., Pryke, J., Samways, M., 2019. Contribution of common vs. rare species to species diversity patterns in conservation corridors. Ecological Indicators 104, 279–288.
- Van Wilgen, B., Govender, N., Biggs, H., Ntsala, D., Funda, X., 2004. Response of savanna fire regimes to changing fire-management policies in a large African national park. Conservation Biology 18, 1533–1540.
- Vasconcelos, H.L., Pacheco, R., Silva, R.C., Vasconcelos, P.B., Lopes, C.T., Costa, A.N., Bruna, E.M., 2009. Dynamics of the leaf-litter arthropod fauna following fire in a neotropical woodland savanna. PLOS ONE 4, e7762.
- Vaz, A.B., Vieira, M.L., Pimenta, R.S., Morais, P.B., Sobral, M.E., Rosa, L.H., Rosa, C.A., 2012. Diversity and antimicrobial activity of fungal endophyte communities associated with plants of Brazilian savanna ecosystems. African Journal of Microbiology Research 6, 3173–3185.

- Ward, D.F., New, T.R., Yen, A.L., 2001. Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. Journal of Insect Conservation 5, 47–53.
- Warren, S., Scifres, C., Teel, P., 1987. Response of grassland arthropods to burning: a review. Agriculture, Ecosystems & Environment 19, 105–130.
- Wigley-Coetsee, C., Strydom, T., Govender, D., Thompson, D.I., Govender, N., Botha, J., Simms, C., Manganyi, A., Kruger, L., Venter, J., 2022. Reflecting on research produced after more than 60 years of exclosures in the Kruger National Park. KOE-DOE-African Protected Area Conservation and Science 64, 1674.
- Wittkuhn, R.S., McCaw, L., Wills, A.J., Robinson, R., Andersen, A.N., Van Heurck, P., Farr, J., Liddelow, G., Cranfield, R., 2011. Variation in fire interval sequences has minimal effects on species richness and composition in fire-prone landscapes of south-west Western Australia. Forest Ecology and Management 261, 965–978. Yekwayo, I., Pryke, J.S., Gaigher, R., Samways, M.J., 2018. Only multi-taxon studies
- Yekwayo, I., Pryke, J.S., Gaigher, R., Samways, M.J., 2018. Only multi-taxon studies show the full range of arthropod responses to fire. PLOS ONE 13, e0195414.
- Zambatis, N. 2006. Average monthly and seasonal temperatures (C) of the Kruger National Park. Unpublished report. SANParks, Skukuza. Available at: http: //www. sanparks. co. za/parks/kruger/conservation/scientific/weather/rainfall/ 2006/temps\_rainfall\_averag es.pdf Accessed 1 August 2022.