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Grass and woody species composition and diversity beneath mistletoe-infected and uninfected *Sclerocarya birrea* (marula) trees in two South African semi-arid savanna protected areas

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ABSTRACT

Mistletoes increase understorey resource heterogeneity by altering animal visitations, litterfall, and soil moisture, thus support diverse understorey plants. However, their impact on understorey species composition and diversity in protected areas with small to large-sized herbivores remains unclear. We compared grass and woody species under mistletoe-uninfected and infected marula (*Sclerocarya birrea* subsp. *caffra*) trees in the Sabie and Sabi Sand Game Reserves, with differing mean annual rainfall, 500 mm and 610 mm, respectively. Species composition varied slightly between sites and with infection level. Total species evenness was 8% higher in the wetter site, where woody species diversity indices were up to 52% higher. In contrast, grass species richness and diversity were up to 33% higher in the drier site. Functional dissimilarity (FDis), Functional divergence (FDiv), and Rao's quadratic entropy (RaoQ) were up to 23% higher in the wetter site. Infected trees had 4% greater total cover abundance, and 32% higher woody species richness than uninfected trees. Additionally, eight woody and five grass species were exclusive to infected trees, compared to two woody and three grass species under uninfected trees indicating mistletoephily. RaoQ was 8% lower beneath uninfected than infected trees. Tree height significantly influenced total cover abundance and evenness and grass species richness and evenness. Overall, rainfall had a greater effect than mistletoe infection on understorey plants, suggesting moisture limitations and that mistletoe effects are additive. Thus, by enhancing resource availability and supporting mistletoephily, the interaction of mistletoes with other factors such as rainfall influence plant heterogeneity in these low-altitude semi-arid savannas.
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1. Introduction

Localised understorey nutrient hotspots and high zoochorous dispersal by diverse fauna visiting mistletoes, coupled with increased germination and recruitment, have been shown to significantly increase understorey plant productivity and diversity of mistletoe-infected trees (Maponga 2021; Mellado and Zamora, 2017). Mistletoes are chlorophytic hemi-parasitic plants in the order Santalales that obtain 60% of their carbohydrates through a haustorium attached to the host while photosynthesising the remaining 40% (Dzerefos and Witkowski, 1997; Mathiasen et al., 2008; Watson, 2001). Studies from Mediterranean pinelands (Hódar et al., 2018; Mellado and Zamora, 2017) and semi-arid savannas (Maponga et al., 2021, 2024, 2025; Mlambo and Mundava, 2024; Ndagurwa et al., 2016) consistently show that mistletoe-infected trees support more species-rich and functionally diverse understorey plant communities compared with uninfected trees, a phenomenon referred to as mistletoephily (Maponga et al., 2021, 2024). While these studies show the ecological significance of mistletoe infection on understorey plant trait plasticity, species composition, and functional diversity, a comprehensive understanding of other underlying biotic (i.e., host and mistletoe characteristics) and abiotic factors (e.g., rainfall and land use) and their broader implications remains unstudied in semi-arid

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savannas. The response of understorey plants can depend on the interaction between these factors (Maponga, 2021; Zamora and Mellado, 2019). A recent study has explored the effects of non-nitrogen-fixing mistletoe-infected trees on understorey species composition and diversity in Zimbabwe's semi-arid savannas (Mlambo and Mundava, 2024). However, further research is needed to expand on these findings, particularly to understand the broader ecological implications and the underlying mechanisms driving these patterns. Moreover, all these previous studies were done in similar semi-arid savannas (in Zimbabwe), but in areas with only small (e.g., rabbits) to medium-sized mammalian herbivores, mostly livestock (e.g., goats and cows). Therefore, knowledge gaps exist on how mistletoe-infected trees within protected areas with free-ranging small up to very large-sized herbivores influence understorey species composition and diversity in semi-arid savannas.

Large trees create understorey fertility islands through nutrient deposition and hydraulic lift, thus supporting more diverse understorey communities than intercanopy microhabitats (Ludwig et al., 2003, 2004; Tessema and Belay, 2017). Furthermore, by lodging mistletoes within their canopies, trees further broaden understorey species and resource heterogeneity, thus increasing patchiness in semi-arid savannas (Maponga et al., 2021, 2024, 2025; Ndagurwa et al., 2016, 2018). Mistletoes acquire significant amounts of nutrients and disproportionate amounts of water from their hosts, thus triggering host foliage loss, which increases host leaf litter quantities and turnover rates (Ndagurwa et al., 2014a; Press and Phoenix, 2005). Thus, mistletoes play the role of an ecological Robin Hood by redistributing nutrients that would have otherwise been locked up in the host for a longer period (Griebel et al., 2017; Watson et al., 2022). Mistletoes have relatively higher leaf litterfall (by up to 156%), turnover, and decompose more rapidly (by up to 75%) compared to their host tree's leaves (March and Watson, 2007; Mellado et al., 2016; Ndagurwa et al., 2015, 2020). Furthermore, mistletoe litter also facilitates rapid decomposition of the host's more recalcitrant litter, resulting in higher microbial and arthropod activity, thus augmenting soil nutrient concentrations (by up to 72%) within infected tree subcanopies (Krasylenko et al., 2022; Ndagurwa et al., 2014b, 2015, 2020). These favourable conditions improve the understorey plant nutrient qualities, thus attracting a more diverse range of mammalian herbivores.

Animals visit large trees for their shade, nutritious fruits, foliage, and understorey plants. Mistletoes further increase this attraction by providing nectar, fruit, and foliage and associated arthropods (Griebel et al., 2017; Krasylenko et al., 2022; Ndagurwa et al., 2014b; Okubamichael et al., 2011, b; Oliver et al., 2024; Watson, 2002). The attracted diverse fauna further increases subcanopy nutrients through their excreta and regurgitation, which contains zoochorous seeds, thus increasing the understorey taxonomic and functional diversity (Hódar et al., 2018; Krasylenko et al., 2022; Maponga et al., 2021; Mellado and Zamora, 2016; Okubamichael et al., 2011). However, there is also a possibility of a negative feedback loop on the understorey plant composition and diversity through excessive feeding and trampling by these visiting animals (Maponga, 2021).

In semi-arid savannas, understorey plants constitute 70% of the plant community; therefore, it is important to understand the factors that influence their distribution (Coverdale et al., 2016; Siebert and Scogings, 2015). This study investigated how *Sclerocarya birrea* subsp. *caffra* (marula) infected by the prevalent mistletoe species, *Erianthemum dregei* (Eckl. & Zeyh.) Tiegh. and *Pedistylis galpinii* (Schinz ex Sprague) influence understorey plant communities in two semi-arid savanna protected areas with different mean annual rainfall (MAR). Marula is a large keystone tree species in African savannas that is targeted by both large herbivores, particularly elephants (Jacobs and Biggs, 2002) and the two mistletoe species (Dzerefos et al., 2003). Similar to Mellado and Zamora (2017), our main aim focused on understorey woody-plant communities; however, grasses also have a competitive relationship with woody plants. For instance, high grass productivity coupled with high fire intensity suppresses the density of woody plant species, while high grazing reduces fire fuel load and hence supports the woody plants (Higgins et al., 2000). Hódar et al. (2018) also found that Poaceae species had the most significant responses to mistletoe infection effects on understorey plant species composition and diversity. Therefore, here we ask: (i) Do marula understorey grass and woody species assemblages, taxonomic and functional diversity, and herbivory differ between the Sabie (MAR 500 mm) and Sabi Sand (MAR 610 mm) Game Reserves; (ii) Does the presence of mistletoes on marula trees result in unique understorey grass and woody species assemblages, and result in differences in species composition, functional diversity, and herbivory? We predicted that the wetter site and mistletoe-infected trees would have higher grass and woody species and functional diversity, resulting in different understorey assemblages (Kermavnar and Kutnar, 2020; Maponga et al., 2021; Osem et al., 2012; Suter et al., 2017; Thompson and Eldridge, 2005). In areas with <650 mm, woody cover increases with MAR (Sankaran et al., 2005). Similarly, Donzelli et al. (2013), noted that in dry savannas, as MAR declines, water becomes highly limiting compared to nutrient availability and vice versa, thus we expect differences in growth form abundance with MAR variations. Also, we anticipated that herbivory would be higher under mistletoe-infected trees (Maponga, 2021) and in the wetter areas compared to the uninfected and drier areas, resulting in a different suite of plant species. Other factors such as fire frequency, severity (intensity, duration, and impact), and length of time postfire may also influence grass and woody species composition (Cousins et al., 2018; Govender et al., 2006; Higgins et al., 2000).

2. Methods

2.1. Description of study area

The study was conducted in the adjoining Sabie (also known as Sabi Sabi, 24°55′1S, 31°30′15″ E) and Sabi Sand Game Reserves (24° 50′15″ S, 31°20′30″ E) in Bushbuckridge, Mpumalanga Province, South Africa. In 1993, fences between these reserves, Manyeleti Game Reserve, and Kruger National Park were removed (de Boer et al., 2015), allowing herbivores to roam freely across these areas. This connectivity facilitates a fairly even distribution of wildlife during the growing season. Sabie and Sabi Sand Game Reserves differ in altitude, mean annual rainfall (MAR), and size. Sabie is situated at 381 m with a MAR of 500 mm and covers 54 km^2, whereas Sabi Sand is located at 465 m with a MAR of 610 mm and spans 440 km^2 (excluding Sabie Game Reserve and MalaMala) (Dzerefos et al., 2003; Fig. 1). Henceforth, we refer to Sabie Game Reserve as the drier site and Sabi Sand as the wetter site. The rainy season is from October to April and mean monthly temperatures range between 17 °C and 28 °C (Balme et al., 2017; Smith and Fitchett, 2020). Both areas are underlain by granite (Dzerefos et al., 2003; Funston, 1992; Smith and Fitchett, 2020) on Tonalite Sandveld (Sabi Sand, pers comm). They house the 'Big 5′ and herbivore species include elephant - *Loxodonta africana* (Blumenbach, 1797), impala - *Aepyceros melampus* (H Lichtenstein, 1812), kudu - *Tragelaphus strepsiceros* (P S Pallas, 1766), blue wildebeest - *Connochaetes taurinus* (Burchell, 1823), warthog - *Phacochoerus africanus* (Gmelin, 1788), common duiker - *Sylvicapra grimmia* (Linnaeus, 1758), and bushbuck - *Tragelaphus scriptus* (Pallas, 1766) (de Boer et al., 2015).

The sites are a mosaic of open savanna, and the common trees are *Combretum* spp., *Dichrostachys cinerea, Terminalia sericea, S. birrea,* and *Senegalia nigrescens* (Dzerefos et al., 2003; Thomas et al., 2008). Dominant grasses include *Megathyrsus maximum, Heteropogon contortus, Digitaria eriantha, Pogonarthria squarrosa, Perotis patens, Dactyloctenium australe, Themeda triandra,* and *Chloris virgata* (Thomas et al., 2008). Using MCD64A1.061 MODIS Burned Area Monthly Global 500m in Google Earth Engine (over the period between the years

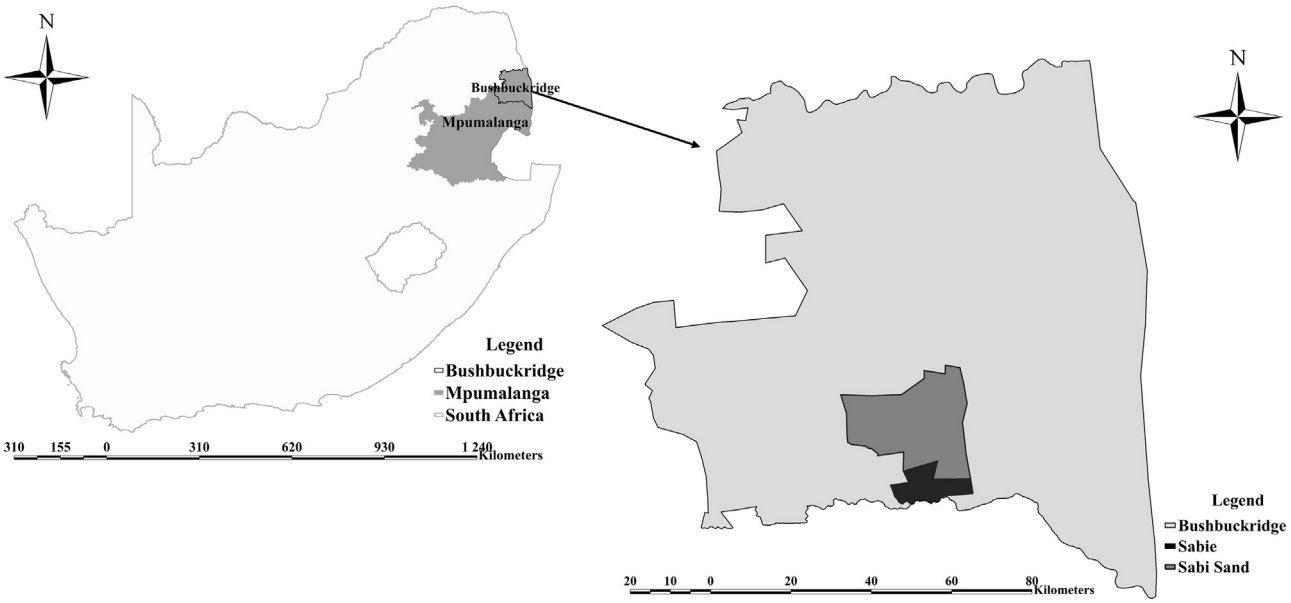

Fig. 1. Location of Sabie and Sabi Sand (including MalaMala) Game Reserves in Bushbuckridge, Mpumalanga, South Africa.

2000 and 2023), two fires (i.e., 10th of October 2011 and 17th of September 2021) directly affected the study plot in Sabi Sand (Fig. S1). However, in Sabi Game Reserve, six fires were recorded between 2001 and 2020, and the last significant fire to affect the plot was on the 16th of September 2015 (Fig. S2).

Our study host tree, marula, has high socio-ecological and economic importance to both human, plant, and wildlife communities in which it occurs (Helm et al., 2011). Its height ranges from 10 to 15 m (Helm and Witkowski, 2012). Marulas are deciduous and dioecious, i.e., having male and female in different individuals (Cook et al., 2017; Helm et al., 2011; Shackleton et al., 2002). Female trees produce fruits (with up to 4 seeds/samara) between March and June, and each tree can produce up to 8000 fruits (Cook et al., 2017; Jacobs and Biggs, 2002b).

2.2. Experimental design

Fieldwork was conducted from January to February 2024. Within a 1 km radius at each site, we selected 10 infected (>3 mistletoes/tree) and 10 uninfected marula trees. However, in Sabie Game Reserve (drier site) finding mistletoe-infected trees was more challenging, which may have influenced tree size variations, and the criteria used to define and select infected trees. Nonetheless, we selected trees matched for canopy size and tree height, ensuring they were not influenced by nearby large trees, or located on/near large termite mounds (Tessema and Belay, 2017; Maponga et al., 2021).

The long and short canopy diameters (D_1 and D_2) of the trees were measured using a tape measure, and the canopy area was calculated using Eq. 1.

$$Canopy\ area\ (m^2) = \pi\left(\frac{D1}{2} \times \frac{D2}{2}\right) \quad (1)$$

Height was measured using a measuring pole (m). Stem circumference at ground level was measured using a tape measure and then converted to stem diameter.

The number and species of mistletoes per tree were recorded. For each mistletoe individual, we measured the diameter of the woodrose (i.e., excess of host tissue in response to mistletoe infection, also known as hypertrophy (Dzerefos and Witkowski, 1997)) and the long and perpendicular crown diameter of the mistletoes, which we used to calculate mistletoe area. Underneath each infected and uninfected tree, we recorded grass and woody species found within 8 × 1 m^2 quadrats per tree (4 at the bole and 4 at the edge) in the four cardinal directions (n = 320 quadrat samples). Most identifications were done up to species level in the field. The few that could not be identified were removed to the lab at Wits Rural Campus for further identification. We assigned percentage cover-abundance for each species that was recorded within each quadrat using the Walker scale (Walker, 1976). Percentage herbivory (percentage of grazed and browsed plants within each quadrat) was also estimated using the Walker scale.

For functional traits, we recorded categorical traits, including life form, plant succession, photosynthetic pathway, grass leaf blade type, evergreen/deciduous, annual/perennial, palatability (grazing value, grazing status, leaf and fruit palatability), fruit type, presence of spinescence, nitrogen fixation, preferred habitat, and type of seed dispersal (Table S1 and Table S2). We used published articles, handbooks (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2016), field guides (Van Oudtshoorn, 2014; Palgrave, 2015), and online databases such as the Encyclopaedia of Life, Global Biodiversity Information Facility, SANBI, Flora of Mozambique, Zambia, and Zimbabwe, Tree SA, and the Tree Atlas of Namibia to obtain species functional traits.

2.3. Statistical analysis

Tree and mistletoe structural variables for each site and infection category were compared using General Linear Models (GLM) in SPSS. ANOSIM (ANAlysis Of SIMilarity) was conducted to assess species compositional similarity using Bray or Euclidean distance. We used the *R*-statistic to interpret the ANOSIM results with ANOSIM *R*-statistic of ≥ 0.30 regarded as significant (Muvengwi et al., 2024). Species composition among sites and in relation to mistletoe infection were compared using non-metric multidimensional scaling (NMDS), using the vegan package in *R*.

Biodiversity *R* was then used to calculate grass and woody cover abundance, evenness, richness, and Shannon diversity using cover abundances. Functional diversity was analysed in *R* using the package *FD* and the functions gowdis and dbFD, and because the data were categorical, the correction 'lingoes' was applied (Laliberté et al., 2013; Villéger et al., 2008). The following functional diversity indices were calculated: functional richness (FRic), functional evenness (FEve),

functional divergence (FDiv), functional dissimilarity (FDis), and Rao's quadratic entropy (RaoQ) (within each site (n = 160) and infection category (n = 160), total n = 320 quadrats).

We then analysed the effects of site, infection status, and tree height on the cover abundance of grasses and trees and both combined, as well as herbivory, using a generalized linear mixed model (GLMM) with a beta-binomial error distribution and a logit link function. We considered tree height because previous studies have demonstrated its significant association with mistletoe infection (Ndagurwa et al., 2012; Okubamichael et al., 2014) and its influence on understorey species diversity (Maponga, 2021). Since the response variables were proportional data, binomial distributions were used for modelling. Specifically, the beta-binomial distribution was chosen to account for overdispersion in the proportion data. In all the models in this study, tree was included as a random effect to account for repeated measurements within trees.

For total, grass and tree species richness, we used a GLMM with Poisson error distribution with a log link function, appropriate for count data. Tree characteristics (height, stem diameter and canopy area), total, grass and tree species evenness and Shannon diversity were modelled using linear mixed models (LMM). Similarly, all the functional diversity indices were analysed using LMMs.

These models were fitted using the *glmmTMB* and *lme4* packages in R. We assessed the significance of fixed effects using Type II Wald chi-square tests, performed with the Anova function from the *car* package. Model summaries were examined using the summary function to evaluate fixed effects estimates, standard errors, and significance levels.

Similar to Witkowski et al. (2001), we compared the grazing status of each grass species, classifying them as decreasers (species abundant in well-managed rangelands but declining with overgrazing) and increasers (species common in underutilised or overgrazed areas) (Van Oudtshoorn, 2014) both between and within sites.

3. Results

The tree characteristics did not vary between the drier and wetter sites. However, mistletoe-infected trees were significantly shorter (11.5 ± 0.14 m vs 12.0 ± 0.14 m) and with canopy areas that were smaller (158 ± 11.4 m^2 vs 212 ± 10.9 m^2) than uninfected trees, respectively.

A total of 306 mistletoes comprising 278 *Erianthemum dregei* and 28 *Pedistylis galpinii* were recorded in this study. Infected marulas had 13.0 ± 1.43 living mistletoes/tree with woodrose sizes of 8.19 ± 0.42 cm and mistletoe area of 1.21 ± 0.90 m^2, as well as 2.83 ± 0.55 dead mistletoes/tree. However, mistletoe attributes did not vary with site ($P > 0.05$, Table 1).

3.1. Species composition

We recorded 63 understorey plant species, comprising 27 grass and 36 woody species (Table 2). Grasses were predominantly Poaceae, with one sedge species (Cyperaceae), while woody species were from 17 families, of which 28% were Fabaceae (Table S3). The overall relative plant cover-abundance was 12% for woody species and 88% for grasses. *Megathyrsus maximus* (58%) was the most dominant species across all study sites, followed by *Urochloa mosambicensis* (16%) and *Digitaria eriantha* (6%). Among tree species, *Flueggea virosa, Euclea natalensis, Diospyros mespiliformis*, and *Dichrostachys cinerea* were the most dominant trees across all sites (Table 2). Five grasses (i.e., *Cyndon dactylon, Tricholaena monachne, Sporobolus nitens, Sporobolus africanus, Melinis repens* subsp. *repens*) were exclusive to infected trees, while three grass species (i.e., *Urochloa* sp., *Melinis repens* subsp. *grandiflora*, and *Loudetia simplex*) occurred only beneath uninfected trees (Table 2). Similarly, eight woody species occurred only beneath infected trees, while two woody species were found exclusively beneath uninfected trees (Table 2).

The NMDS (Fig. 2a-c) and ANOSIM results show that species assemblages had very little variation between sites (R = 0.04) or with mistletoe infection (R = 0.02). Understorey species composition beneath infected trees in the drier site and uninfected trees in the wetter site showed greater variation relative to other pairwise comparisons (R = 0.11, Table 3). Likewise, the ANOSIM of grass species alone showed low variations between site (R = 0.04) and infection (R = 0.01) and grass species composition beneath infected trees in the drier site and uninfected trees in the wetter site showed greater variation relative to other pairwise comparisons (R = 0.11, Table 3). Woody species composition also showed small variations between sites (R = 0.02) or with infection (R = 0.01).

3.2. Diversity indices

Total species evenness was 8% lower at the drier compared to the wetter site (Table 4), while other diversity indices and herbivory did not significantly differ between sites ($P > 0.05$). Infected tree microhabitats had 4% greater total cover abundance than uninfected microhabitats (Table 4), but no significant differences were observed in other diversity indices and herbivory. Tree height significantly influenced total cover-abundance and evenness (Table 4), with scatter plots showing that both increased with tree height (Fig. S3).

Site had significant effects on all grass species diversity indices (Table 4). Grass cover-abundance was 10% higher in the drier than wetter site. Similarly, grass species richness and diversity were between 23–33% higher in the drier than the wetter site. Conversely, grass evenness was 13% higher in the wetter than the drier site.

Grass species diversity indices did not differ significantly ($P > 0.05$) beneath infected and uninfected trees (Table 4). However, tree

Table 1
Mean (± SE) tree height, stem diameter, canopy area, number of *Erianthemum dregei* and *Pedistylis galpinii*, living and dead mistletoes/tree, woodrose size and mistletoe area for mistletoe infected and uninfected marula trees at Sabie (drier site) and Sabi Sand (wetter site) Game Reserves. χ^2 and (P value) of the generalised linear mixed models (GLMM) and linear mixed models (LMMs) are shown for each factor. Significant P values appear in bold. Lower-case letters show within-site differences between infection presence. df = 1, 36 and mistletoe variables df = 1, 18.

Parameters	Sabie (Drier site)		Sabi Sand (Wetter site)		Effects		
	Infected	Uninfected	Infected	Uninfected	Site	Infection	Site × Infection
Height (m)	11.23 ± 0.94[a]	11.89 ± 0.28[b]	11.70 ± 0.19	12.14 ± 0.17	1.19 (0.27)	7.77 (**0.005**)	0.32 (0.57)
Stem diameter (cm)	60.70 ± 3.34	68.60 ± 3.02	70.06 ± 2.20	70.52 ± 2.76	1.21 (0.27)	2.09 (0.15)	1.65 (0.20)
Canopy area (m^2)	153.27 ± 12.98	190.88 ± 14.12	162.37 ± 21.84[a]	233.58 ± 13.96[b]	1.19 (0.28)	11.89 (**0.001**)	1.14 (0.29)
No. of *E. dregei*	156		122				
No. of *P. galpinii*	22		6				
Mistletoes/tree	14.70 ± 3.00		11.33 ± 2.83			0.24 (0.63)	
Dead mistletoes/tree	3.10 ± 1.13		2.56 ± 1.11			0.003 (0.96)	
Woodrose sizes (cm)	7.88 ± 0.72		8.50 ± 1.00			0.92 (0.35)	
Mistletoe area (cm^2)	1.26 ± 0.20		1.17 ± 0.15			1.21 (0.29)	

Table 2
Mean (± SE) percentage cover-abundance of understorey grasses and trees within 1m^2 quadrats under mistletoe-infected and uninfected marula trees at Sabie and Sabi Sand Game Reserves. Species name Authorities also given. Blank spaces show that there were no recordings of that species.

	Sabie Infected trees	Sabie Uninfected trees	Sabi Sand Infected trees	Sabi Sand Uninfected trees
Grasses	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Aristida congesta Roem. & Schult.	0.13 ± 0.07	0.03 ± 0.03		
Bothriochloa insculpta (Hochst. ex A.Rich.) A.Camus	1.94 ± 0.81	0.25 ± 0.25		
Chloris virgata Sw.	0.06 ± 0.04	0.26 ± 0.10		
Cyndon dactylon (L.) Pers.			1.63 ± 0.78	
Dactyloctenium sp.	0.01 ± 0.01	0.11 ± 0.08		
Digitaria eriantha Steud.	9.24 ± 1.93	7.13 ± 1.67	0.42 ± 0.12	0.28 ± 0.15
Eragrostis cylindriflora Hochst.	0.03 ± 0.03	0.35 ± 0.14	0.08 ± 0.06	
Eragrostis superba Peyr.	0.98 ± 0.26	2.91 ± 1.34	0.72 ± 0.67	0.02 ± 0.02
Heteropogon contortus (L.) Roem. & Schult.	1.55 ± 0.95	0.03 ± 0.03	2.46 ± 0.94	0.32 ± 0.171
Hyperthelia dissoluta (Steud.) Clayton			0.42 ± 0.35	0.80 ± 0.57
Loudetia simplex (Nees) C.E.Hubb.		0.01 ± 0.01		
Melinis repens (Wild.) Zizka subsp. *repens*	0.13 ± 0.09			
Melinis repens (Willd.) Zizka subsp. *grandiflora* (Hochst.) Zizka A. Rich.	0 ± 0	0.03 ± 0.03	0 ± 0	0.02 ± 0.02
Megathyrsus maximum Jacq.	42.28 ± 3.18	41.04 ± 3.19	39.99 ± 2.82	49.64 ± 2.06
Perotis patens Gand.	0.10 ± 0.06	0.01 ± 0.01		
Pogonarthria squarrosa (Roem. & Schult.) Pilg.	0.01 ± 0.01		0.28 ± 0.15	0.18 ± 0.08
Schmidtia pappophoroides Steud. ex J.A. Schmidt	0.21 ± 0.11	0.54 ± 0.25	0.25 ± 0.19	
Kyllinga sp.	0.85 ± 0.38	0.39 ± 0.09	0.24 ± 0.05	0.38 ± 0.11
Sporobolus africanus (Poir.) Robyns & Tournay	0.10 ± 0.07			
Sporobolus nitens Stent			0.06 ± 0.06	
Sporobolus pyramidalis P. Beauv.	1.13 ± 0.56	0.76 ± 0.35	0.21 ± 0.15	0.06 ± 0.06
Themeda triandra Forssk.	1.35 ± 0.89	0.06 ± 0.06		0.20 ± 0.13
Tricholaena monachne (Trin.) Stapf & C.E. Hubb.	0.04 ± 0.04			
Urochloa deflexa (Schumach.) H.Scholz	0.28 ± 0.15	0.03 ± 0.03		
Urochloa nigropedata (Munro ex Ficalho & Hiern) A.M.Torres & C.M. Morton	0.01 ± 0.01	0.26 ± 0.20		
Urochloa trichopus (Hochst.) Stapf (Hack.) Dandy	9.85 ± 2.10	13.85 ± 2.23	13.65 ± 2.61	11.51 ± 2.06
Urochloa sp.		0.10 ± 0.07		
Woody plants				
Albizia harveyi E. Fourn.	0.09 ± 0.07	0.10 ± 0.10	0.49 ± 0.28	0.11 ± 0.11
Berchemia discolor (Klotzsch) Hemsl.	0.06 ± 0.06			
Cissus cornifolia (Baker) Planch.	0.08 ± 0.06			
Combretum apiculatum Sond. subsp. *apiculatum*	0.21 ± 0.14	0.58 ± 0.45		
Combretum collinum Fresen. subsp. *gazense* (Swynn. & Baker f.) Okafor	0.29 ± 0.25	0.13 ± 0.13	1.21 ± 0.58	0.11 ± 0.11
Combretum hereroense Schinz	0.58 ± 0.48			
Combretum zeyheri Sond.		0.38 ± 0.38		
Commiphora africana (A. Rich.) Engl.	0.11 ± 0.06	0.06 ± 0.06		
Dalbergia melanoxylon Guill. & Perr.	0.10 ± 0.07	0.35 ± 0.17	0.06 ± 0.06	
Dichrostachys cinerea (L.) Wight & Arn.	0.04 ± 0.03	0.28 ± 0.15	0.63 ± 0.39	2.38 ± 0.66
Diospyros mespiliformis Hochst. ex A. DC.	1.53 ± 0.75	0.03 ± 0.02	1.89 ± 0.87	0.51 ± 0.36
Ehretia amoena Klotzsch	0.06 ± 0.06		0.11 ± 0.11	0.34 ± 0.21
Elaeodendron transvaalense (Burtt Davy) R.H. Archer	0.06 ± 0.06			
Euclea divinorum Hiern	0.35 ± 0.26			
Euclea natalensis A. DC.	0.88 ± 0.40		1.24 ± 0.53	2.84 ± 0.88
Flueggea virosa (Roxb.ex Willd.) Voigt	0.60 ± 0.50		5.60 ± 1.53	1.75 ± 0.56
Grewia bicolor Juss.	0.04 ± 0.04	0.21 ± 0.19		
Grewia flavescens Juss.			0.14 ± 0.14	
Gymnosporia buxifolia (L.) Szyszyl.	0.64 ± 0.27	0.05 ± 0.05	0.76 ± 0.28	0.28 ± 0.12
Gymnosporia senegalensis (Lam.) Loes			0.36 ± 0.19	0.11 ± 0.08
Ormocarpum trichocarpum (Taub.) Engl.	0.23 ± 0.14			0.03 ± 0.03
Pavetta schumanniana F.Hoffm. ex K.Schum.	0.13 ± 0.13		0.07 ± 0.07	0.13 ± 0.09
Peltophorum africanum Sond.		0.31 ± 0.31		
Philenoptera violacea (Klotzsch) Schrire		0.25 ± 0.13	0.64 ± 0.41	0.06 ± 0.06
Phyllanthus reticulatus Poir.			0.15 ± 0.11	0.17 ± 0.13
Pterocarpus rotundifolius (Sond.) Druce	0.13 ± 0.13			0.66 ± 0.52
Rhus sp.	0.13 ± 0.13			
Sclerocarya birrea Hochst.	0.18 ± 0.07	0.15 ± 0.08	0.19 ± 0.09	0.17 ± 0.07
Senegalia nigrescens (Oliv.) P.J.H. Hurter	0.13 ± 0.09			
Senna petersiana (Bolle) Lock			0.07 ± 0.07	
Spirostachys africanum Sond.			0.04 ± 0.04	
Strychnos madagascariensis Poir.	0.19 ± 0.11	0.60 ± 0.27	0.39 ± 0.20	0.14 ± 0.07
Strychnos spinosa Lam.			0.03 ± 0.03	0.09 ± 0.09
Terminalia sericea Burch. ex-DC.	0.10 ± 0.07	0.73 ± 0.48	0.50 ± 0.31	0.17 ± 0.08
Vachellia exuvialis (I.Verd.) Kyal. & Boatwr.	0.03 ± 0.03	0.11 ± 0.10		
Ziziphus mucronata Willd.	0.03 ± 0.03	0.55 ± 0.40		0.01 ± 0.01

height had a significant effect on grass species richness and evenness. Grass species richness showed a negative relationship with tree height, whilst grass evenness was positively associated with tree height (Fig. S3).

Woody cover-abundance, richness, and diversity were between 32–52% higher in the wetter than drier site (Table 4). In contrast, woody species evenness was higher (0.97 ± 0.01) in the drier compared to the wetter site (0.92 ± 0.01).

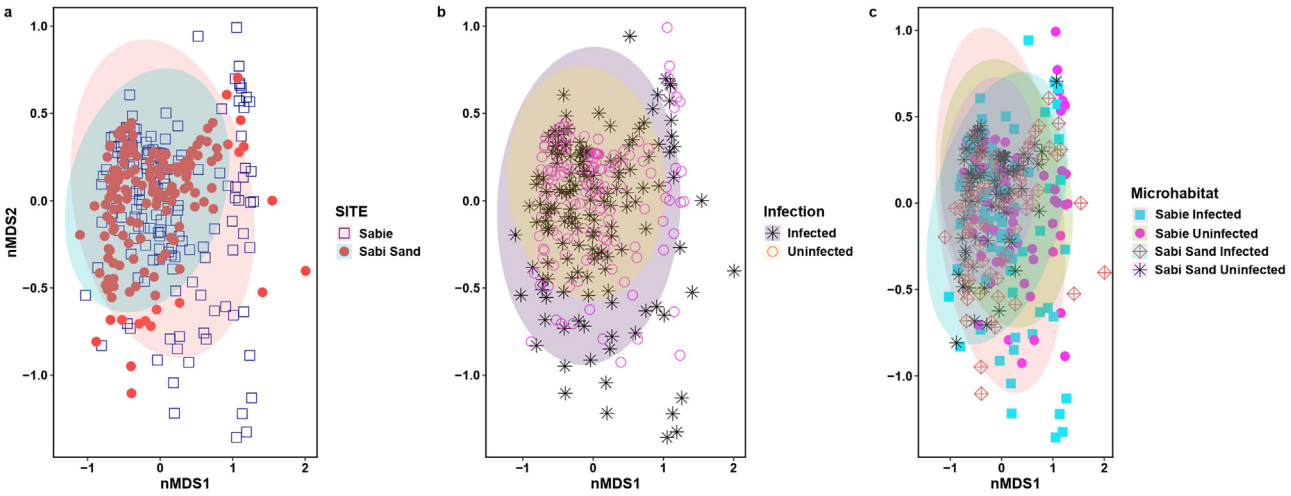

Fig 2. Non-metric multidimensional scale (nMDS) plots of total understorey plants (a) between Sabie (drier site) and Sabi Sand (wetter site) Game Reserves (stress value -0.21), (b) infected and uninfected microhabitats (stress value - 0.21), and (c) microhabitats from the interaction of site and infection (stress value - 0.21). The symbols represent the quadrats (1 m × 1 m) sampled underneath each tree.

Woody species richness was higher by 32% within mistletoe-infected than uninfected microhabitats (Table 4). Evenness was higher within uninfected (0.97 ± 0.01) than mistletoe-infected microhabitats (0.92 ± 0.01). However, tree height had no significant effect on all the woody diversity indices. Lastly, there was no significant interactive effects between site and infection on total, grass and woody diversity indices.

Tree height had a significant negative association with total species richness, living and number of dead mistletoes, woodrose sizes, and mistletoe area (Table 5). Similarly stem diameter showed a negative relationship with mistletoe area. However, both tree height and stem diameter had a significant positive association with species evenness.

3.3. Functional diversity

FDis, FDiv and RaoQ were higher (6–23%) at the wetter than the drier site (Fig. 3, Table S5), whereas FRic and FEve, did not differ between sites. RaoQ was also marginally (8%) higher beneath infected than uninfected trees, while other functional diversity indices showed no significant differences between infected and uninfected trees.

Sabie Game Reserve had a 70% higher cover-abundance of grasses that were both decreasers/Increaser II compared to Sabi Sand (Table 6 and Table S5). While Sabi Sand-infected microhabitats had between 25–34% lower cover-abundances of decreasers compared to the other three microhabitats (Table 6).

4. Discussion

Overall, total, grass, and woody species composition were relatively similar between mistletoe-infected and uninfected marula trees, as well as between the drier and wetter sites. However, except for evenness, grasses had much higher diversity indices in the drier than the wetter site, while woody species showed the opposite trend. Understorey microhabitats of infected trees had greater total cover abundance, higher woody species richness and greater RaoQ compared to uninfected trees. Following previous studies (Ndagurwa et al., 2016, 2018; Maponga et al., 2021, 2024, 2025; Mlambo and Mundava, 2024) these variations in the understorey plant community likely reflect contrasting responses between grasses and woody plants to changes in resources, e.g., light, soil moisture, seed rain, and nutrients associated with site conditions and mistletoe infection (Donzelli et al., 2013; Maponga et al., 2021; Mellado and Zamora, 2017; Ndagurwa et al., 2016). The observed differences between sites may also be attributed to the 20% difference in MAR.

4.1. Site effect

Contrary to previous findings (Coverdale et al., 2016; Thompson and Eldridge 2005), total understorey species richness was higher in the drier than wetter site. Grass species dominated the drier sites, while understorey woody plants thrived in the wetter site. This is consistent with woody cover increases with MAR, and grass persistence under water-limited conditions typical in savanna systems (Donzelli et al., 2013; Sankaran et al., 2005). Nonetheless, other unmeasured factors, such as historic levels of herbivory and fire, may have influenced these patterns. A fire in Sabi Sand 4–5 years ago may have initially suppressed woody seedlings while promoting grass biomass accumulation (Govender et al., 2006; Higgins et al., 2000). However, Sabie Game Reserve (drier site) had a higher grass abundance and diversity compared to Sabi Sand, suggesting that fire intensity in Sabi Sand may not have been severe enough to significantly alter tree-grass patterns (Sankaran et al., 2005). Instead, the

Table 3
ANOSIM results for the interaction of site and mistletoe infection. ANOSIM *R*-statistic of ≥ 0.30 were regarded as significant.

		Total Species *R*	Grasses *R*	Trees *R*
Microhabitats				
Sabie Infected	Sabie Uninfected	0.01	0.01	0.01
Sabie Infected	Sabie Sand Uninfected	0.11	0.11	0.04
Sabie Infected	Sabie Sand Infected	0.05	0.04	0.01
Sabie Uninfected	Sabie Sand Uninfected	0.09	0.10	0.05
Sabie Uninfected	Sabie Sand Infected	0.06	0.04	0.04
Sabi Sand Uninfected	Sabie Sand Infected	0.08	0.05	0.02

Table 4
Selected measures of diversity and percentage herbivory (mean ± standard error) for total species (grasses and woody plants), grasses and woody plants sampled beneath uninfected and infected marula trees at Sabie (drier site) and Sabi Sand (wetter site) Game Reserves. χ^2 and (*P* value) of the generalised linear mixed models (GLMM) and linear mixed models (LMMs) are shown for each factor. Significant *P* values appear in bold. Lower-case letters show differences between microhabitats beneath infected and uninfected trees at each site. *df* = 1, 316.

Site	Sabie (drier site)		Sabi Sand (wetter Site)		Factor			
Infection	Infected	Uninfected	Infected	Uninfected	Site	Infection	Height	Site × Infection
Total species								
Cover-abundance	77.2 ± 1.08[a]	73.0 ± 1.08[b]	75.7 ± 1.14[a]	73.9 ± 1.03[b]	1.67 (0.20)	13.33 (<**0.001**)	9.77 (**0.002**)	1.26 (0.24)
Richness	3.84 ± 0.14	3.46 ± 0.14	3.64 ± 0.15	3.01 ± 0.14	1.70 (0.10)	2.63 (0.10)	1.91 (0.17)	0.35 (0.55)
Evenness	0.58 ± 0.02	0.63 ± 0.02	0.62 ± 0.02	0.70 ± 0.02	4.78 (**0.03**)	2.61 (0.11)	11.49 (<**0.001**)	0.59 (0.44)
Diversity	0.71 ± 0.04	0.65 ± 0.04	0.75 ± 0.04	0.61 ± 0.82	0.00 (1.00)	2.33 (0.12)	0.26 (0.61)	0.42 (0.52)
Herbivory	12.2 ± 1.56	10.9 ± 1.56	9.32 ± 1.65	15.8 ± 1.49	0.02 (0.89)	2.31 (0.13)	0.03 (0.87)	2.79 (0.09)
Grasses								
Cover-abundance	70.3 ± 1.54	68.1 ± 1.54	61.1 ± 1.63	63.8 ± 1.47	10.0 (<**0.001**)	0.01 (0.92)	0.03(0.86)	3.16 (0.08)
Richness	2.94 ± 0.12	2.90 ± 1.41	2.49 ± 0.15	2.00 ± 0.13	11.2 (<**0.001**)	0.24 (0.62)	4.35(**0.04**)	2.74 (0.10)
Evenness	0.66 ± 0.02	0.66 ± 0.02	0.70 ± 0.02	0.81 ± 0.02	8.21 (**0.004**)	0.52 (0.47)	5.41(**0.02**)	1.53 (0.22)
Diversity	0.50 ± 0.04	0.51 ± 0.04	0.38 ± 0.04	0.30 ± 0.04	6.17 (**0.01**)	0.004 (0.98)	1.73 (0.19)	0.06 (0.81)
Woody plants								
Cover-abundance	6.94 ± 1.47	3.85 ± 1.47	14.6 ± 1.55	10.1 ± 1.40	6.09 (**0.01**)	3.62 (0.06)	3.07 (0.08)	0.01 (0.93)
Richness	0.90 ± 0.10[a]	0.56 ± 0.10[b]	1.15 ± 0.11	1.01 ± 0.10	6.78 (**0.001**)	3.75 (**0.05**)	0.81 (0.37)	0.12 (0.73)
Evenness	0.96 ± 0.01	0.98 ± 0.02	0.88 ± 0.01[b]	0.96 ± 0.01[a]	6.50 (**0.01**)	7.71 (**0.005**)	0.10 (0.75)	0.01 (0.94)
Diversity	0.14 ± 0.03	0.06 ± 0.03	0.23 ± 0.03	0.18 ± 0.03	6.46 (**0.01**)	1.84 (0.18)	0.01 (0.92)	0.29 (0.59)

fire could have contributed to increased woody species diversity in Sabi Sand through post-fire resprouting (Higgins et al., 2000), and fire-stimulated germination of soil-stored woody seeds (Cousins et al., 2018; Witkowski and Garner, 2000).

Table 5
Regression analyses: The relationship between height (m), diameter (cm), canopy area (m^2), mistletoe number and grazing (%), abundance, richness, evenness, Shannon diversity, mistletoe numbers, woodrose size, mistletoe area (m^2). -/+ on slope shows negative or positive associations.

Parameter		**Regression** R^2	*P*	**Slope**
Height	Herbivory	0.01	0.53	
	Abundance	0.06	0.13	
	Richness	**0.15**	**0.01**	-
	Evenness	**0.21**	**0.003**	+
	Shannon Diversity	0.02	0.43	
	Mistletoe numbers	**0.15**	**0.01**	-
	Woodrose sizes	**0.12**	**0.03**	-
	Mistletoe area	**0.15**	**0.01**	-
	Dead mistletoe	**0.10**	**0.05**	-
Stem Diameter	Herbivory	0.01	0.48	
	Abundance	0.02	0.35	
	Richness	0.08	0.08	
	Evenness	**0.12**	**0.03**	+
	Shannon Diversity	0.002	0.78	
	Mistletoe numbers	0.09	0.06	
	Woodrose sizes	0.07	0.11	
	Mistletoe area	**0.15**	**0.01**	-
	Dead mistletoe	0.02	0.44	
Canopy area	Herbivory	< 0.001	0.97	
	Abundance	< 0.001	0.95	
	Richness	0.08	0.08	
	Evenness	0.04	0.21	
	Shannon Diversity	0.02	0.42	
	Mistletoe numbers	**0.10**	**0.05**	-
	Woodrose sizes	**0.24**	**0.001**	-
	Mistletoe area	**0.23**	**0.002**	-
	Dead mistletoe	0.04	0.20	
Mistletoe numbers	Herbivory	0.03	0.30	
	Abundance	0.006	0.64	
	Richness	0.02	0.40	
	Evenness	0.05	0.17	
	Shannon Diversity	< 0.001	0.89	
	Woodrose sizes	**0.51**	< **0.001**	+
	Mistletoe area	**0.49**	< **0.001**	+
	Dead mistletoe	**0.45**	< **0.001**	+

Because grass-rich microhabitats often exhibit lower functional diversity compared to other plant growth forms (Maponga et al., 2021), the higher abundance of grasses, particularly decreaser species in the drier site explains lower RaoQ, FDiv, and FDis compared to the wetter site (Laliberté et al., 2013; Maponga et al., 2021). Therefore, drier sites are dominated by species with traits that are adaptable to low moisture availability, leading to trait convergence due to abiotic filtering (Kermavnar and Kutnar, 2020; Maponga et al., 2021). Conversely, the wetter site had higher FDis, FDiv, and RaoQ, showing greater niche differentiation and occupancy and resource partitioning than the drier site (Kermavnar and Kutnar, 2020; Suter et al., 2017). Nonetheless, differences in FDis, FDiv, and RaoQ can also be attributed to differences in nutrient availability between sites.

4.2. Mistletoe infection effect

Although the large, uninfected trees are likely more facilitative (Ludwig et al., 2004; Tessema and Belay, 2017), grass species richness and diversity tended to be higher beneath the smaller, mistletoe-infected marula trees. Therefore, despite their smaller size, mistletoe-infected trees may be augmenting more resources (nutrients and water) within their subcanopies, due to higher light incidence, litterfall, rapid decomposition of host and mistletoe litter, and significantly greater hydraulic lift compared to large, uninfected trees. Not only does this show that infected trees play a more substantial facilitative role in supporting understorey plants (Maponga, 2021; Ndagurwa et al., 2014a, 2016, 2020), but it also shows that mistletoe infection can alter tree size effects in savanna. Additionally, five grass species occurred exclusively beneath infected trees, suggesting misletoephily (Maponga et al., 2021) and niche partitioning in response to enhanced resource availability (Hódar et al., 2018; Maponga et al., 2021). However, on a broader scale, the high presence of increaser II grasses within infected tree microhabitats, indicates that higher rainfall and herbivore activity attracted by the effects of mistletoes is changing the grass composition by initially high levels of grazing and trampling, and reducing the grazing capacity over time (Maponga, 2021).

Woody species richness was higher beneath infected than uninfected trees, with eight woody species including *Combretum hereroense* and *Euclea divinorum*, occurring exclusively beneath infected trees, whereas only two woody species i.e., *Combretum zeyheri* and *Peltophorum africanum* were unique to uninfected trees. Species associated with nutrient-rich environments, such as *Diospyros*

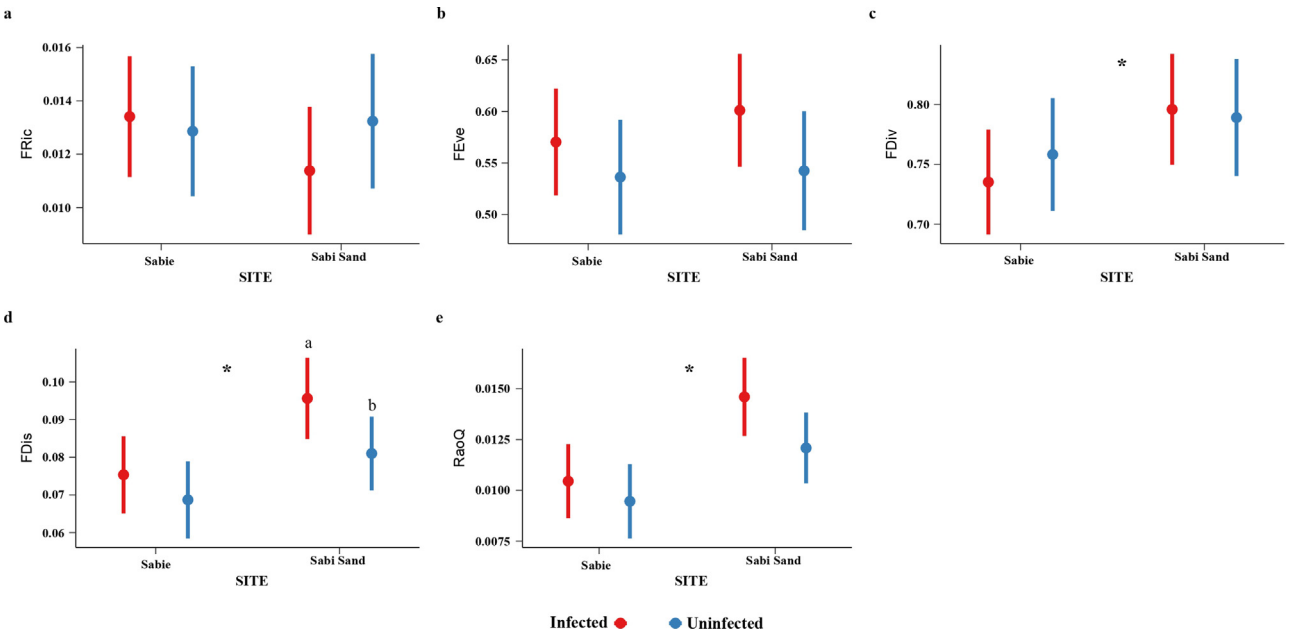

Fig. 3. The effects of site (Sabie Game Reserve, 500 mm MAR, Sabi Sand Game Reserves, 610 mm MAR) and mistletoe infection on functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional disimmilarity and RaoQ. Asteriks show differences between sites.

Table 6
Cover-abundance of the grass species per microhabitat (Sabie infected, Sabie uninfected, Sabi Sand infected, and Sabi Sand uninfected), classified into functional categories of Decreaser, Decreaser/Increaser II, Increaser I, Increaser I/Increaser II, Increaser II, Increaser III and unknown. Upper case letters show differences between sites ($P < 0.05$). For the functional category totals, percentages are shown in brackets.

		Sabie		Sabi Sand	
Species	Grazing status	Infected	Uninfected	Infected	Uninfected
Aristida congesta	Increaser II	10	2	0	0
Bothriochloa insculpta	Increaser II	22	2	0	0
Chloris virgata	Increaser II	5	21	0	0
Cyndon dactylon	Increaser II	0	0	117	0
Dactyloctenium sp.	Unknown	1	9	0	0
Digitaria eriantha	Decreaser	739	570	30	25
Eragrostis cylindriflora	Increaser II	2	28	6	0
Eragrostis superba	increaser II	78	233	52	2
Heteropogon contortus	Increaser II	124	2	177	28
Hyperthelia dissoluta	Increaser I	0	0	30	70
Kyllinga sp.	Unknown	68	31	17	33
Loudetia simplex	Increaser I/Increaser II	0	1	0	0
Megathyrsus maximus	Decreaser	3382	3283	2879	4368
Melinis repens subsp. *repens*	Increaser II	10	0	0	0
Melinis repens subsp. *grandiflora*	Increaser II	0	2	0	2
Perotis patens	Increaser II	8	1	52	38
Pogonarthria squarrosa	Increaser II	1	0	20	16
Schmidtia pappophoroides	Decreaser/Increaser II	17	43	18	0
Sporobolus africanus	Increaser III	8	0	0	0
Sporobolus nitens	Increaser II	0	0	4	0
Sporobolus pyramidalis	Increaser II	90	61	15	5
Themeda triandra	Decreaser	108	5	0	18
Tricholaena monachne	Increaser II	3	0	0	0
Urochloa deflexa	Decreaser	1	21	0	0
Urochloa nigropedata	Increaser II	155	20	0	0
Urochloa sp.	Unknown	0	8	0	0
Urochloa trichopus	Increaser II	788	1108	983	1013
	Total				
	Decreaser	4230 (75.3)	3879 (71.16)	2909 (66.11)	4411(78.51)
	Decreaser/Increaser II	17 (0.30)^{A}	43 (0.79)^{A}	18 (0.41)^{B}	0(0)^{B}
	Increaser I	0 (0)	0(0)	30 (0.68)	70(1.25)
	Increaser I/Increaser II	0 (0)	1 (0.02)	0 (0%)	0(0)
	Total Increaser II	1296 (23.1)	1480 (27.15)	1426 (32.41)	1104(19.65)
	Total Increaser III	8 (0.14)	0 (0)	0 (0)	0(0)
	Total Unknown	69 (1.2)	48 (0.88)	17 (0.39)	33(0.59)

mespiliformis, Flueggea virosa, and *Philenoptera violacea* (Joseph et al., 2014; Maponga et al., 2021; Ndagurwa et al., 2018), were particularly abundant beneath infected trees, whereas *Pterocarpus rotundifolius*, a species adapted to nutrient-poor soils unless growing on termite mounds (Joseph et al., 2014), was more common beneath uninfected marulas. Additionally, the presence of 2–3 m tall shrubs suggests the potential for mixed woodland patches developing within the resprouting or dead marulas' zone of influence, similar to patterns observed in Mediterranean Pinelands (Mellado and Zamora, 2017). These findings highlight the role of mistletoe-infected microhabitats as key sites for woody plant recruitment and regeneration, likely due to enhanced soil resources (Ludwig et al., 2004; Maponga, 2021; Ndagurwa et al., 2014a, 2016, 2020).

Mistletoe-infected trees attract a greater diversity of faunal visitors and seed dispersers, particularly avian species, which enhances seed dispersal thereby promoting higher understorey woody species richness compared to uninfected trees (Maponga et al., 2021, 2024; Mellado and Zamora, 2016, 2017). While both infected and uninfected marulas attract frugivores, mistletoe presence diversifies available food resources, drawing a wider range of specialist and generalist dispersers. This results in a richer "seed rain" and "seed bank," particularly favouring endozoochorous species with drupe-type fruits, such as *D. mespiliformis, E. divinorum*, and *F. virosa* (Dudley, 2000; Joseph et al., 2014), other good examples (or better even) of mistletoephily (Maponga et al., 2021, 2024). In addition, faunal visitors may also be responding to different cues associated with infected and uninfected marula canopies (Jayanth et al., 2024; Okubamichael et al., 2011a, b). Consequently, plant diversity is greater beneath infected than uninfected trees (Krasylenko et al., 2022; Maponga et al., 2021; Mellado and Zamora, 2016, 2017; Watson et al., 2022).

The wider range of animal visitors to infected trees often increases dung piles and dung pile scattering, facilitating secondary seed dispersal by dung beetles, squirrels, banded mongooses, baboons, birds, and others feeding on dung or its contents (Cook et al., 2017; Dudley, 2000; Midgley et al., 2012). While seed aggregation can intensify understorey woody plant competition (Dudley, 2000), plants beneath uninfected trees, may experience thinning due to lower soil resources, whereas the nutrient-rich infected tree microhabitats may support higher woody plant densities (Maponga et al., 2024). Therefore, the greater woody species richness beneath infected trees likely results from enhanced seed dispersal and improved environmental conditions, which promote woody plant establishment, potentially offsetting the impacts of herbivory.

The low number of conspecific plants compared to heterospecifics suggests multiple factors influence marula understorey survival. A hard seed coat, high predation by small mammals and birds near parent trees, and high moisture and light requirements may hinder germination and establishment (Coetsee et al., 2023; Cook et al., 2017; Mellado and Zamora, 2017; Midgley et al., 2012). However, diplochorous dispersal can mitigate seed predation and localised competition (Dudley, 2000; Midgley et al., 2012; Cook et al., 2017). Nonetheless, targeted browsing by smaller herbivores (e.g., impala), fire, and poor rainfall may further threaten marula seedling survival (Jacobs and Biggs, 2002b; Cook et al., 2017).

Infected tree microhabitats had higher RaoQ than uninfected microhabitats, suggesting greater trait variation and niche differentiation, while uninfected trees may have had species with similar traits due to niche-based exclusion (Kermavnar and Kutnar 2020; Maponga et al., 2021). This pattern is likely due to the favourable environmental conditions beneath infected trees that support species with a wide suite of traits (Maponga, 2021), which allows a variety of responses to disturbances and resource availability. In contrast, the lower RaoQ, species diversity, and richness beneath uninfected trees may lead to inefficient resource utilisation and poor niche occupancy due to high functional homogeneity and redundancy (Kermavnar and Kutnar, 2020; Magnago et al., 2014; Maponga et al., 2021). Further, although species composition variations between infected and uninfected tree microhabitats were small, they were sufficiently substantial to contribute towards the significant differences that we observed in RaoQ suggesting the importance of combining taxonomical and functional diversity indices to better understanding the broader effects of mistletoe infection.

5. Conclusion

In conclusion, grasses were more diverse in drier sites, while woody plants thrived at the wetter site. However, mistletoe presence enhanced woody, but not grass species richness. Overall, site (rainfall) effects on species and functional diversity indices were more pronounced than mistletoe infection indicating that the effects of mistletoes are additive. The variations in plant species between sites and mistletoe-infection microhabitats increase functional trait heterogeneity with important consequences for many ecosystem processes such as nutrient retention, nutrient cycling, and resilience to disturbances of this savanna system. Future studies should explore how the interaction of mistletoes with other tree species, environmental factors (e.g., soil type, fire), and animals (e.g., herbivores) influence understorey plant communities in savanna ecosystems. Finally, our findings contribute to the growing body of evidence supporting mistletoes as "ecosystem engineers" that create resource and plant spatial heterogeneity within semi-arid savannas.

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Declarations

The authors have no competing interests to declare that are relevant to the content of this article.

Declaration of competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.sajb.2025.02.032.

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