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Responses of Ground-Dwelling Arthropods to Long-Term Prescribed Fire Regimes in a Savanna-Protected Area ☆

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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 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 long-term 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., ~ 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

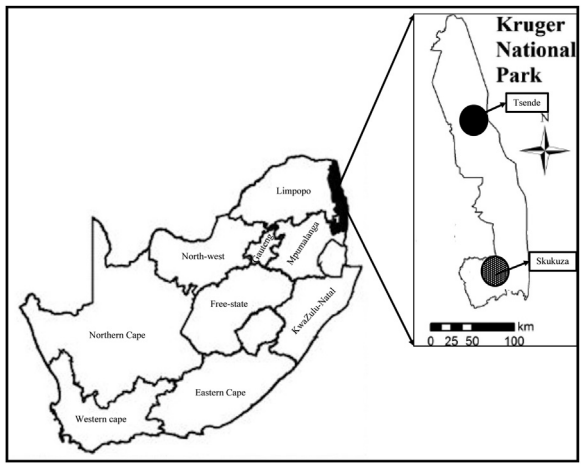

Figure 1. South African map displaying the geographic location of Kruger National Park and two selected experimental burnt plots, namely Tsende *(shaded circle)* and Skukuza *(dotted circle)*.

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 2×5 grid transect with a trap set (two individual pitfall traps) placed 2 m apart (Munyai and Foord 2015). The first pair of pitfall

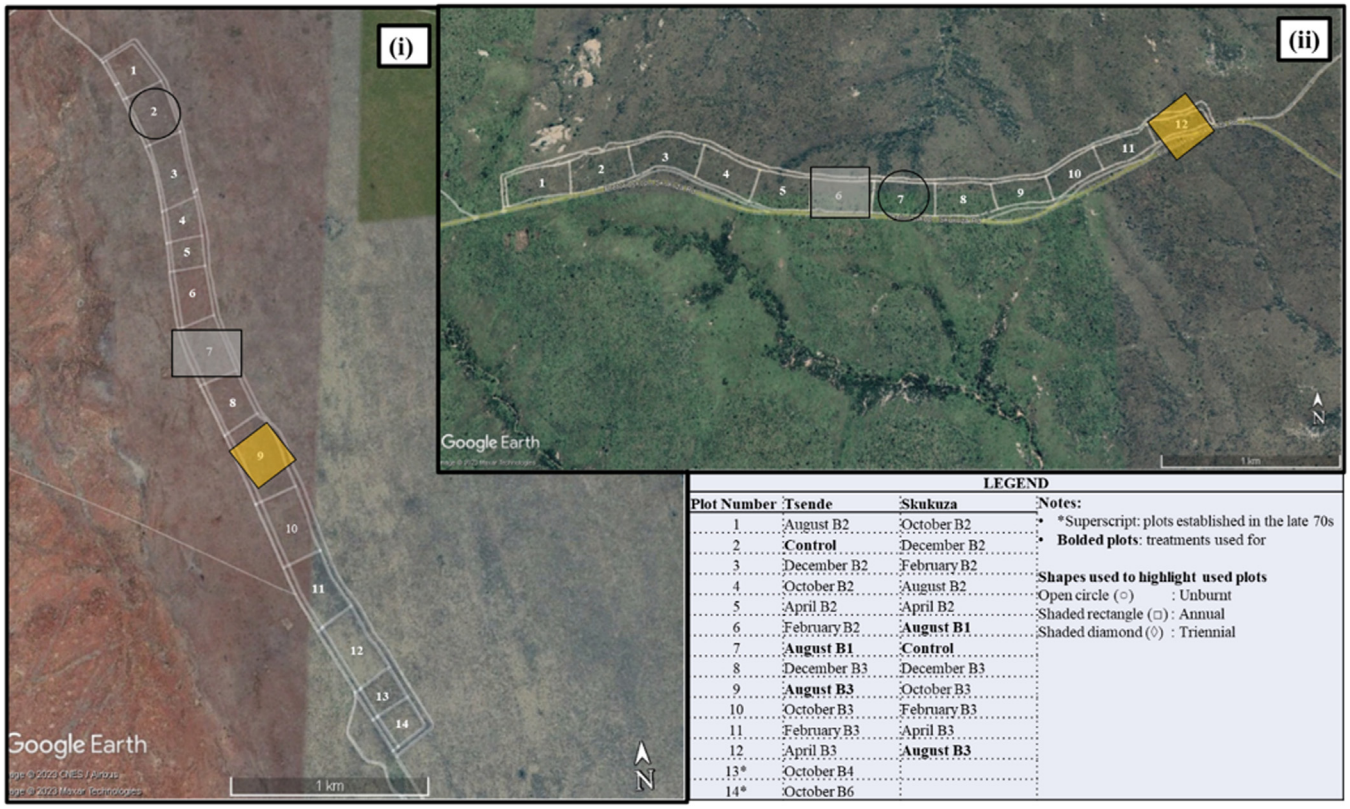

Figure 2. Aerial images showing the layout of Tsende (**i**) and Skukuza (**ii**) strings of experimental burnt plots. Treatment plots on both strings were described, and those used for the experiments (i.e., Unburnt [○], annually [□] and triennially [◊]) were highlighted.

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 ± 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 10-cm 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 coverage-based 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 χ^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[1]	93.4	73.7	117.8	169
Chao2	93.6 ± 13.1	69.6 ± 3.7	110.8 ± 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

[1] ICE indicates incidence-based coverage estimator; MM, Michaelis-Menten.

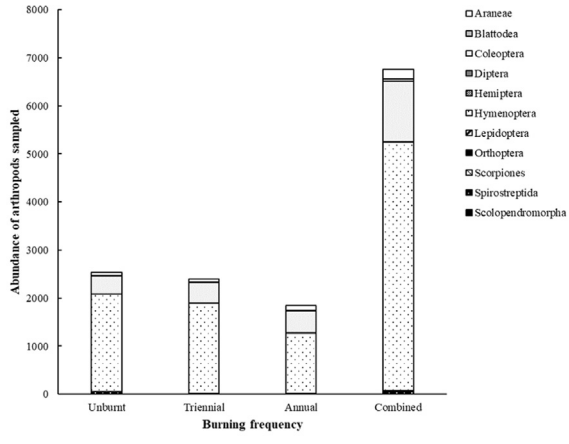

Figure 3. Abundance of arthropods sampled at the unburnt, annually burnt, and triennially burnt experimental burnt plots, solely and combined.

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, $P = 0.399$) 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,

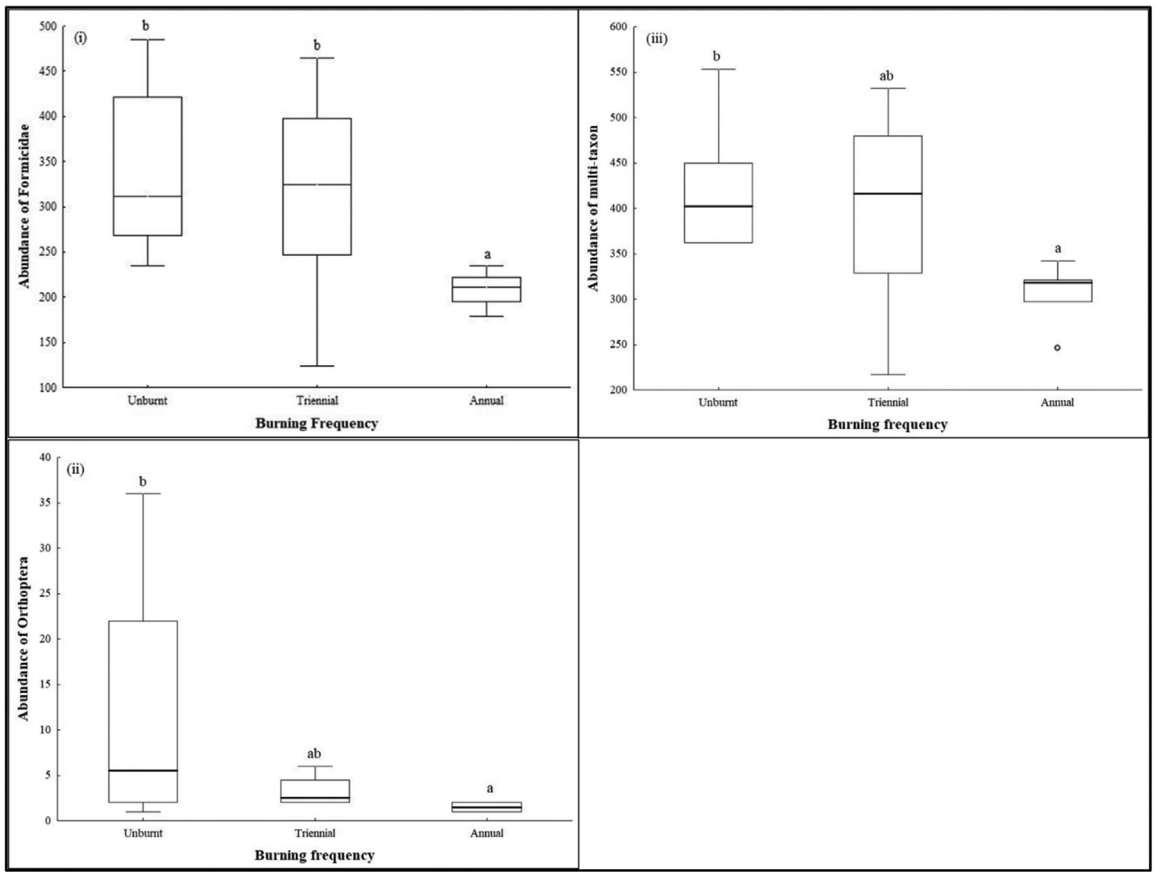

Figure 4. Boxplots showing the abundance of Formicidae (i), Orthoptera (ii), and multitaxon (iii) arthropods collected at the unburnt, triennially burnt, and annually burnt experimental burnt plots of Kruger National Park. Different letters above the bars show significant differences between treatments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

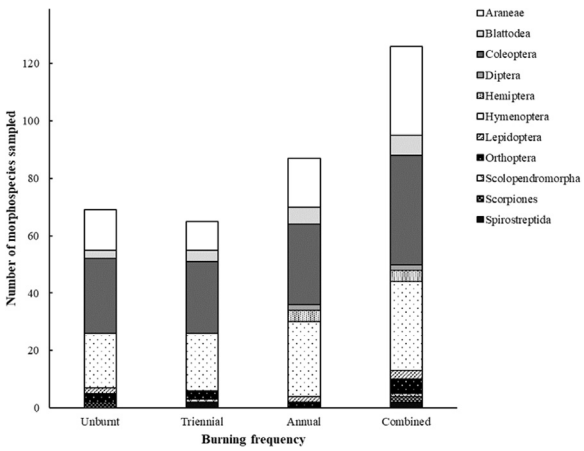

Figure 5. Number of arthropod species sampled at the unburnt triennially and annually burnt plots solely and combined.

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**	≠
Triennial	Annual	1.1929	0.1324	=

[1] = indicates similarity; ≠, dissimilarity.

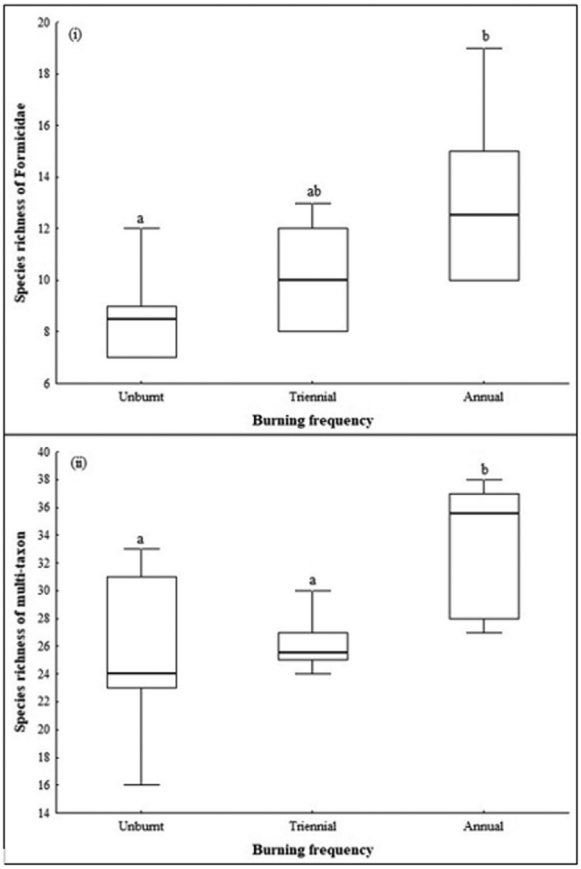

Figure 6. Boxplot showing the species richness of Formicidae (i) and multitaxon (ii) sampled at the annually, triennially burnt, and unburnt plots of Kruger National Park. Different letters above the bars show significant differences between treatments (Dunn's test: $P < 0.05$).

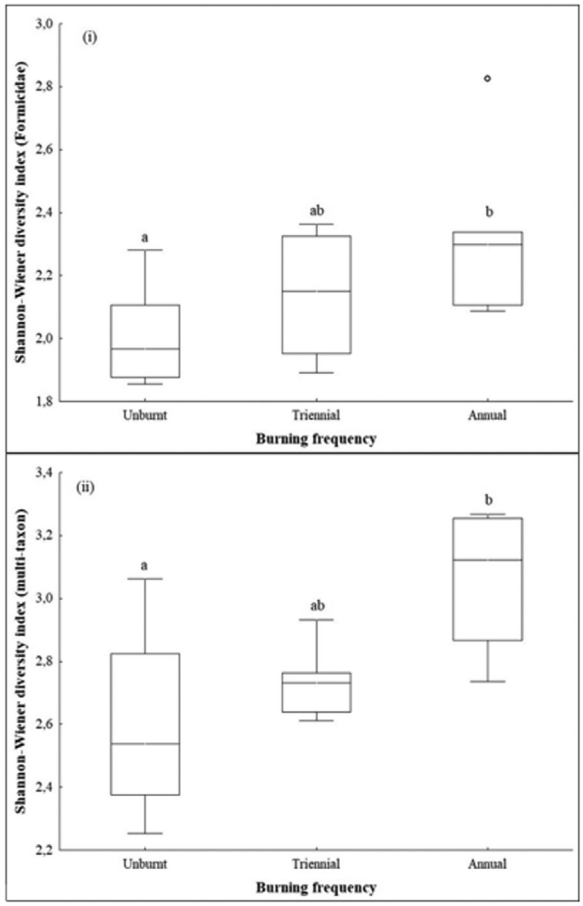

Figure 7. Boxplot showing the diversity (Shannon-Wiener diversity index) of arthropods (i.e., Formicidae [i] and multitaxon [ii]), sampled at the unburnt, annually burnt, and triennially burnt experimental burnt plots of Kruger National Park. Different letters above the bars show significant differences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

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 arthropod 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

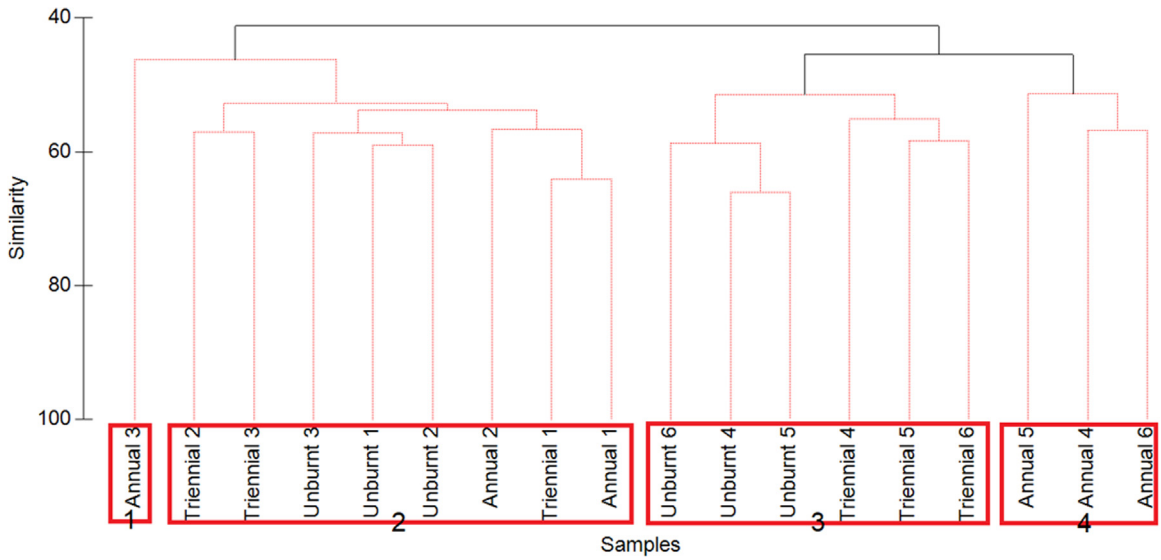

Figure 8. Classification tree showing arthropod assemblage similarities across unburnt, triennially burnt, and annually burnt plots at Kruger National Park. The group-average linking on Bray-Curtis species similarities was used to measure the similarities.

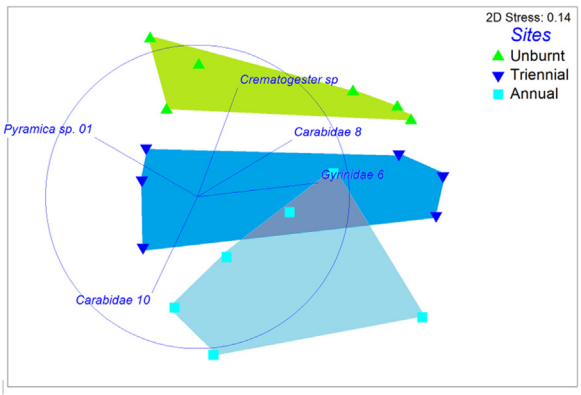

Figure 9. Nonmetric multidimensional scaling (nMDS) ordination showing the resemblance of arthropod species across unburnt, triennially burnt, and annually burnt plots surveyed at KNP. Polygons represent different plots, namely unburnt (green), triennially (dark blue), and annually burnt (light blue).

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 trienni-

ally 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 short-term 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.

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