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RESEARCH ARTICLE

The effects of fire frequency on vegetation structure and mammal assemblages in a savannah-woodland system

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Abstract

Fire frequency affects vegetation structure and composition in savannah- woodlands, with the potential indirect consequence of affecting the habitat choice and space use of large mammals. Understanding these responses can assist with the development of appropriate fire management policies to conserve co-existing species with different habitat requirements. In a natural experiment in Majete Wildlife Reserve, Malawi, we compared vegetation composition, woody plant structure and large (>5 kg) mammal assemblages on 10 frequently and 10 infrequently burnt 30-ha plots, that had fire return intervals of <2.5 and >6 years, respectively, between 2001 and 2019. Fire frequency had little effect on woody plant composition, but did affect grass species composition. Frequent burning reduced mean tree height from 4 to 3 m, woody plant cover from 59% to 35%, and resulted in the dominance of short-statured, less-palatable grasses. Many mammal species showed clear preferences for either frequently burnt (e.g. buffalo, zebra, kudu, impala and sable) or infrequently burnt (e.g. nyala, bush pig, baboon, common duiker and vervet monkey) areas, while others (e.g. elephants and black rhinoceros) were not selective. We conclude that establishing a mosaic of patches exposed to different fire frequencies would allow for the persistence of all mammal species in the area by creating an optimal range of habitat types.

KEYWORDS
camera trap, fire management, fire return interval, Malawi, pyric herbivory, species richness estimator, woody cover

Résumé

La fréquence des incendies affecte la structure et la composition de la végétation dans les savanes boisées,avec la conséquence indirecte potentielle d'affecter les choix d'habitat et d'utilisation de l'espacedes grands mammifères. La compréhension de ces réponses peut aider le développement de politiques de gestion des incendies appropriées pour la conservation des espèces cohabitantes ayant des exigences différentes en matière d'habitat. Dans le cadre d'une étude réalisée dans la réserve naturelle de Majete, au Malawi, nous avons comparé la composition de la végétation, la structure des plantes ligneuses et les groupements de grandsde grands mammifères (>5 kg) sur 10 parcelles de 30 ha brûlées fréquemment et 10 parcelles brûlées rarement avec des intervalles de retour du feu<2,5 et >6 ans, respectivement entre

2001 et 2019. Alors que la fréquence des feux affecte peu la composition des plantes ligneuses, son effet sur la composition des espèces herbacées est considérable. Les brûlis fréquents ont réduit la hauteur moyenne des arbres de 4 à 3 m, la couverture des plantes ligneuses de 59 % à 35 % et le nombre d'espèces d'herbacés de 59% à 35%. Ils ont aussi entraîné la dominance d'espèces herbacéesmoins appétissantes et de petite taille. De nombreuses espèces de mammifères ont montré une nette préférence pour les zones fréquemment brûlées (par exemple, le buffle, le zèbre, le koudou, l'impala et la zibeline) ou peu brûlées (par exemple, le nyala, le cochon de brousse, le babouin, le Céphalophe commun et singe vervet), tandis que d'autres (par ex.les éléphants et les rhinocéros noirs) ne montrent pas de préférence. Nous concluons que l'établissement d'unemosaïque de parcelles exposées à différentes fréquences de feu permettrait la persistance de toutes les espèces de mammifères dans la région en créant une gamme optimale de types d'habitats.

1 | INTRODUCTION

Fire is able to modify the structure, function and dynamics of savannah-woodland ecosystems (Bond & Archibald, 2003; Bond & Parr, 2010; Scholes & Walker, 1993) and is therefore managed in protected areas to achieve conservation goals by promoting preferred elements of fire regimes (i.e. fire size, intensity, season and frequency) (Nieman et al., 2021a). One such element that is often closely monitored and manipulated is fire frequency (Scholes & Archer, 1997). Fire frequency may be reduced to increase woody cover (Gandiwa & Kativu, 2009; Roques et al., 2001), to promote the regeneration of trees (Bond & Midgley, 2001; Prior et al., 2006) or to ensure the survival of tall trees (Furley et al., 2008), particularly in areas with high elephant densities (Vanak et al., 2012). A reduction in fire frequency may also prevent the spread of invasive alien species (te Beest et al., 2015), or protect fire-sensitive species or communities (Eby et al., 2015; Pfab & Witkowski, 2000). Conversely, high fire frequencies favour grasses and reduce woody biomass, allowing herbaceous vegetation to become dominant (Anderson et al., 2020), thus maintaining open ecosystems in areas that would otherwise be closed (Bond et al., 2005; Hoffmann et al., 2012). Furthermore, variations in fire frequencies can change plant species composition and diversity (Anderson et al., 2007; Archibald et al., 2005; Furley et al., 2008; Fynn et al., 2005), with decreased fire frequencies or complete fire exclusion typically resulting in decreased species richness and diversity (Furley et al., 2008; Savadogo et al., 2008; Smith et al., 2013; Uys et al., 2004).

Changes in the ratio of woody to herbaceous plants, and vegetation composition, due to changes in fire frequency may influence herbivory patterns (Smith et al., 2013), herbivore assemblages (Sensenig et al., 2010; Smit & Prins, 2015) and predator assemblages (Hopcraft et al., 2010). Small-bodied herbivores have to consume high-quality forage due to their small gastrointestinal systems, and thus, short ingesta retention times (Owen-Smith, 1988; du Toit & Owen-Smith, 1989), while larger herbivores can extract nutrition from poorer-quality food, provided that they can obtain it in sufficient quantities (Wilmshurst et al., 2000). Additionally, smaller herbivores are more vulnerable to predation (Hopcraft et al., 2012; Sinclair et al., 2003) and are thus more likely to avoid areas with dense vegetation (Riginos, 2015), potentially resulting in the selection of sub-optimal habitats (Burkepile et al., 2013). Conversely, mega-herbivores such as elephants and rhinoceros are not significantly constrained by predation and may thus prefer areas of high tree and shrub densities that have more browse available (Riginos, 2015; Smit & Prins, 2015). Herbivores thus face a constant trade-off between selecting optimal habitats that increase food quantity and quality, while minimising predation risk. The responses vary between species based on their body size, diet, susceptibility to predation and escape tactics (Burkepile et al., 2013; Hopcraft et al., 2010). Most predators rely on cover to increase hunting success (Balme et al., 2007; Eby et al., 2014; Loarie et al., 2013), and predators are thus expected to maximise prey capture rates by choosing landscapes with dense vegetation cover (Hopcraft et al., 2005). However, prey availability across the landscape might vary, presenting a trade-off between the probability of finding prey and actually capturing prey (Balme et al., 2007; Hopcraft et al., 2005).

Although the broad trends in mammal responses to resource gradients (Hopcraft et al., 2010) and the immediate response of mammal species to fire have been well-studied (Eby et al., 2014; Green et al., 2015; Sensenig et al., 2010; Zavala & Holdo, 2005), different species may also respond differently to the longer-term effects of fire (Bell, 1971; Kimuyu et al., 2017). Understanding mammal responses to differences in long-term mean fire frequency is thus necessary for the management and conservation of species and habitats. Additionally, such understanding can aid in the development of fire management policies in savannah-woodland ecosystems—especially if extremes on either end of the fire frequency spectrum could result in the reduction of the

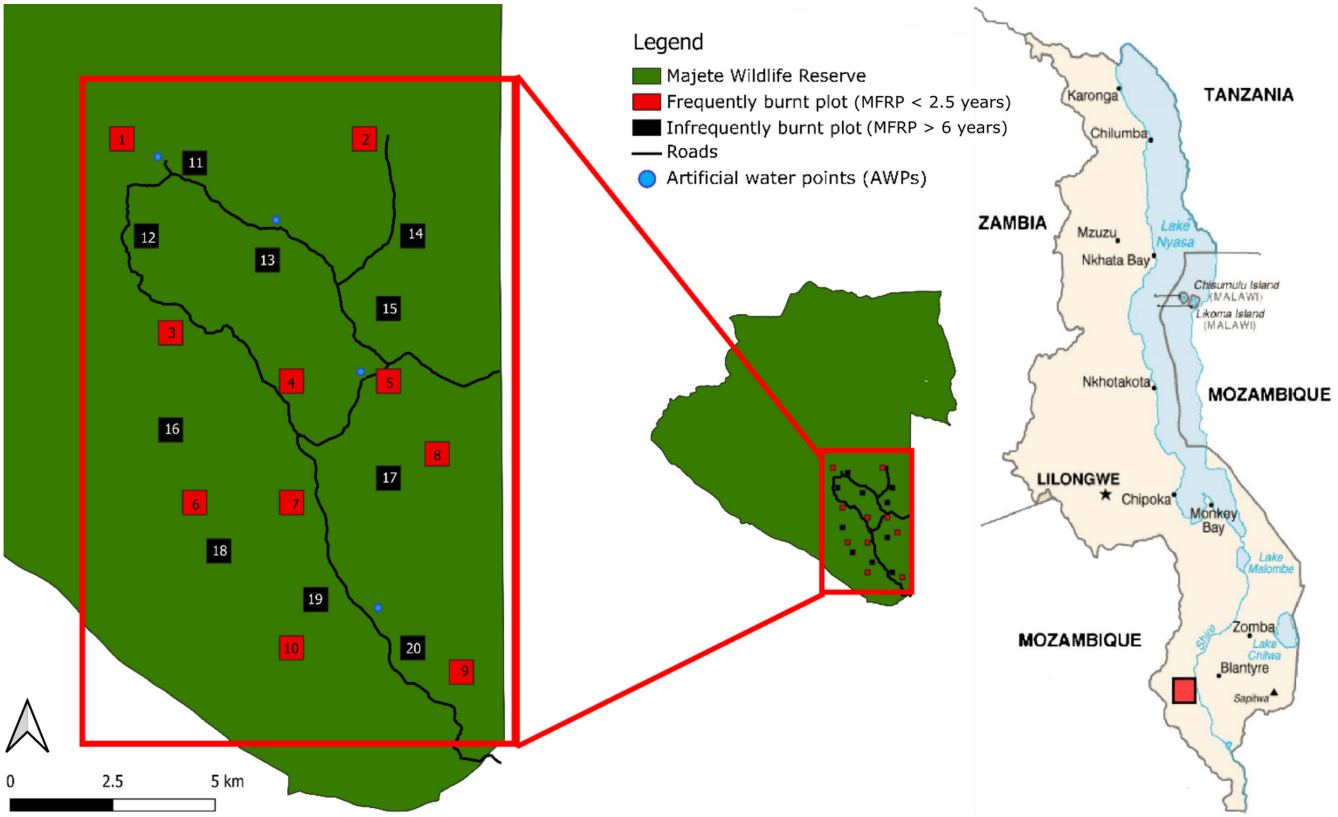
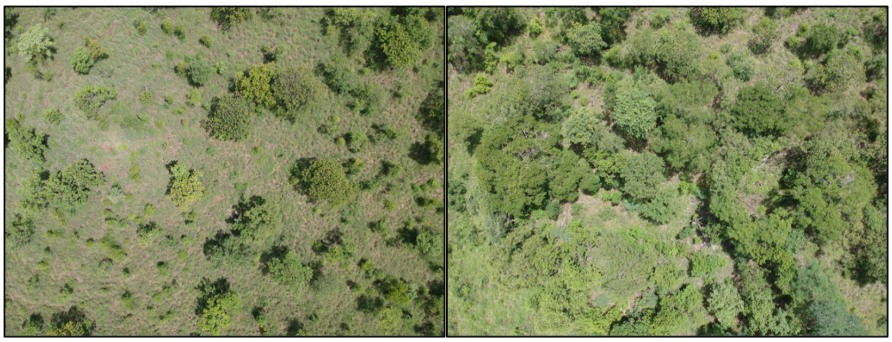


FIGURE 1 Study area located in the south-eastern corner of Majete Wildlife Reserve, showing the location of the 20 sampling sites that either experience high (>6 years) or low (<2.5 years) fire frequencies (MFRP, mean fire return period)

FIGURE 2 Example of the aerial photographs used to estimate canopy cover at frequently burnt (left) and infrequently burnt (right) plots



preferred habitat of any particular species. For example, changes in fire policy to incorporate fine-scale patchiness within the matrix (i.e. patch mosaic burning) in the Kruger National Park, South Africa, have led to improved habitat to aid in the conservation of rare roan antelope (*Hippotragus equinus*) (Kroger & Rogers, 2005). Furthermore, developing long-term datasets on mammal responses to differences in fire components may assist adaptive management decisions, particularly with regard to uncertainty in fire dynamics and future global change. The aims of this study were to determine whether patches of habitat experiencing markedly different long-term fire frequencies in an African savannah-woodland protected area have correspondingly different (i) woody and grass floristic composition, (ii) woody cover and density, and (iii) large (>0.5 kg) mammal assemblages.

2 | METHODS

2.1 | Study area

The study area (~148 km^2; Figure 1) is situated in the south-eastern corner of Majete Wildlife Reserve (MWR, ~700 km^2), in the Lower Shire Valley in the south of Malawi. The vegetation in the study area comprises floristically rich shrublands and woodlands dominated by the genera *Combretum*, *Terminalia*, *Vachellia*, *Senegalia* and *Sclerocarya* (Nieman et al., 2021b). Miombo species (*Brachystegia* and *Julbernadia*) dominate the remainder of MWR, but are mostly absent from the study area. The area has a tropical climate (Staub et al., 2013) with three distinct seasons: the wet season (December to March), the cool dry season (April to August) and the hot dry

season (September to November). The topography is relatively gentle, with only a few rocky outcrops, and elevation is typically below 250 m asl. Mean annual precipitation ranges between 680 and 800 mm (Hall-Martin, 1972). Soils are shallow, stony, lithosols of poor nutrient status, with fertile alluvial soil occurring along a few seasonal river beds (Bell, 1984). No perennial rivers occur in the study area, but seasonal streambeds and waterholes contain ample water for a few months during the wet season. Additionally, four artificial water points supply water to animals in the study area throughout the year. An estimated 39 large mammal species (>0.5 kg) occur in the study area (Bell, 1984; Clarke, 1983; Unpublished management reports). Fires occur at intervals of 4–6 years, and although managers of the MWR wish to promote low-intensity fires in the early dry season, most burning is in the form of unplanned wildfires of high-intensity during the late-dry season (Nieman et al., 2021c).

2.2 | Study plot selection

Twenty 30-ha plots were chosen for study based on their past (2001–2019) fire frequencies as determined by Nieman et al. (2021c) using remotely sensed Moderate Resolution Imaging Spectroradiometer (MODIS) images. Ten 'infrequently burnt' plots (30 ha) were selected in areas that experienced three or less fires between 2001 and 2019 (mean fire return period >6 years), and 10 'frequently burnt' plots were selected in areas that experienced between 8 and 13 fires (mean fire return period <2.5 years) over the same time period (Figure 1). A plot was considered to have burnt in any given year if >30% of the MODIS pixels on that plot burned. Sites that burnt in 2019 were not selected to eliminate the potential short-term effects of fire, that is ash fertilisation, and the influx of species to recently burnt sites (Eby et al., 2014). The selected plots were at similar elevation (range: 201–289 m, mean = 225.1 m), occurred on relatively homogenous soils and in a similar vegetation type as noted in the study area description. Plots were also evenly distributed along a gradient of distance from permanent water points (Frequently burnt plots: range: 608–3889 m, mean = 2248.7 m; Infrequently burnt plots: range: 649–4351 m, mean = 2002.1 m), roadways (Frequently burnt: range: 247–2714 m, mean = 1028.4 m; Infrequently burnt: range: 435–2298 m, mean = 1018.2 m), and fences (Frequently burnt: range: 985–8379 m, mean = 3743.3 m; Infrequently burnt: range: 1860–7735 m, mean = 3965.3 m).

2.3 | Data collection

Data collection took place during the wet season (January to April) of 2020. Data collection was confined to the wet season to ensure that vegetation was in an optimal growing condition (i.e. forage material was not a limiting factor affecting the habitat choice of mammals), and that water resources were evenly and abundantly distributed throughout the study area (to eliminate the effect of species aggregating around a few artificial water points). Sampling in the wet season also reduced the potential interfering effects from dry season fires (e.g. the influx of herbivores to burnt sites due to the abundance of nutritious post-fire regrowth, changes in movement patterns of mammals escaping fires, or potential destruction of cameras or removal of biomass by fire).

2.4 | Vegetation sampling

The floristic composition of both grasses and woody vegetation, as well as the structure of woody vegetation, was assessed on each of the frequently and infrequently burnt plots. First, both woody (tree and shrub) and grass species that occurred within a 15 m radius of the 30-ha plot centroid were recorded. Species were identified on site where possible, and a physical sample was taken for further identification where uncertainty existed. Woody and grass assemblages were tested for similarity between frequently and infrequently burnt plots using an analysis of similarity (ANOSIM). Grass species were additionally categorised as either Decreaser (species that decrease when rangeland is under- or overgrazed), Increaser I (species that increase when rangeland in under- and/or selectively grazed), or Increaser II (species that increase when rangeland is overgrazed) species (Trollope et al., 1990). Secondly, canopy cover of trees was estimated from aerial photographs taken from 50 m directly above the plot centroid using a drone (DJI™ SPARK™) (Figure 2). Canopy cover as a percentage of total ground area was determined by overlaying each photograph with a grid of 1900 squares (0.05 m^2), and counting the number of grid cells that were >50% covered by the canopies of woody plants. The canopy cover at each plot was thereafter compared between frequently and infrequently burnt plots using a non-parametric Mann–Whitney *U*-test for independent samples. Finally, the stem circumference, total tree height, stem height (distance from the ground to the first branch) and total number of stems was measured for each tree or shrub species within the circular plot of 15 m radius. In single-stemmed plants, stem circumference was measured just above the buttress swelling, while in forked plants, stem circumference was measured just below the fork. If the fork was too low to permit measurement, the thickest stem was measured. Stem and tree heights were measured with a 3-m graduated pole, which was further raised up by a person of known body height when needed. For taller trees, a rangefinder (Nikon PROSTAFF 5) was used to estimate height. The medians of all measurements of woody plants were compared between frequently and infrequently burnt plots with the use of non-parametric Mann–Whitney *U*-tests. In all analyses, *p*-values <0.05 were considered significant.

2.5 | Large mammal assemblages

Large mammal species occurrence on plots was established using two Cuddeback X-Change™ camera traps (Model 1279) in each plot (total of 40 cameras). Initially, the cameras were placed at random

locations in the study area, but when only 3.28 independent photo events per trap (range: 0–11) were recorded in the 546 camera trap nights (2 weeks), we decided to move the camera traps to active game trials to increase the photo capture rate (Burton et al., 2015). Two camera traps were placed within 50 m of the plot centroid in each of the 20 plots, spaced 200–250 m apart and mounted 30–45 cm off the ground on trees near active game trails (Rich et al., 2016). A 1-min delay was set between successive capture events, and nocturnal photographs were captured with Xenon white flash assistance. The camera traps remained in place for 12 weeks (January to April 2020) and were checked every 2 weeks to replace the batteries, download the photographs and to ensure that the cameras were still operational. Vegetation obstructing the camera view was trimmed at each visit to prevent false trigger events, but not to such an extent that the habitat was noticeably transformed. To minimise autocorrelation in the data, a 30-min lapse between same-species photo events was used to determine independent events at the same camera station (Drouilly & O'Riain, 2019; Rich et al., 2016).

The completeness of the dataset (i.e. whether a sufficient representative proportion of the mammal assemblage present in the study area was captured) was evaluated by generating sample-based rarefaction curves (R package 'vegan' – Oksanen et al., 2019), where sampling size was deemed sufficient when the rarefaction curve approached an asymptote (i.e. when the expected number of species did not increase with the addition of more individuals to the sample) (Begossi, 1996). Species richness and diversity values were calculated and compared between frequently and infrequently burnt plots, based on the observed species richness (N_{obs}), including the Shannon's diversity index (H'), Simpson's diversity (λ) and reciprocal diversity ($1/\lambda$) indices. Values of N_{obs} may however be heavily dependent on sampling effort, and six non-parametric incidence-based species richness estimators were therefore also used to estimate the expected species richness that would be reached if sampling continued indefinitely (Colwell & Coddington, 1994; Gotelli & Colwell, 2001). The estimators used were as follows: Chao 2, a bias-corrected form of Chao 2 (Chao 2-bc); iChao 2, the incidence-based coverage estimator (ICE); and two Jackknife estimators (Jack 1 and Jack 2). These estimators assume a closed community (i.e. community composition does not change throughout the duration of the study), and Jackknife estimators assume temporal consistency in species' capture probability (Burnham & Overton, 1978). Since the survey was limited to a single season, the first assumption is assumed to be met. However, due to differences in species behaviour, the probability of capture could vary temporally. For each of the calculations, the sample order was randomised 100 times to compute mean statistics at each sample order (Colwell & Coddington, 1994; Palmer, 1991).

Photo capture rates (i.e. detection frequency or the relative abundance index [RAI]) for each species at each camera station was calculated as the number of independent photo events expressed as a percentage of camera trap days. The RAI of species does not necessarily reflect the true abundance of a species in a community (Sollmann et al., 2013), but can provide relative findings for comparative studies (Drouilly et al., 2018). The mean capture rate of each species in frequently burnt or infrequently burnt plots was then compared using a non-parametric Mann–Whitney *U*-test. Measures of species richness and photo capture rates can provide a good estimate of the effects of fire frequency on species assemblages, but may also be biased due to the variability in detection rates between species, thereby potentially creating a false representation of the effects of fire frequency histories (Zipkin et al., 2010). We therefore calculated the detection probability (p) of all species in an occupancy modelling framework (R package 'unmarked' – Fiske & Chandler, 2011) to ensure that there was no significant difference between plot types that could invalidate the results. Plot type was included as a covariate variable, and detection histories were set at 14-day intervals (total of six detection periods). Model selection was based on Akaike information criterion (AIC) values, where the lowest AIC value was considered the best-fit model. All analyses were conducted in R v4.0.2.

3 | RESULTS

3.1 | The effect of fire frequency on vegetation

3.1.1 | Plant species composition

The species composition of tree and shrub assemblages was not significantly different between frequently and infrequently burnt plots (ANOSIM: $R = 0.1168$; $p > 0.05$), and the most species-rich genus found on both frequently and infrequently burnt plots was *Combretum* (seven species). A total of 27 and 26 woody species were recorded in frequently and infrequently burnt plots respectively. Genera found at >1 of the frequently burnt plots were *Combretum*, *Diospyros*, *Senegalia*, *Terminalia*, *Pseudolachnostylis*, *Colophospermum*, *Pterocarpus* and *Vachellia*, and the most frequently recorded species (≥4 plots) were *Diospyros kirkii*, *Combretum apiculatum*, *Combretum zeyheri* and *Terminalia mollis*. Genera found at >1 of the infrequently burnt plots included *Combretum*, *Diospyros*, *Senegalia*, *Terminalia*, *Pterocarpus*, *Colophospermum* and *Diplorhynchus*, while the most frequently recorded species (≥4 plots) were *Diospyros kirkii*, *Combretum zeyheri*, *Combretum adenogonium*, *Senegalia nigrescens* and *Terminalia sericea*. A total of 13 grass species were found on all plots combined, with nine species each on the frequently and infrequently burnt plots respectively. The grass species most often recorded at frequently burnt plots (≥3 plots) were *Heteropogon contortus*, *Digitaria eriantha* and *Schmidtia pappophoroides*. The grass species most often recorded at infrequently burnt plots (≥3 plots) were *Digitaria eriantha*, *Panicum maximum* and *Ischaemum afrum* (Table 1). Infrequently burnt plots were thus characterised by palatable Decreaser species with high forage values, while frequently burnt plots were characterised by less-palatable Increaser II species with relatively lower forage values (Table 2).

TABLE 1 Number of plots on which woody and grass species were recorded at frequently ($n = 10$) and infrequently burnt ($n = 10$) plots

Life form	Species	Frequently burnt	Infrequently burnt
Trees and shrubs	*Allophylus africanus*	1	0
	Bolusanthus speciosus	1	0
	Brachystegia boehmii	0	1
	Brachystegia spiciformis	0	1
	Bridelia cathartica	1	0
	Colophospermum mopane	2	2
	Combretum adenogonium	3	4
	Combretum apiculatum	4	3
	Combretum hereroense	1	2
	Combretum imberbe	1	3
	Combretum molle	2	1
	Combretum mossambicense	0	1
	Combretum zeyheri	4	4
	Commiphora mollis	1	1
	Cremaspora triflora	0	1
	Dalbergia melanoxylon	1	0
	Diospyros kirkii	5	6
	Diospyros mespiliformis	2	3
	Diplorhynchus condylocarpon	1	2
	Hyphaene coriacea	0	1
	Mundulea sericea	1	0
	Philenoptera violacea	1	0
	Phoenix reclinata	0	1
	Pseudolachnostylis maprouneifolia	3	1
	Pterocarpus rotundifolius	2	3
	Searsia tenuiervis	1	0
	Senegalia burkei	2	1
	Senegalia galpinii	2	2
	Senegalia nigrescens	2	4
	Sterculia quinqueloba	1	0
	Terminalia mollis	4	2
	Terminalia sericea	2	4
	Vachellia nilotica	2	1
	Ziziphus mucronata	0	1
Grasses	*Aristidia adscensionis*	2	0
	Digitaria eriantha	3	7
	Eragrostis rigidor	1	0
	Eragrostis superba	2	1
	Heteropogon contortus	4	2
	Hyparrhenia hirta	2	1
	Ischaemum afrum	0	3
	Panicum deustum	0	2
	Panicum maximum	1	3
	Rottboelia cochinchinensis	2	0
	Schmidtia pappophoroides	3	0
	Sporobolus festivus	0	1
	Urochloa mosambicensis	0	2

TABLE 2 Categories and palatability characteristics of grass species associated with either frequently or infrequently burnt plots (Roodt, 2011; van Oudtshoorn, 2012). See text for a definition of categories

Preference for fire frequency	Grass species	Category	Palatability
Species associated with frequently burnt areas	*Aristidia adscensionis*	Increaser II	Low
	Eragrostis rigidor	Increaser II	Low, except when green
	Eragrostis superba	Increaser II	Average
	Heteropogon contortus	Increaser II	Only palatable in the wet season
	Hyparrhenia hirta	Increaser I	High
	Rottboelia cochinchinensis	Increaser I	Low
	Schmidtia pappophoroides	Increaser II	High
Species associated with infrequently burnt areas	*Digitaria eriantha*	Decreaser	High
	Ischaemum afrum	Decreaser	Low
	Panicum deustum	Decreaser	High
	Panicum maximum	Decreaser	High
	Sporobolus festivus	Increaser I	High
	Urochloa mosambicensis	Increaser II	High

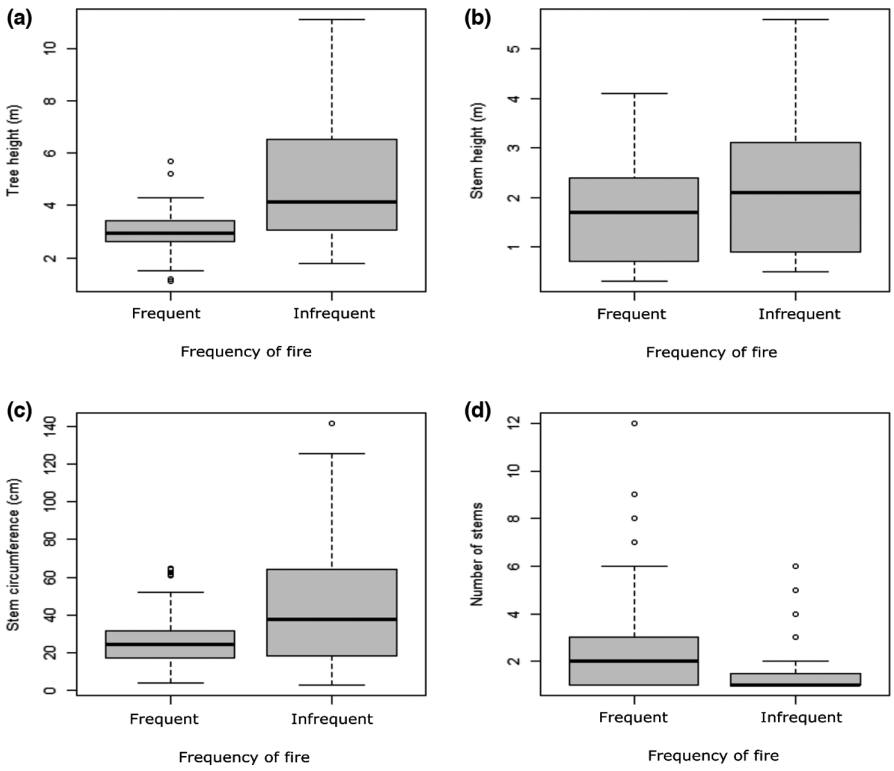


FIGURE 3 Measurements of tree and shrub (a) total height, (b) stem height, (c) stem circumference and (d) total number of stems in frequently burnt and infrequently burnt plots. Box and whisker diagrams indicate the median, 25th and 75th percentiles respectively; open circles show outliers

3.1.2 | Woody plant structure

Frequent burning significantly reduced the cover, height and stem diameter of woody vegetation, and resulted in more multi-stemmed plants. Woody canopy cover was significantly lower on frequently versus infrequently burnt plots (medians of 35% and 58% respectively; $W = 100$; $p < 0.0001$). The stem circumference, stem height, tree height and number of stems were measured for 205 and 211 trees or shrubs in the frequently and infrequently burnt plots respectively.

Median tree height was significantly higher in infrequently burnt plots (median = 4.10 m) than in frequently burnt plots (median = 2.94 m) ($W = 4284$; $p < 0.001$; Figure 3a). Median stem height was also higher in infrequently burnt plots (median = 2.10 m) than in frequently burnt plots (median = 1.70 m) ($W = 3548.5$; $p < 0.05$; Figure 3b) Median stem circumference was significantly greater in

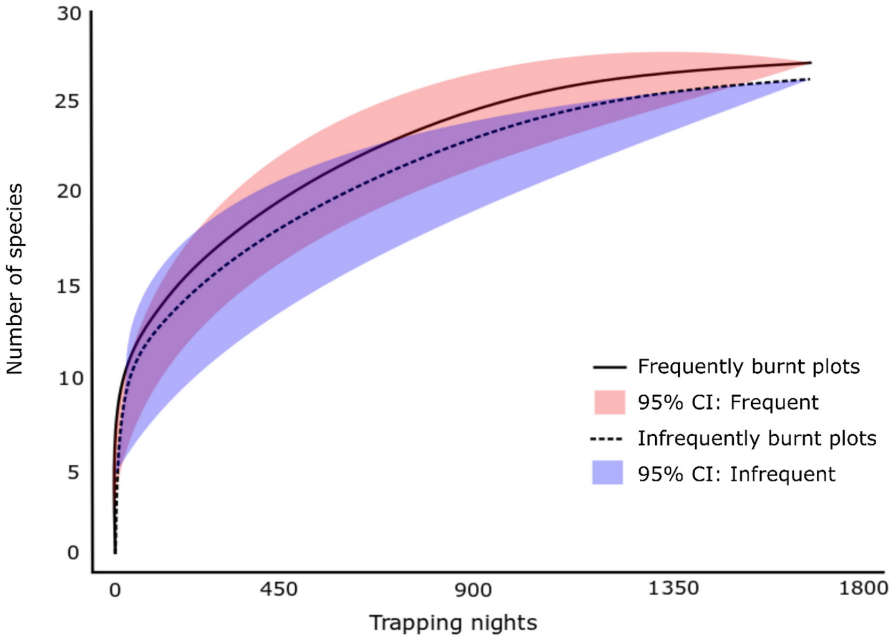


FIGURE 4 Rarefaction curves for frequently burnt and infrequently burnt plots in the study area of Majete Wildlife Reserve, expressed over the same sampling effort (camera trap nights). Shaded polygons represent 95% confidence intervals (CI) drawn from 100 sample-order randomisations

TABLE 3 Observed and estimated (±SE) species richness for mammal species in 10 frequently and 10 infrequently burnt plots

	Frequently burnt	Infrequently burnt	Combined
Number of species recorded (N_{Obs})	27	25	29
Trapping nights	1598	1633	3231
Photo events$_{Total}$	1286	1440	2726
Chao2	27.8 ± 1.4	25.9 ± 1.6	30.0 ± 1.8
Chao2-bc	27.5 ± 1.0	25.4 ± 1.0	29.3 ± 0.9
iChao2	28.0 ± 0.8	26.0 ± 1.1	30.0 ± 1.2
ICE	28.7 ± 2.0	26.8 ± 1.6	29.8 ± 1.3
Jack 1	29.9 ± 2.4	27.6 ± 2.5	31.0 ± 2.0
Jack 2	28.3 ± 3.9	26.2 ± 3.8	31.0 ± 3.3
Simpson's diversity	0.15	0.28	0.20
Simpson's reciprocal	6.53	3.57	4.88
Shannon diversity	3.27	2.83	3.15

infrequently burnt plots (median = 38 cm) than in frequently burnt plots (median = 22 cm) ($W = 3621.5$; $p < 0.05$; Figure 3c). Woody species in frequently burnt plots had significantly more stems (median = 2) than in infrequently burnt plots (median = 1) ($W = 2054$; $p < 0.001$; Figure 3d).

3.2 | The effect of fire frequency on large mammal assemblages

Data were obtained from 3231 camera trap nights (1598 on frequently burnt plots and 1633 on infrequently burnt plots). Nine camera traps were affected by disruptions due to technical failures or animal disturbance, resulting in the loss of 129 camera trap nights. A total of 29 mammal species were recorded, all of which were >5 kg in body size. Species richness was higher in frequently burnt plots (27, compared to 25 in infrequently burnt plots). However, the rarefaction curve for both frequently burnt and infrequently burnt plots followed a similar trend, with a relatively steep initial ascent indicating a high proportion of abundant species, and eventually reaching a near asymptote indicating that most of the mammals in the study area had been recorded (Figure 4). All species richness estimators produced species richness values higher than the observed species richness, indicating that up to five species were missed in this survey in both the frequently burnt and infrequently burnt plots (Table 3). The community in the frequently burnt plots was slightly more diverse ($H'_{frequent} = 3.27$; $1/\lambda_{frequent} = 6.53$) than the one in infrequently burnt plots ($H'_{infrequent} = 2.83$; $1/\lambda_{infrequent} = 3.57$).

The number of photo events was higher on infrequently burnt plots (Tables 4 and 5). The most commonly recorded (>100 independent capture events) species in frequently burnt plots were warthog (*Phacochoerus africanus*) (400 capture events), impala (*Aepyceros melampus*) (196 capture events), kudu (*Tragelaphus strepsiceros*) (129 capture events) and sable antelope (*Hippotragus niger*) (108 capture events). The most commonly recorded (>100 independent capture events) species in infrequently burnt plots were warthog (733 capture events) and yellow baboon (*Papio cynocephalus*) (108 capture events). Nine species were detected only five times or less for the duration of the sampling period, and two species were detected only once.

The probability of detection (p) of all species was not significantly affected by fire frequency, and the mean p in both frequently burnt and infrequently burnt plots was 0.04 (range: 0.004–0.32). Several species had particularly low detection rates, for example aardvark (*Orycteropus afer*) ($p = 0.0042$), civet (*Civettictis civetta*) ($p = 0.0047$), serval (*Leptailurus serval*) ($p = 0.0054$), Cape porcupine (*Hystrix africaeaustralis*) ($p = 0.0057$) and Lichtenstein's hartebeest (*Alcelaphus*

TABLE 4 Total photograph events, mean capture rate (i.e. detection probability) with Mann–Whitney *U*-test statistics (*W*-value and *p*-value), naïve occupancy, and detection probability (*p*) for all species with >10 independent capture events at frequently burnt and infrequently burnt plots. Models were considered significant at $p < 0.05$ (ns = $p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ****$p < 0.0001$)

Species	Predominant feeding guild	Total events: frequent	Total events: infrequent	Mean capture rate: frequent	Mean capture rate: infrequent	*W*-value	*p*-value	Detection probability (*p*): overall
Species that significantly preferred infrequently burnt areas								
Warthog (*Phacochoerus africanus*)	Herbivore: Grazer	400	733	25.03	44.89	121.5	0.035*	0.316
Bush pig (*Potamochoerus larvatus*)	Omnivore	2	19	0.13	1.16	114	<0.01**	0.015
Grey duiker (*Sylvicapra grimmia*)	Herbivore: Browser	42	93	2.63	5.70	108.5	0.013*	0.047
Nyala (*Tragelaphus angasii*)	Herbivore: Browser	8	57	0.50	3.49	84	<0.001***	0.045
Baboon (*Papio cynocephalus*)	Omnivore	29	108	1.81	6.61	53.5	<0.0001****	0.051
Species that significantly preferred frequently burnt areas								
Impala (*Aepyceros melampus*)	Herbivore: Mixed-feeder	196	71	12.27	4.35	240.5	<0.01**	0.123
Kudu (*Tragelaphus strepsiceros*)	Herbivore: Browser	129	62	8.07	3.80	286	0.020*	0.069
Cape buffalo (*Syncerus caffer*)	Herbivore: Grazer	92	50	5.76	3.06	268.5	0.049*	0.068
Sable (*Hippotragus niger*)	Herbivore: Grazer	108	65	6.76	3.98	270.5	0.047*	0.058
Waterbuck (*Kobus ellipsiprymnus*)	Herbivore: Grazer	92	48	5.76	2.94	267.5	0.048*	0.050
Zebra (*Equus quagga*)	Herbivore: Grazer	55	18	3.44	1.10	256.5	0.014*	0.043
Species that had no significant preference for either plot type								
Elephant (*Loxodonta africana*)	Herbivore: Mixed-feeder	68	46	4.26	2.82	185	>0.05 ns	0.060
Bushbuck (*Tragelaphus sylvaticus*)	Herbivore: Browser	16	29	1.00	1.78	197	>0.05 ns	0.032
Reedbuck (*Redunca arundinum*)	Herbivore: Grazer	8	3	0.50	0.18	211.5	>0.05 ns	0.024
Black rhinoceros (*Diceros bicornis*)	Herbivore: Browser	6	5	0.38	0.31	210	>0.05 ns	0.024

TABLE 5 Total photograph events, mean capture rate (i.e. detection probability) with Mann–Whitney *U*-test statistics (*W*-value and *p*-value), naïve occupancy, and detection probability (*p*) for all species with <10 independent capture events at frequently burnt and infrequently burnt plots. Models were considered significant at $p < 0.05$ (ns = $p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ****$p < 0.0001$)

Species	Predominant feeding guild	Total events: frequent	Total events: infrequent	Mean capture rate: frequent	Mean capture rate: infrequent	*W*-value	*p*-value	Detection probability (*p*): overall
Species with an inclination towards infrequently burnt areas								
Honey badger (*Mellivora capensis*)	Omnivore	0	3	0.00	0.18	190	>0.05 ns	0.042
Spotted hayena (*Crocuta crocuta*)	Carnivore	2	6	0.13	0.37	188	>0.05 ns	0.014
Vervet monkey (*Chlorocebus pygerythrus*)	Omnivore	0	8	0.00	0.49	160	0.040*	0.021
Cape porcupine (*Hystrix africaeaustralis*)	Herbivore: Roots, tubers and bulbs	2	6	0.13	0.37	169	>0.05 ns	0.006
Species with an inclination towards frequently burnt areas								
Eland (*Tragelaphus oryx*)	Herbivore: Mixed-feeder	5	0	0.31	0.00	220	>0.05 ns	0.021
Sharpe's grysbok (*Raphicerus sharpei*)	Herbivore: Browser	7	2	0.44	0.12	212	>0.05 ns	0.017
Lichtenstein's hartebeest (*Alcelaphus buselaphus lichtensteinii*)	Herbivore: Grazer	2	0	0.13	0.00	220	>0.05 ns	0.006
Leopard (*Panthera pardus*)	Carnivore	3	1	0.19	0.06	210.5	>0.05 ns	0.010
Lion (*Pantera leo*)	Carnivore	5	3	0.31	0.18	219.5	>0.05 ns	0.009
Aardvark (*Orycteropus afer*)	Insectivore (ants and termites)	4	1	0.25	0.06	221	>0.05 ns	0.004
Species with no clear inclination towards either plot type								
Serval (*Leptailurus serval*)	Carnivore	1	1	0.06	0.06	199.5	>0.05 ns	0.005
Caracal (*Caracal caracal*)	Carnivore	1	0	0.06	0.00	210	>0.05 ns	0.009
Civet (*Civettictis civetta*)	Carnivore	2	1	0.13	0.06	210	>0.05 ns	0.005
Cheetah (*Acinonyx jubatus*)	Carnivore	1	0	0.06	0.00	210	>0.05 ns	0.008

buselaphus lichtensteinii) ($p = 0.0057$). A total of 12 species had mean captures rates that were significantly different between plot types. The mean capture rate of buffalo (*Syncerus caffer*) ($W = 268.5$; $p < 0.05$), impala ($W = 240.5$; $p < 0.01$), kudu ($W = 286$; $p < 0.05$), sable antelope ($W = 270.5$; $p < 0.05$), waterbuck (*Kobus ellipsiprymnus*) ($W = 267.5$; $p < 0.05$) and zebra (*Equus quagga*) ($W = 256.5$; $p < 0.05$) was significantly higher on frequently burnt plots, while the mean capture rate of yellow baboon ($W = 53.5$; $p < 0.0001$), bush pig (*Potamochoerus larvatus*) ($W = 114$; $p < 0.01$), common duiker (*Sylvicapra grimmia*) ($W = 108.5$; $p < 0.05$), nyala (*Tragelaphus angasii*) ($W = 84$; $p < 0.001$), vervet monkey (*Chlorocebus pygerythrus*) ($W = 160$; $p < 0.05$) and warthog ($W = 121.5$; $p < 0.05$) was significantly higher in infrequently burnt plots.

4 | DISCUSSION

4.1 | The effect of fire frequency on vegetation

Fire frequency had no detectable effect on the floristic composition of most trees and shrubs in the plots sampled in this study, and this is similar to the findings of other studies in African savannahs (Gandiwa & Kativu, 2009; Nefabas & Gambiza, 2007; Nyazika et al., 2017; Sabiti & Wwin, 1988; Shackleton & Scholes, 2000; Tafangenyasha, 1997). The exceptions were miombo species of the genus *Brachystegia*, and palm species of the genera *Hyphaene* and *Phoenix*, which were only present on infrequently burnt plots. The distribution of *Brachystegia* is predominantly determined by edaphic and topographical factors (Munishi et al., 2011), but tree regeneration may be impaired by excessively frequent fires (Ryan & Williams, 2011), thus potentially explaining their absence from frequently burnt plots. Similarly, excessive fires may limit the recruitment of palm species by killing seedlings (Martins & Shackleton, 2017), while the absence of fire may allow sufficient time for fallen fruits to become buried and germinate (Fanshawe, 1967). Although the floristic composition of woody plants was unaffected by fire frequency, this was not the case with woody plant structure, where increases in fire frequency resulted in marked decreases in woody plant cover, height and stem diameters, mirroring findings elsewhere (see, for example, Case & Staver, 2017; Enslin et al., 2000; Gandiwa & Kativu, 2009; Higgins et al., 2007; Kennedy & Potgieter, 2003; Nyazika et al., 2017; Russell et al., 2019; Shackleton & Scholes, 2000; Sweet, 1982). Frequent fires decrease seedling establishment and post-fire regeneration rates of woody species, ultimately resulting in more open, less dense vegetation. Similarly, frequent fires may confine trees to smaller size classes by maintaining them within a 'fire trap' (Bond & van Wilgen, 1996). Consequently, the incidence of tall trees significantly decreases, and savannah-woodland landscapes may eventually be converted to shrublands (Tainton et al., 1993), or even to grasslands (Furley et al., 2008). In addition, as commonly shown (Gandiwa & Kativu, 2009; Jacobs & Biggs, 2001; Kennedy & Potgieter, 2003; Shackleton & Scholes, 2000; Walters, 2000), the number of stems on individual plants increased on frequently burnt plots, possibly due to basal coppicing due to repeated burning.

Grass species composition, on the contrary, was affected by fire frequency. Infrequently burnt plots were associated with the dominance of tall-statured grasses (*P. maximum* and *I. afrum*), while frequently burnt plots were associated with the dominance of a few shorter-statured grasses (*H. contortus* and *S. pappophoroides*). These findings are also in line with other studies (Frost & Robertson, 1987; Fynn et al., 2005; Plumptre et al., 2010; Smith et al., 2013). In their selection of preferred habitats, therefore, mammal species would be responding to differences in woody plant species structure, combined with changes to both the structure and composition of grass species.

There were noticeable differences in grass species assemblages between the frequently and infrequently burnt plots. Grasses have much faster life cycles than woody plants, and grass species composition can change relatively rapidly in response to changes in fire frequency and levels of herbivory. Increases in fire frequency result in increases in grass richness, evenness and diversity (Smith et al., 2013), because fire opens up the landscape, allowing new species to establish (Savadogo et al., 2008). Fire, in combination with grazing, can also change the balance between Decreaser, Increaser I and Increaser II species (Archibald et al., 2005; Trollope et al., 1990). Palatable Decreaser species typical of infrequent burning and shaded landscapes, and with high forage values (*P. maximum*, *I. afrum*, *P. deustum* and *D. eriantha*) were mostly found on infrequently burnt plots, while Increaser II species (*H. contortus*, *S. pappophoroides*, *A. adcensionis* and *R. cochinchinensis*) typically associated with frequent burning, and with relatively lower forage values, were mostly found on frequently burnt plots (Table 2) (van Oudtshoorn, 2012; Roodt, 2011). *H. contortus*, although sometimes classified as a Decreaser species, has better germination success when burnt (Orr & Paton, 1997) and is often associated with regularly burnt areas (van Oudtshoorn, 2012; Plumptre et al., 2010). Our findings suggest that frequently burnt areas are dominated by Increaser grasses characterised by relatively low palatability, which may also be as a result of heavy grazing by large mammals that occurs in association with regular burning.

4.2 | The effect of fire frequency on large mammal assemblages

Mammal species assemblages were similar in frequently burnt and infrequently burnt plots, and both types are thus utilised to some degree by most of the larger mammals in the study area. There were however a number of species that displayed a clear preference for either frequently burnt or infrequently burnt plots (Tables 4 and 5), indicating that the contrasting habitats created by differences in fire frequency are favoured by different species depending on their behaviour, body size, digestive strategy and metabolism, foraging mode and predator-avoidance behaviour (Burkepile et al., 2013; Hopcraft et al., 2010; Smit & Prins, 2015).

The current species richness in MWR is not accurately known, but based on historical accounts (Bell, 1984; Clarke, 1983), and present unpublished reports, it is estimated that between 37 and 42 mammal species (>0.5 kg) are present, not including arboreal

(e.g. *Galago* species) or semi-aquatic species such as hippopotamus (*Hippopotamus amphibius*) and otters (either *Aonyx capensis* or *Hydrictis maculicollis*). This study thus accounted for 69.0%–78.4% of the mammal species present in MWR. The majority of the species that were not recorded included smaller species that often go undetected by camera traps (Kelly & Holub, 2008; Tobler et al., 2008), such as scrub hare (*Lepus saxatilis*), genet species (genus *Genetta*) and mongoose species (genera *Herpestes*, *Galerella* and *Mungos*), and niche-specific species that are unlikely to use game trials (Kolowski & Forrester, 2017), such as klipspringer (*Oreotragus oreotragus*) and the yellow-spotted rock hyrax (*Heterohyrax brucei*). When excluding these species, the values produced by the species richness estimators appear more credible, predicting the absence of only a few species that are known to be present in MWR, but occur at extremely low densities, such as ground pangolin (*Smutsia temminckii*) and the recently introduced giraffe (*Giraffa camelopardalis*).

Frequent fire continually removes moribund material and stimulates new grass regrowth with increased levels of N, P, K, Mg and Cu (Anderson et al., 2020; Eby et al., 2014; van de Vijver et al., 1999), thus often attracting grazing species (Burkepile et al., 2013). The enhancing effects of fire by providing high-quality new regrowth for grazers are most pronounced immediately after fires, and typically only last for less than a year (Green et al., 2015; van de Vijver et al., 1999). Additionally, continued frequent fires may decrease soil nutrients and plant forage quality over time (Anderson et al., 2007; Blair, 1997). Nonetheless, Kimuyu et al. (2017) found herbivore preferences for burnt areas can still be seen many years after a fire, potentially explaining the increased preference for open-structured, frequently burnt plots shown by the pure grazers sable antelope, waterbuck, buffalo and plains zebra in this study, as found elsewhere (Burkepile et al., 2013, 2016; Kingdon et al., 2013; Mandinyenya et al., 2020; Traill, 2004; Wirtz & Kaiser, 1988). Similarly, the mixed-feeding impala showed a strong preference for frequently burnt plots in this study (Ford et al., 2014). Frequent fires may also result in increased foliar nitrogen levels, and decreased non-structural carbohydrate defence compounds (Ferwerda et al., 2006), potentially attracting browsing species to frequently burnt sites, as found for kudu in this study. Typically, however, browser species such as kudu are known to favour densely wooded habitats (Burkepile et al., 2013, 2016) characteristic of infrequently burnt areas, as shown for nyala, common duiker and bushbuck (*Tragelaphus sylvaticus*) in this study.

Conversely, because infrequently burnt areas typically have higher forage quantities of low quality, they are favoured by larger-bodied species that are able to persist on poorer-quality diets (Owen-Smith, 1988; Sensenig et al., 2010; van Soest, 1996). Larger-bodied species are also less vulnerable to predation and are therefore more comfortable to inhabit densely wooded areas that are typically avoided by most smaller herbivores (Burkepile et al., 2013; Ford et al., 2014). In general, this difference was not obvious from this study, as the three largest-bodied species recorded, namely buffalo (~650 kg), black rhinoceros (*Diceros bicornis*) (~1000 kg) and elephant (*Loxodonta africana*) (~5500 kg), did not show any preference for infrequently burnt areas. Due to their large body size, buffalo have previously been shown to opt for higher forage quantities rather than quality (Hopcraft et al., 2012), and to inhabit infrequently burnt areas (Burkepile et al., 2016). Buffalo have however also previously been shown to avoid extremely dense areas, potentially due to the increased risk of predation from lions and to prefer open-structured habitats (Mandinyenya et al., 2020; Valls-Fox et al., 2018); as corroborated in this study, where buffalo showed a clear preference for frequently burnt plots with a lower density of woody plants. Black rhinoceros were captured at comparatively low rates and showed no indication of preferring either habitat type, despite their general tendency to select habitats of dense vegetative cover (Odendaal-Holmes et al., 2014). This can probably be explained by black rhinoceros' preference for intermediate habitats (Anderson et al., 2020), since very infrequent fires would allow trees to outgrow optimal browse height, while very frequent fires would reduce browse availability (Anderson et al., 2020; Higgins et al., 2007; Holdo et al., 2014). Elephants, on the contrary, are mixed-feeders, and are therefore able to inhabit a wide variety of habitats (Codron et al., 2006). This study showed that fire frequency did not greatly influence the habitat choice of elephants, as found elsewhere (Burkepile et al., 2016), although a slight preference was given to infrequently burnt plots with increased woody cover, similar to findings of Harris et al. (2008).

For omnivorous species, it is possible that vegetation structure plays a more important role in determining habitat preferences than either vegetation quality or quantity. For example, as corroborated in this study, primates such as yellow baboons (and presumably likewise, vervet monkeys) have been shown to prefer forested areas, even when the majority of the landscape consisted of open areas (Bentley-Condit, 2009), and bush pigs have been shown to prefer less disturbed habitats of greater post-fire age (Jenkins et al., 2003), characteristic of infrequently burnt plots in this study. In contrast to previous findings that showed a preference for frequently burnt plots by warthogs (Burkepile et al., 2013, 2016; Plumptre et al., 2010), warthogs in this study preferred infrequently burnt areas. Warthogs however occurred in extremely high densities in MWR, explaining their high prevalence at both plot types.

This study found no support for differences in predator habitat use between frequently and infrequently burnt plots. Relatively low capture rates were however obtained for all eight predator species recorded in this study, and additional sampling could provide further information on their responses to fire frequency.

5 | CONCLUSIONS

It is well understood that herbivore abundances are regulated by both top-down processes (such as predation), and by bottom-up processes (through primary production, which is in turn regulated by underlying environmental factors). Since topography, soil and water characteristics, and the history of disturbances such as drought and floods were relatively homogenous in the study area, as well as the distribution of predators, we may assume that any variations in herbivore assemblages are predominantly a result of variations in vegetation

quality, quantity and structure, which in turn is strongly influenced by fire frequency (Hopcraft et al., 2010). The single season sampled in this study, however appropriate, may have biased findings related to the habitat preferences of mammal species. The pressures influencing mammal distributions in the dry season, such as food and water shortage, or even fire itself, are not present in the wet season, potentially changing the diet and consequently the habitat preferences of herbivore species (Arsenault & Owen-smith, 2011; Havarua et al., 2014). It is therefore possible that forage quality and quantity could play a larger role in determining large mammal habitat choices in the dry season. This study supports the growing recognition of the pronounced impact of fire on the functioning (Anderson et al., 2007; Bond & Keeley, 2005) and structure (Higgins et al., 2007) of savannah-woodland ecosystems. Specifically, the decreases in woody cover that have been associated with increases in fire frequency elsewhere, were confirmed in MWR, as was the dominance of the grass sward by short-statured increaser grasses; both of which presumably influenced the resultant composition of large mammal assemblages.

The prevailing fire regime in MWR is one of frequent fires, where 57% of the area burns at intervals of 2 years or less, and a further 30% burns at intervals of 3–5 years (Nieman et al., 2021c). The optimal mix of fire frequencies that would adequately cater for the habitat preferences of all large mammal species in MWR is not known, so whether the current regime is optimal is also unknown. In addition, whether or not managers will be able to maintain an optimum mix of vegetation with a desired range of fire frequency histories is currently untested. We conclude that the adoption of a fire management policy that promotes a mosaic of patches exposed to different fire frequencies could maintain a range of habitat types that should allow for the continued support of the diverse range of mammals that occupy MWR. For this purpose, a patch mosaic burning policy could be applied. Patch mosaic burning takes annual rainfall into account, and sets a target for area to be burnt in a series of point ignitions across the fire season, based on rainfall in the preceding two years (Brockett et al., 2001). While this should create a relatively diverse mosaic of fire frequencies, it will be necessary to monitor both the resultant fire patterns and trends in large mammal populations. The preferences of individual mammal species for either frequently or infrequently burnt areas reported here could aid in interpreting any negative trends. For example, a decline in mammals that prefer infrequently burnt areas could be related to increases in the proportion of land subjected to frequent fire, leading to changes in the burnt area targets that could be implemented to counter undesirable trends.

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CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTIONS

This study was collaboratively conceived and designed by all authors. WAN sourced the data, conducted the analyses and co-wrote the paper with BvW, FGTR and CJT. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The data presented in this article are available from the authors upon request.

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