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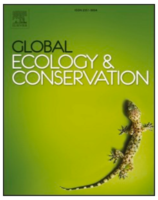

Original Research Article

Woody densification and its management shape insect and bat communities in an African savanna.

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ABSTRACT

Understanding management-driven interactions is critical for savanna biodiversity conservation. Vegetation management alters ecosystem structure, potentially impacting higher trophic levels, including insects vital to insectivorous bat communities. Our study in MalaMala Game Reserve, South Africa, examined five management approaches (densified, intermediate woody cover, summer mow, winter mow, rest) within an experimental design, assessing their effects on vegetation (tree density, grass height), insect abundance and richness (via light traps), and bat activity and richness (via acoustic monitoring). Habitat management significantly influenced habitat structure, producing contrasting responses in insect and bat communities. Specifically, insect abundance and richness increased with woody plant cover, whereas bat activity decreased. Low tree density and short grass areas supported high bat activity, but had the lowest insect abundance and species richness, likely due to bats' mobility and adaptable foraging behaviours. Intermediate woody cover and taller grass hosted diverse insect communities with moderate bat activity. Dense woody cover hosted the richest insect communities but the lowest bat activity, favouring clutter-specialist bats like *Rhinolophus smithersi*, which prefer thick vegetation. Our findings highlight the nuanced interactions within savanna ecosystems and the importance of maintaining heterogeneous landscapes with a range of vegetation structures to support diverse insect and bat communities. Mixed habitat management practices that create habitats with varying woody plant densities and herbaceous layer heights can enhance insect abundance and bat diversity across landscapes. This study underscores the complex interplay between vegetation, prey availability, and bat foraging, providing important insights for savanna biodiversity conservation.

1. Introduction

Savanna ecosystems, covering approximately one-third of Earth's land surface and supporting one-fifth of the global population, are characterized by a mosaic of woody plants and grasses, with a natural gradient of woody cover (Mistry and Beradi, 2000; Solbrig,

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1993). This vegetation structure, regulated by factors such as water availability, soil conditions, fire frequency, and herbivory, is critical for maintaining ecosystem integrity (Beerling and Osborne, 2006; Charles-Dominique et al., 2015; Parr et al., 2014; Scheiter and Higgins, 2009), and supports diverse wildlife, including large herbivores, smaller mammals, birds, insects, and bats (du Toit and Cumming, 1999; Krüger and McGavin, 1998; Mishra and Young, 2020; Monadjem and Reside, 2008). However, savannas are highly sensitive to global and local stressors, such as increased CO_2, altered rainfall regimes and land-use changes, which can disrupt the woody plant-grass balance, leading to bush encroachment or densification, reduced habitat heterogeneity, and declines in biodiversity and ecosystem function (Buitenwerf et al., 2012; Charles-Dominique et al., 2015; Eldridge et al., 2011; Soto-Shoender et al., 2018). Habitat management strategies, such as mechanical tree clearing, mowing, and prescribed burning, are implemented to maintain savanna heterogeneity, which is essential for species reliant on these environments, such as insectivorous bats and their insect prey (Charles-Dominique et al., 2015; Parker et al., 2023; Schmitt et al., 2022).

An important area warranting further investigation is how various habitat management approaches that alter woody plant density and grass height influence taxa dependent on African savanna vegetation. Of particular interest are insectivorous bats and their insect prey, both of which provide critical ecosystem services. Bats contribute to pest control, pollination, and seed dispersal, playing a vital role in maintaining ecological balance (Ducummon, 2000; Kalka et al., 2008; Leelapaibul et al., 2005; McCracken et al., 2012; Williams-Guillen et al., 2008). Similarly, insects are crucial for pollination, decomposition, and serve as a primary food source for many insectivores, including bats (Parr et al., 2014; Schowalter, 2017). Habitat management can independently affect both insects and bats, although their responses are often linked through predator-prey interactions (Jacobs and Bastian, 2016). Moreover, the diversity and abundance of insect taxa, such as Lepidoptera (moths), Coleoptera (beetles), and Isoptera (termites), are intricately linked to the vegetation structure of savanna ecosystems, which provides critical habitat and resources (e.g., food and shelter), influencing bat foraging behaviour, health, and reproductive success (Kalka et al., 2008). According to optimal foraging theory, bats should select habitats that maximise energy intake by balancing prey abundance with foraging efficiency (Balza et al., 2020; Emlen, 1966; MacArthur and Pianka, 1996). However, habitat management altering vegetation structure, may disrupt this balance, misaligning prey availability with foraging needs and affecting population dynamics (Appel et al., 2023). Thus, understanding how different habitat management strategies affect both prey availability and bat foraging behaviour is crucial for maintaining healthy insect and bat populations and, ultimately, the ecosystem services that both bats and insects provide.

Nearly a quarter of bat species face extinction risk due to habitat loss and fragmentation driven by agricultural expansion and other land-use changes (Boyles et al., 2011; Jones et al., 2003; Mickleburgh et al., 2002; Voigt and Kingston, 2016). In particular, South Africa's north-eastern savannas support a rich diversity of bat species (Schoeman and Monadjem, 2018), but these populations are influenced by various factors, including food availability, predation risk, and social dynamics (Brigham and Fenton, 1986; Fenton and Rautenbach, 1986). Vegetation structure plays a critical role in bat foraging behaviour (Shapiro et al., 2020), because changes in woody cover can alter hunting efficiency. Increased woody cover, for instance, reduces the open spaces that bats rely on for foraging, creating challenges for species that depend on clutter-free or edge environments (Cooper-Bohannon, 2016; Monadjem et al., 2020). To support healthy bat populations and maintain their essential role in ecosystem functioning, conservation and management efforts must prioritise the preservation of suitable habitat structure.

While extensive research has explored the effects of land-cover change on bat richness and activity in forest ecosystems (e.g., Estrada-Villegas et al., 2010; Ferreira et al., 2017; Grindal and Brigham, 1998; Hendel et al., 2024; Pinto and Keitt, 2008; Williams-Guillén and Perfecto, 2011), fewer studies have focused on savanna ecosystems, despite their ecological importance (Meyer et al., 2016; Monadjem and Reside, 2008; Mtsetfwa et al., 2018; Weier et al., 2018). However, Monadjem and Reside (2008) found that riparian vegetation in savannas supports higher bat activity due to increased prey availability, while Mtsetfwa et al. (2018) reported that bat community composition shifts across conservation-agriculture boundaries, with open habitats favouring open-air foragers. Similarly, Weier et al. (2018) showed that natural vegetation in savanna orchards enhances bat activity by supporting insect prey. However, the specific impacts of habitat management practices, such as mowing or woody plant clearing, on both insect and bat communities in savannas remain largely underexplored. This knowledge gap is critical, because savannas face increasing woody densification due to global change factors like elevated CO_2 and altered fire regimes (Stevens et al., 2017), which may disrupt trophic interactions. Our study addresses this gap by examining how specific habitat management strategies, influence vegetation structure, insect abundance and bat activity in a South African semi-arid savanna. These insights are vital for informing savanna conservation strategies that support bat diversity and ecosystem functioning. We hypothesized that moderate woody plant density and grass height would support more diverse and abundant bat and insect communities compared to structural extremes (i.e., areas experiencing unchecked woody densification or low woody plant density and grass height). This hypothesis is based on the principle that intermediate vegetation structure provides a balance of open spaces for foraging bats and complex habitats for diverse insect populations, maximising resource availability and niche diversity (Crist et al., 2006; Cromsigt et al., 2009; du Toit and Cumming, 1999). However, we also recognize that the relationship between vegetation structure, prey abundance, and bat foraging behaviour is complex. It is possible that certain management strategies, although promoting desirable vegetation characteristics, may misalign with the prey abundance patterns expected under predator-prey theory. This misalignment could influence bat population dynamics in ways that might not be predicted by focusing solely on vegetation structure, highlighting the need for a deeper exploration of predator-prey relationships in managed savanna systems.

2. Materials and methods

2.1. Study site

We conducted our research in MalaMala Game Reserve, which spans 133 km^2 in South Africa, during the wet season in January-February 2022. The reserve shares an unfenced boundary with the Kruger National Park to the east, thereby forming part of the Greater Kruger National Park (>20,000 km^2) conservation area (Fig. 1). The region experiences an average annual rainfall of approximately 620 mm, with the rainy season extending from October to March (Schulze, 2008). According to the 2024 South African National Biodiversity Institute (SANBI) national vegetation classification, MalaMala Game Reserve lies entirely within the Savanna Biome (SANBI, 2024). The natural vegetation at the study site is characterized by a mixed Combretum/Terminalia woodland (Gertenbach, 1983).

2.2. Habitat management and experimental design

At our study site, the savanna includes areas subjected to distinct habitat management approaches, resulting in varying levels of woody plant density and grass height. These approaches include: (1) "densified" areas where natural woody densification has occurred as a result of no management interventions, (2) savanna areas with intermediate woody plant cover maintained by management burns conducted on a fire return frequency of 3–5 years, which falls within Kruger National Park's mean fire return frequency of 4.5 years (Govender et al., 2006), and (3) areas that were cleared of woody plants in the 1960s to create grass-dominated landscapes with minimal tree cover (< 5 trees/ha; Schmitt et al., 2022). These tree-cleared areas were maintained in this state between 1960 and 2015 via annual mowing. In 2019, we established three replicated tree-cleared management sites, each subjected to three different mowing approaches – summer mow, winter mow and rest – arranged in a randomised block design (Fig. 1). Mowing habitat management approaches have been applied annually since 2019 (i.e., for three years at the time of our study). Austral summer mows (hereafter "summer mows") were conducted during the wet season (i.e., late December to mid-January), austral winter mows (hereafter "winter mows") during mid-to-late June, while the rest areas have remained unmowed since 2015. Tree-cleared areas varied in size

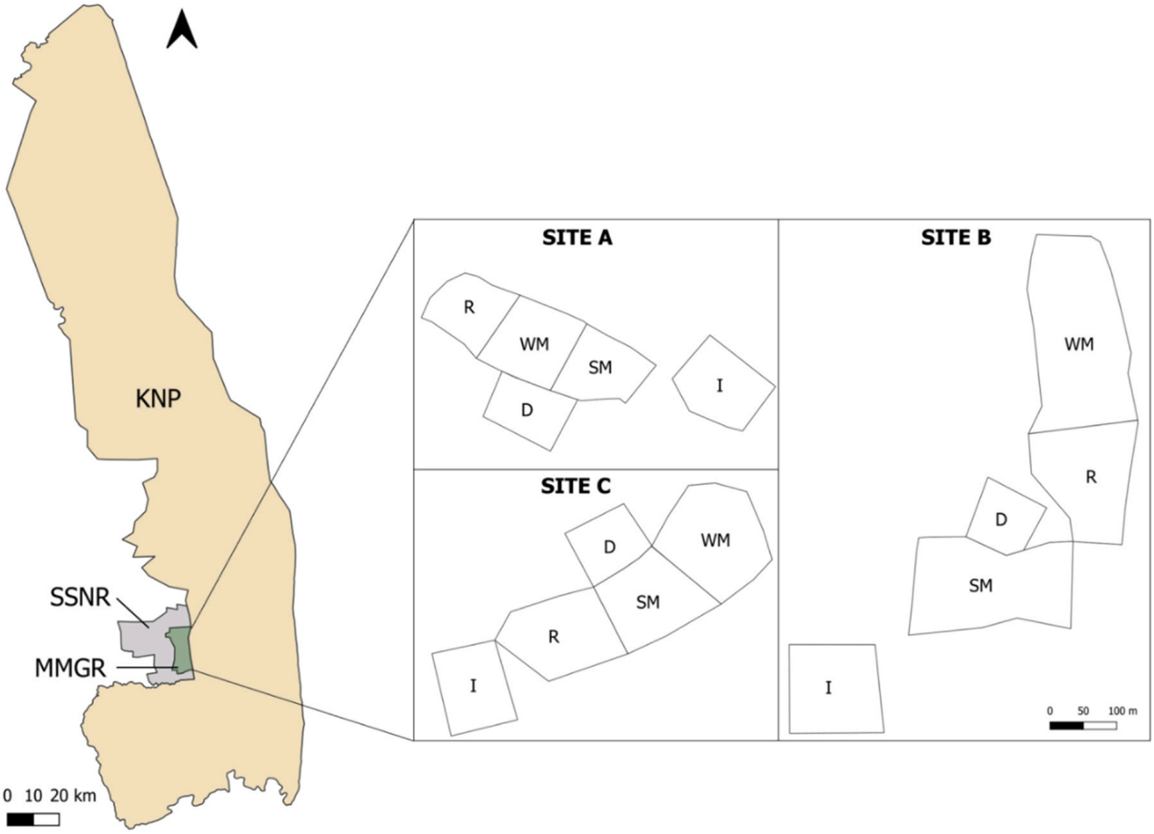

Fig. 1. Location of our study site, MalaMala Game Reserve (MMGR) in South Africa, situated between Sabi Sands Nature Reserve (SSNR) and Greater Kruger National Park (KNP). The inset illustrates the randomized design of our habitat management approaches (i.e., areas that have experienced woody densification (D), areas with intermediate woody cover from natural fire return (I), summer mow (SM), winter mow (WM) and rest (R)) within each study site.

(approximately 3.5–10.5 ha), with mow habitat management approach plots within sites ranging from 1 to 4 ha and positioned adjacently (Fig. 1). Thus, at our study site, we had five habitat management approaches: (1) densified, (2) intermediate woody cover, (3) rest, (4) summer mow, and (5) winter mow. Ultimately, all habitat management approaches were replicated across three separate sites with all approaches being adjacent to each other at each site and the sites located 0.5–1.5 km apart (Fig. 1).

2.3. *Vegetation survey*

During the wet season (i.e., February) of 2022, we measured tree density (trees/100 m^2) and grass height (cm) for each habitat management approach plot at each site. Tree density was estimated by counting the number of trees, defined as any woody vegetation taller than 0.5 m (Blaum et al., 2009; McCleery et al., 2018), in a 10 × 10 m plot surrounding the location of the bat detector (see below). Grass height was measured using two 25 m transects within each habitat management approach plot that were spaced 10 m apart, sampling the area that immediately surrounded the location of the bat detector. We took three measurements of grass height at every meter along each transect ($n = 75$ measurements per transect). For analysis, the three measurements were averaged per meter, yielding 25 average grass height measurements per transect. Winter mows had occurred ~8 months prior, while summer mows were implemented ~1.5 months before data collection.

2.4. *Insect light trapping*

We used a standardized light-trapping approach to capture nocturnal winged insects in each habitat management approach, including Lepidoptera, Hemiptera and Diptera, which are key prey for insectivorous bats (Bohmann et al., 2011). We deployed battery-operated light traps in each habitat management approach for one night during the new moon phase (i.e., darkest phase of the lunar cycle when insects are most attracted to the traps) in January to February 2022. To avoid interference with bat sampling, light trapping was conducted immediately after bat sampling concluded.

Light traps were activated at dusk and deactivated at dawn, with all captured insects preserved in 70 % ethanol for morphospecies level identification (Oliver and Beattie, 1996). This resolution is adequate for detecting taxonomic responses to habitat management (Benton et al., 2002; Farrell et al., 2015). Each morphospecies was recorded upon first occurrence, with the number of individuals logged by location, using consistent nomenclature. All morphospecies were classified to the family level by the same individual (TO; see Table S1) to ensure consistency in identification and minimize observer bias. Voucher specimens were preserved and retained at the University of KwaZulu-Natal.

2.5. *Bat sampling*

We deployed five SM4BAT FS song meter detectors (Wildlife Acoustics, Concord, MA, USA) across the five habitat management approaches at each site to record insectivorous bat echolocation calls. Bat acoustic sampling was conducted sequentially at each site between 26 January and 9 February 2022, with detectors deployed for five consecutive nights per sites (15 sampling nights per habitat management approach and 75 sampling nights in total). This sampling period was selected to minimize lunar illumination while also keeping sites temporally close. As a result, most sampling occurred during the waning crescent to new moon phases, with some sampling extending into the waxing crescent and first quarter (Table S2). To account for any potential differences in lunar illumination among sites, we included "site" as a random effect in our models. Minimum nighttime temperatures, which can also influence bat activity, were generally consistent across the sampling period (Table S2). Gumede et al., (2025) demonstrated that five consecutive nights of sampling sufficiently describe the insectivorous bat communities in our study area. For the tree-cleared areas (rest, summer mow, winter mow), detectors were placed in the center of each plot. In intermediate woody cover and densified plots, detectors were placed 20 m inside each plot to ensure sampling occurred within the core of the habitat type, avoiding edge effects given the sampling range of the detectors.

We followed bat call identification protocols from (Brinkley et al., 2021; Gumede et al., 2025; Parker, 2022; Parker and Bernard, 2018, 2023). Kaleidoscope Pro software version 5 (Wildlife Acoustics, Concord, MA, USA) was used to analyse and identify each bat call series recorded. In addition, we used a Kruger National Park-specific cluster analysis tool (Brinkley et al., 2021) to cluster all echolocation call recordings from each site into putative species categories based on their call characteristics, namely minimum call frequency (Fmin) in kHz, characteristic call frequency (Fc) or frequency at the flattest portion of the call (kHz), maximum call frequency (Fmax) in kHz and call duration (ms). Even though Kaleidoscope's cluster analysis tool automatically identifies each recording, the software is not completely accurate (Brinkley et al., 2021; Rydell et al., 2017). Thus, each of the individual bat call sequences within the resultant clusters was also manually identified to species-level using a call reference library and published literature (Brinkley et al., 2021; Gumede et al., 2025; Monadjem et al., 2020; Parker, 2022; Parker and Bernard, 2018, 2023). The recorded call sequences were only positively identified to species level if there was a sequence of three or more pulses recorded. This approach avoided misidentification of species due to possible noise, social calls, or insufficient call statistics. If a call sequence could not be positively identified, it was excluded.

Manual identification of bat calls followed a deliberate three-phase process to minimize Type I statistical errors (Parker, 2022; Parker and Bernard, 2023). In the first phase, we made use of the known ranges of the Fmin of southern African bats to putatively identify the call sequences to species. The second phase then used the known ranges of the Fc or Fmax to corroborate the identifications made in the first phase. Only if a recording fell within the known ranges of the first two call characteristics was it retained for the final phase. The final phase corroborated the retained species assignments using the known ranges of either the Fmax or Fc for southern

African bats (Gumede et al., 2025; Parker, 2022; Parker and Bernard, 2023).

2.6. Data analysis

2.6.1. Vegetation structure

To analyze vegetation responses to different habitat management approaches, we used generalized linear mixed models (GLMMs) with the *glmmTMB* and *lme4* packages in R version 4.4.1 (Bates et al., 2024; Brooks et al., 2024; R Development Core Team, 2024). For all vegetation analyses, "site" was included as a random effect to account for variability between sites. Mean tree density across habitat management approaches was modeled using a negative binomial distribution with a log link function, while the effects of habitat management approaches on grass height were analyzed using a Gamma distribution with a log link function. Model diagnostics, including checks for overdispersion, residuals versus fitted values, and outliers, were performed using the *DHARMa* package (Hartig, 2016). Likelihood ratio tests compared the full models against null models (without habitat management approach) to assess the significance of habitat management approach effects. Post-hoc comparisons between habitat management approaches were performed using estimated marginal means with the *emmeans* package (Lenth, 2024), followed by pairwise contrasts to assess significant differences.

2.6.2. Community composition

We analyzed the community compositions of insects and bats using non-metric multidimensional scaling (nMDS) and Bray-Curtis dissimilarities, employing the *vegan* package in R (Oksanen et al., 2024). To test for significant differences in community composition across habitat management approaches in the nMDS ordination, we applied permutational multivariate analysis of variance (PERMANOVA). Separate PERMANOVAs were conducted for insect and bat communities. These analyses used a nested design (e.g., block) to ensure permutations were constrained within the variable "site". To identify the species driving the observed differences between habitat management approaches, we employed the *envfit* function to plot species vectors on the ordination plots. For bats, we set alpha = 0.05 and for insects, we set alpha = 0.01 to limit the number of morphospecies displayed (n = 2) on the ordination plots.

2.6.3. Patterns of species richness and abundance/activity

We investigated differences in insect richness and abundance, as well as bat species richness and activity (i.e., number of passes), across the five habitat management approaches using GLMMs and generalized linear models (GLMs). For insect species richness, we fitted a Poisson GLMM using habitat management approach as a fixed effect and site as a random effect to account for site variability, with the *lme4* package. For insect abundance, we detected overdispersion in the Poisson GLMM and, therefore, used a Negative Binomial (NB) GLMM fitted with the *glmmTMB* package. For this model, we maintained the same fixed and random effect's structure. For bat species richness, we initially attempted a Poisson GLMM, but convergence issues and potential unreliability due to a singular fit, led us to use a Poisson GLM. However, underdispersion led us to fit a Quasi-Poisson GLM instead. Attempts to fit a NB GLMM failed to converge, with near-zero random effect variance. For bat activity, we identified a NB GLMM as the most suitable model. We performed model diagnostics, including checks for overdispersion, residuals versus fitted values, and outliers, using the *DHARMa* package. We compared the full models against null models (without habitat management approach) using likelihood ratio tests to assess the significance of habitat management approach effects. We conducted post-hoc comparisons using the *emmeans* package and reported Tukey-adjusted p-values to determine significant differences between habitat management approaches.

We found that the different habitat management approaches significantly affected insect richness and abundance, as well as bat species richness and activity (see below). Therefore, we assessed whether environmental variables (e.g., tree density and grass height) and the abundance of their prey (insects for insectivorous bats) or predators (insectivorous bats for insects) influenced these observed

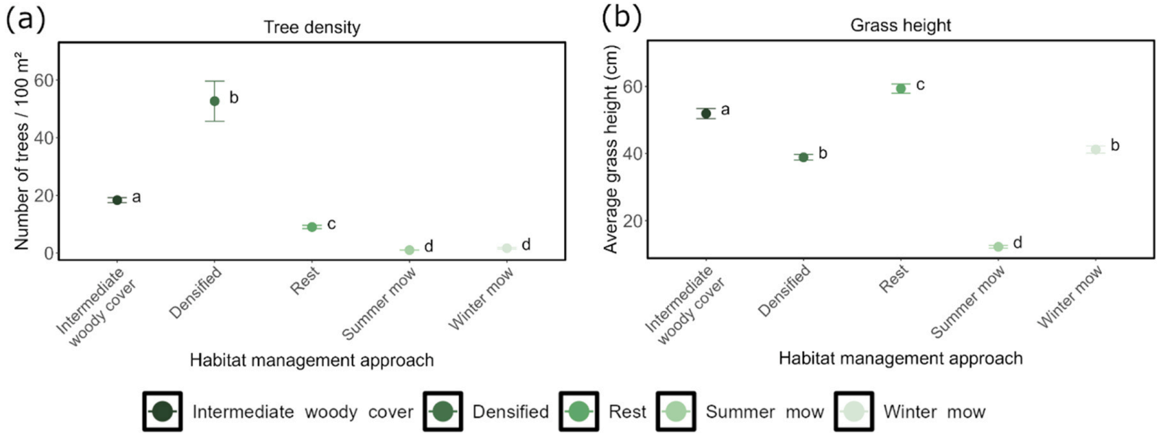

Fig. 2. Vegetation measurements across habitat management approaches (mean ± SE). Panel (a) shows tree density and (b) shows grass height. Means that do not share a common letter indicate significant differences (α = 0.05).

patterns. To determine the factors influencing insect abundance, we modelled insect abundance (dependent variable) against average grass height, tree density, and the activity of bats. Similarly, we modelled the activity of bats (dependent variable) against average grass height, tree density, and the abundance of insects. For insect abundance and bat activity, we employed GLMs with a gamma distribution and a log link function. Initially, "site" was included as a random factor, but was removed due to non-significance based on singular fit and the lack of improvement in deviance explained. We assessed all possible combinations of predictor variables, including a null model ($n = 8$). Multicollinearity among predictor variables was tested and variables were excluded if their variance inflation factor (VIF) exceeded four (Micheal and Abiodun, 2014). Model selection was performed using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2004).

3. Results

3.1. *Vegetation structure*

The five habitat management approaches differed significantly with respect to both average tree density ($\chi^2 = 50.53$, df = 4, $P < 0.001$) and average grass height ($\chi^2 = 949.71$, df = 4, $P < 0.001$; Fig. 2). Densified areas exhibited the highest tree density, with a mean of 52.70 ± 6.94 (SE) trees/100 m^2, followed by intermediate woody cover habitats (18.30 ± 0.88 trees/100 m^2) and then rest areas, which only had an average of 9 ± 0.58 trees/100 m^2 (Fig. 2a). Both summer mow and winter mow areas recorded the lowest tree densities, with the summer mow averaging just 1 ± 0 tree/100 m^2 and winter mow slightly higher at 1.67 ± 0.33 trees/100 m^2 (Fig. 2a). Regarding grass height, the rest habitat management approach had the tallest grass with a mean of 59.40 ± 1.36 cm, followed by the areas with intermediate woody cover at 51.90 ± 1.50 cm (Fig. 2b). Winter mow and densified areas had similar grass heights of 41.20 ± 1.09 cm and 38.90 ± 0.87 cm, respectively (Fig. 2b). In contrast, summer mow areas had significantly shorter grass, averaging only 12.20 ± 0.42 cm (Fig. 2b).

3.2. *Habitat management approach effects on community composition, species richness, and abundance*

3.2.1. *Insects*

We collected 1142 individual insects, representing 10 orders, which were subsequently identified to 106 morphospecies (Table S1).

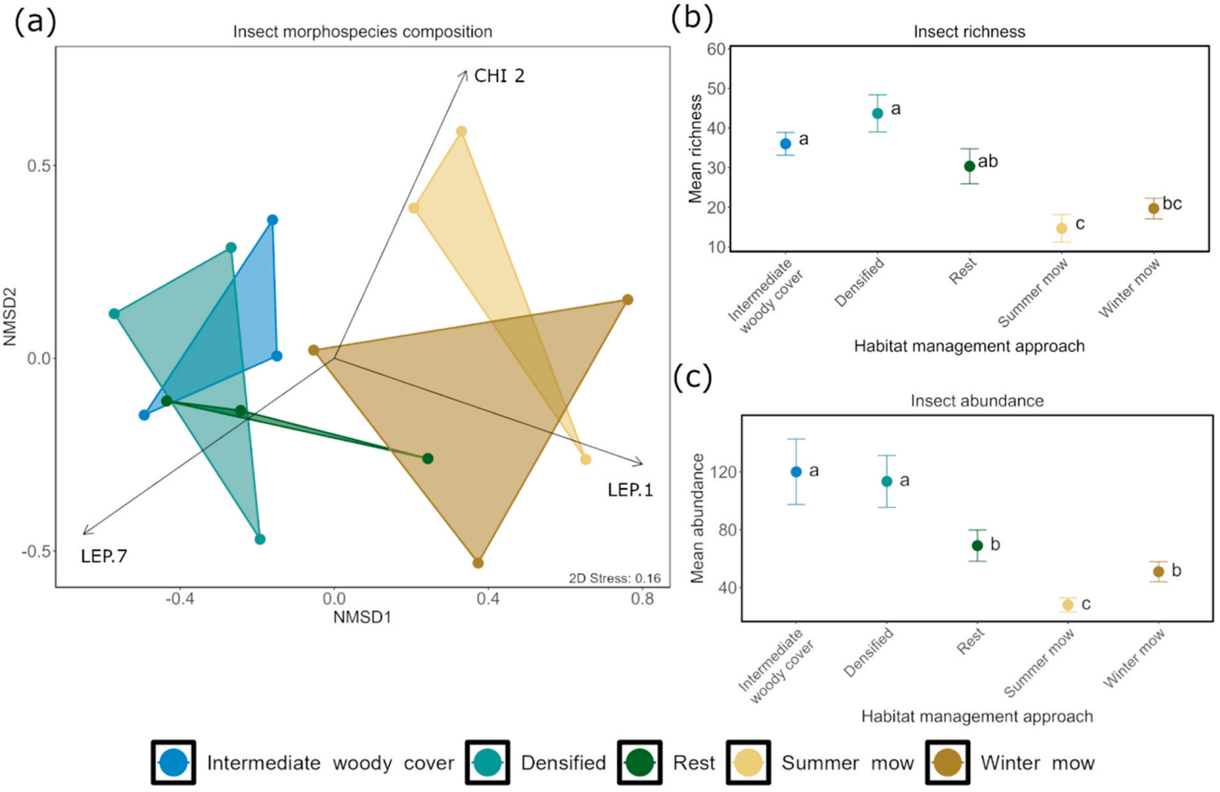

Fig. 3. Habitat management approach effects on insects. Plot (a) depicts variations in insect morphospecies community composition across habitat management approaches, with arrows representing species vectors that are significantly associated with each habitat management approach ($\alpha = 0.01$). Plot (b) shows patterns of insect richness (mean ± SE) and plot (c) displays patterns of insect abundance across habitat management approaches. In plots (b) and (c), means that do not share a common letter indicate significant differences ($\alpha = 0.05$).

Of the 11 orders, five made up ~94 % of all collected insects: Diptera: ~28 %, Hemiptera: ~26 %, Lepidoptera: ~24 %, Coleoptera: ~8 %, and Hymenoptera: ~8 % (Fig. S1). Insect community composition was significantly influenced by habitat management approaches (PERMANOVA pseudo$F_{4,14} = 1.60$, $P = 0.003$; Fig. 3a). The intermediate woody cover, densified and rest areas had the most similar species composition and were characterized by “LEP 7” (Order: Lepidoptera, Suborder: Glossata, Family: Unknown), a very small, nectar-feeding moth. By contrast, the summer and winter mow areas were characterized by Morphospecies “LEP 1” (Order: Lepidoptera, Suborder: Glossata, Family: Unknown), a very small, nectar-feeding dark moth and “CHI 2” (Order: Diptera, Suborder: Nematocera, Family: Chironomidae), a small dark midge and nectar feeder.

We found that both insect richness ($\chi^2 = 59.03$, df = 4, $P < 0.001$, Fig. 3b) and abundance ($\chi^2 = 26.93$, df = 4, $P < 0.001$, Fig. 3c) were significantly influenced by habitat management approach. Intermediate woody cover (35.67 ± 2.91 species (mean ± SE)), densified (43.33 ± 4.63 species) and rest (30.33 ± 4.41 species) areas exhibited similar levels of mean insect richness, with no significant differences among them. In contrast, summer mow areas showed significantly lower richness (14.67 ± 3.48 species) compared to intermediate woody cover, densified, and rest areas. Winter mow areas also had lower richness (19.660 ± 2.60 species) and was only significantly different from the intermediate woody cover and densified areas, but not from rest areas.

Intermediate woody cover (119.67 ± 22.26 insects/light trap) and densified (113 ± 18.14 insects/light trap) areas exhibited similar and significantly higher insect abundance compared to the other habitat management approaches (Fig. 3c). Summer mow areas had the lowest insect abundance (28 ± 4.93 insects/light trap), which was significantly lower than all other habitat management approaches. The rest (69 ± 10.79 insects/light trap) and winter mow (51 ± 6.93 insects/light trap) areas had similar intermediate levels of insect abundance, which were significantly distinct from the intermediate woody cover, densified and summer mow areas. Our model selection process identified tree density and grass height as the best predictors of insect abundance (Table S3). Specifically, insect abundance increased as a function of both tree density ($\beta = 0.36 \pm 0.09$ (SE), $t = 4.21$, $P = 0.001$) and grass height ($\beta = 0.34 \pm 0.09$, $t = 3.93$, $P = 0.002$).

3.2.2. Bats

We recorded 10,716 individual bat echolocation calls from 14 putative species, of which 50 % were open-air foragers, ~43 % were clutter-edge foragers and ~7 % were clutter foragers (Table 1). Like the insects, we found that bat community composition was significantly different across habitat management approaches (PERMANOVA pseudo$F_{4,14} = 2.24$, $P = 0.025$, Fig. 4a). Five putative bat species were significantly associated with the differences in community composition among habitat management approaches. We observed that the open-air, little free-tailed bat (*Chaerephon pumulis*) was distinctly associated with the densified areas, whereas the clutter-foraging Smithers’s horseshoe bat (*Rhinolophus smithersi*) was more closely associated with intermediate woody cover areas. We

Table 1
Bat species presence across the five habitat management approaches in MalaMala Game Reserve, South Africa along with their diet and foraging strategies.

Scientific name	Common name	Intermediate woody cover	Densified	Rest	Summer mow	Winter mow	Primary food – order of preference	Foraging strategy
Chaerephon ansorgei	Ansorge’s free-tailed bat	✓	✓	✓	✓	✓	Coleoptera, Trichoptera, Lepidoptera	Open-air
Chaerephon pumulis	Little free-tailed bat		✓	✓	✓	✓	Coleoptera, Hemiptera, Lepidoptera, Hymenoptera, Diptera	Open-air
Miniopterus natalensis	Natal long-fingered bat	✓	✓	✓	✓	✓	Diptera, Hemiptera, Coleoptera, Lepidoptera, Blattodea	Clutter-edge
Mops condylurus	Angolan free-tailed bat	✓	✓	✓	✓	✓	Coleoptera, Hemiptera, Lepidoptera	Open-air
Mops midas	Midas free-tailed bat	✓	✓	✓	✓	✓	Coleoptera, Hemiptera, Lepidoptera	Open-air
Myotis tricolor	Temminck’s myotis			✓	✓	✓	Coleoptera, Hemiptera, Diptera, Neuroptera, Hymenoptera	Clutter-edge
Neoromicia capensis	Cape serotine	✓	✓	✓	✓	✓	Coleoptera, Hemiptera, Diptera, Lepidoptera, Neuroptera	Clutter-edge
Neoromicia nana	Banana bat			✓	✓		Coleoptera, Lepidoptera, Diptera	Clutter-edge
Neoromicia zuluensis	Zulu serotine	✓	✓	✓	✓	✓	Coleoptera, Lepidoptera	Clutter-edge
Pipistrellus rusticus	Rusty pipistrelle			✓	✓	✓	Coleoptera, Lepidoptera, Trichoptera, Diptera	Clutter-edge
Rhinolohpus smithersi	Smithers’s horseshoe bat	✓					Lepidoptera, Coleoptera	Clutter
Scotophilus dinganii	Yellow-bellied house bat	✓	✓	✓	✓	✓	Coleoptera, Hemiptera, Hymenoptera, Blattodea, Diptera	Clutter-edge
Tadarida aegyptiaca	Egyptian free-tailed bat	✓	✓	✓	✓	✓	Diptera, Hemiptera, Coleoptera, Lepidoptera	Open-air
Taphozous mauritiana	Mauritian tomb bat	✓	✓	✓	✓	✓	Lepidoptera, Blattodea, Coleoptera	Open-air

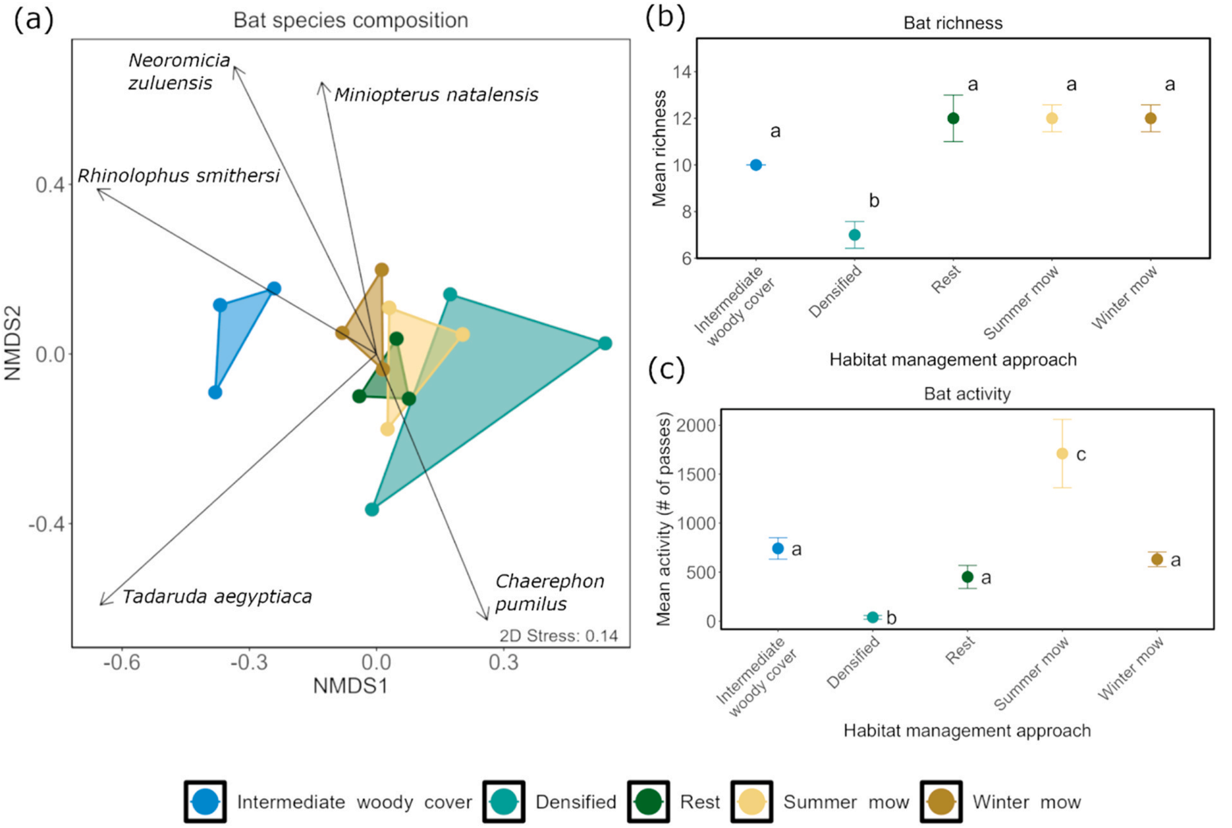

Fig. 4. Habitat management approach effects on bats. Plot (a) depicts variations in bat species community composition across habitat management approaches, with arrows representing species vectors that are significantly associated with each habitat management approach ($\alpha = 0.05$). Plot (b) shows patterns of bat species richness (mean ± SE) and plot (c) displays patterns of bat activity across habitat management approaches. In plots (b) and (c), means that do not share a common letter indicate significant differences ($\alpha = 0.05$).

found that the clutter-edge foraging Zulu serotine (*Neoromicia zuluensis*) and Natal long-fingered bat (*Miniopterus natalensis*) were primarily associated with winter mow areas, whereas the open-air foraging Egyptian free-tailed bat (*Tadarida aegyptiaca*) was notably present in both intermediate woody cover and rest areas.

Similar to the insect data, we found that both bat richness ($\chi^2 = 13.12$, df = 4, $P < 0.001$; Fig. 4b) and activity ($\chi^2 = 34.56$, df = 4, $P < 0.001$; Fig. 4c) were significantly influenced by habitat management approach. Specifically, we found that densified areas (7 species ± 0.58 (mean ± SE)) exhibited significantly lower species richness compared to areas of intermediate woody cover (10 species ± 0) as well as the rest, summer mow and winter mow areas (each with 12 species ± 0.58). We also recorded significantly higher bat activity (1710 passes ± 349) in the summer mow areas compared to the other habitat management approaches (Fig. 4c). The winter mow (630 passes ± 75), rest (451 passes ± 117) and intermediate woody cover (742 passes ± 110) areas had comparable, intermediate levels of bat activity (Fig. 4c), while we observed the lowest bat activity (38.7 passes ± 19) in the densified areas (Fig. 4c). Our model selection process revealed that tree density was the best predictor of bat activity, which negatively influenced bat activity ($\beta = -0.05 \pm 0.009$ (SE), $t = -5.94$, $P < 0.001$; Table S4).

4. Discussion

Our results reveal that habitat management significantly alters the structure of savanna ecosystems, with complex effects that vary across trophic levels. While the direct impact of mowing on grass height is evident, our key finding is that management practices induce structural changes in vegetation that influence insect communities and the bats that prey upon them in nuanced and sometimes opposing ways. These complex relationships highlight the need for careful consideration of management approaches in savanna ecosystems.

Biodiversity within African savannas is intrinsically linked to spatial and temporal heterogeneity (Solbrig et al., 1996). The landscape-scale mosaic of different habitat types, from open areas to densely wooded patches, supports overall biodiversity through complementary resource provision (Cromsigt et al., 2009; du Toit and Cumming, 1999). However, according to Stevens et al. (2017), the densification of African savannas is accelerating. This large-scale increase in woody plant cover can result in the homogenization of savanna habitats and can pose significant risks for savanna ecosystems (Li et al., 2020). Based on our results, a large-scale increase in woody plant cover within a heterogenous landscape may benefit nocturnal flying insect richness and abundance but will result in depauperate bat communities with low richness and activity. These densely wooded habitats provide refugia for insects. However, it is important to note that our study focused on nocturnal flying insects, and patterns may differ for other arthropod groups. For instance, studies on non-flying insects have found that the highest diversity tends to occur at intermediate levels of woody cover, while richness and abundance are often lowest in densely encroached habitats (Blaum et al., 2009; Marquart et al., 2023). Densified habitats may become unsuitable for many bat species due to limited maneuverability and reduced access to prey, particularly for open-air foragers (Kovaříková, 2016). These results suggest that habitat suitability, rather than food availability alone, may be a key driver of reduced bat activity in densified habitats.

To address the negative effects of increased woody densification of savanna ecosystems, land managers can implement mowing regimes (Schmitt et al., 2022). While mowing can significantly reduce the density of woody plants, it can also lead to the homogenization of vegetation structure. Thus, both mowing and woody densified areas represent areas of reduced structural complexity within plots, where structural complexity refers to the diversity and spatial variation of vegetation strata. However, our five habitat management approaches collectively form a landscape-scale mosaic of habitat types, enhancing overall structural complexity and supporting biodiversity through complementary resources (Cromsigt et al., 2009; du Toit and Cumming, 1999). We found that management approaches that reduced woody plant density had a negative effect on insect richness and abundance while resulting in high levels of bat richness and activity. Insect populations are particularly sensitive to environmental changes driven by human land-use practices, such as mowing (Völkl et al., 1993). For example, mowing can directly remove individuals, especially less mobile species, as well as indirectly affect populations by altering vegetation structure, plant composition, and food resources, with cascading effects on microclimates and insect communities (Curry, 1994; Fewkes, 1961; Painter, 1999; Völkl et al., 1993). The high bat activity we observed in mowed areas, especially in summer mow areas, could be due to our acoustic detections being dominated by open-air foraging bats (Table 1). Open-air foraging bats are regarded as generalists (Monadjem et al., 2020) and are particularly flexible in responding to habitat changes, which allows them to thrive in a variety of habitats. Their dominance in our study aligns with other studies in savanna habitats, where these bats tend to hunt insects on the wing above vegetation, exploiting the open areas and responding favorably to landscape simplifications, such as reduced complexity or increased openness, often associated with specific management practices (Freudmann et al., 2015; Heim et al., 2016).

Our results suggest that habitats with intermediate woody plant cover provide suitable features that favor both insect and bat communities. For example, *Rhinolophus smithersi*, a clutter-specialist species, showed a preference for intermediate woody cover areas. This association likely reflects this species' adaptation to maneuvering in denser vegetation and its preference for gleaning prey, such as beetles, off plants or the ground, which are key prey that often thrive in areas with higher vegetation density (Fenton et al., 1977; Russo and Jones, 2003; Toffoli and Rughetti, 2017). Although we did not directly measure beetle abundance, the presence of thicker vegetation suggests increased beetle habitat, supporting the higher *Rhinolophus* activity in these areas. Furthermore, *Rhinolophus* species, which are highly sensitive to habitat change, tend to disappear from areas with even minimal disturbance (Russo and Jones, 2003; Toffoli and Rughetti, 2017), which may explain their absence from the mowed and densified habitats. Ultimately, the structural complexity within intermediate woody plant cover habitats influences species distributions and foraging success, by providing bat foraging sites and roosting habitats (Aguirre, 2002; Avila-Flores and Medellín, 2004; Denzinger and Schnitzler, 2013) and diverse insect foraging niches (Crist et al., 2006; Utsumi et al., 2009).

Habitat structure and herbaceous cover can influence species distributions and animal communities (Aranda and Graciolli, 2015; Brüggeshemke et al., 2022; Prather and Kaspari, 2019; Schmitt et al., 2022). As such, any habitat management practice that affects vegetation structure and cover will also influence the animals relying on the vegetation. Nevertheless, land managers are unlikely to manage vegetation to specifically benefit insect and/or bat communities. However, similar studies at our study site that used the experimental mow plots (e.g., Parker et al., 2023) and quantified large mammal community responses to a gradient of woody plant cover (e.g., Schmitt et al., 2022) found similar results to our study. Specifically, habitats that lacked vegetation structure had depauperate insect and bird communities (Parker et al., 2023) as well as large mammal communities (Schmitt et al., 2022; Stears et al., 2025). While we observed similar responses across many taxa to areas of extremely low woody plant cover within an African savanna, we expect that there will be taxa-specific responses to a gradient of woody plant cover due to intrinsic factors associated with each species. Thus, it is important to understand how entire communities respond to habitat features and modifications to inform management actions to conserve biodiversity. Moreover, it is important to understand whether management actions alter species interactions in ways that may lead to unexpected consequences, such as mismatches between habitat preferences and resource availability.

According to optimal foraging theory, predators like bats should allocate more time to foraging in areas with higher prey density to maximise net energy intake while minimizing energy expenditure (Balza et al., 2020; Emlen, 1966; MacArthur and Pianka, 1996). However, we did not find higher bat activity in habitat management areas with greater insect abundance. In fact, insect abundance was not a key driver of bat activity. As a result, we observed a spatial mismatch in the habitat use of predators and their prey. Specifically, insects had their highest abundance in habitats that had the lowest bat activity and bats had the highest activity in habitats that had the lowest insect abundance. This suggests that vegetation clearing practices, such as mowing, that reduce tree density may create habitats that are ecological traps (Hale and Swearer, 2016) because bats perceive these habitats as suitable based on structural cues, yet low insect availability (only ~28 insects/light trap in summer-mowed areas) in these habitats limit their ability to sustain populations. However, light trap counts may partly reflect predator-avoidance behaviour because flying insects often seek refuge in denser vegetation to reduce predation risk, resulting in a spatial pattern consistent with a "landscape of fear" dynamic (Laundre et al., 2010). Despite this, light traps are a widely used, standardised method for monitoring insects (Kirkeby et al., 2016), and provide a reliable proxy for comparing relative insect abundance across habitats. Ultimately, climate-induced changes, such as increased CO_2 and altered rainfall patterns, may intensify the spatial mismatch between predators and prey, potentially decoupling trophic interactions (Buitenwerf et al., 2012; Charles-Dominique et al., 2015; Eldridge et al., 2011; Soto-Shoender et al., 2018). While disturbances that influence consumer–resource interactions can shape individual behaviour, populations, and even define ecosystem structure and functioning (Karakoç et al., 2018; Stears and McCauley, 2018), further research is needed to determine if the observed spatial mismatch as a result of climate change and vegetation management has the potential to decouple trophic interactions.

Overall, our findings support the notion that habitat management practices that create areas across the landscape with varying woody plant density and grass height can foster diverse and abundant insect populations essential for sustaining bat diversity. The intricate dependencies between vegetation structure, insect availability, and bat habitat use underscore the importance of landscape-scale heterogeneity within African savannas, accommodating both open and cluttered environments to ensure that both aerial and clutter-adapted foragers have access to essential resources. Ultimately, while we recognize that resource managers are unlikely to manage specifically for bat and insect communities, our results can inform conservation policies that encourage mixed management to counter anthropogenically-driven woody densification to maintain savanna biodiversity (Stevens et al., 2017). Future research should focus on larger spatial and temporal scales, as well as species-specific habitat requirements of both bats and insects, to develop more refined management and conservation strategies that account for the complex dynamics of savanna ecosystems.

CRediT authorship contribution statement

Keenan Stears: Writing – review & editing, Visualization, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Jessica Comley:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Parker Daniel:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Terence Olckers:** Writing – review & editing, Formal analysis. **Schmitt Melissa:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Ethics statement

Not applicable.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03875.

Data availability

Research Link Provided
Data from: Woody densification and its management shape insect and bat communities in an African savanna (Zenodo)

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Further reading

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